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USE OF THESIS

ORIGIN AND FATE OF ORGANIC MATTER IN SOUTH-WEST AUSTRALIAN WETLANDS

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ABSTRACT

The development and local distribution of organic soils in Australia have been poorly documented. Within Western Australia, conditions conducive to the accumulation of organic matter are geographically restricted and generally occur in coastal and/or forested landscapes. An extensive system of wetlands with peat soils occurs in the Muir-Unicup region in the far south west of Western Australia. Bokarup Swamp, Kodjinup Swamp and Noobijup Lake are representative of the wetlands occurring in this region. They are shallow (<1m) wetlands dominated by extensive stands of emergent macrophytes and contain deep peat soils. Each wetland has a different recent history of disturbance from fire and altered drainage and water quality. The impacts of these disturbances on wetland processes and development are unknown, and therefore the sustainability of these ecosystems under current management practices needs to be addressed.

This study quantified major carbon inputs (autochthonous and allochthonous) and losses (CO_2 and CH_4 ebullition) to construct an annual carbon budget for the three wetlands. A descriptive model of organic matter accumulation was developed using empirical data from the carbon budgets, $^{14}C/^{210}Pb$ dated profiles and sediment characteristics such as bulk density and carbon content. This thesis provides the only examples of a quantitative carbon budget and a descriptive, predictive model of long-term peat accumulation rates for Australian wetland systems.

Organic matter sources and losses were dominated by a strong seasonal cycle of increased inputs and losses during the summer periods of each year, coinciding with periods of maximum water levels and temperatures. Allochthonous litterfall contributed significant amounts of organic matter but was restricted to the wetland margins. Emergent macrophytes (predominantly *Baumea articulata*) dominated the organic matter supply in each wetland through litterfall and below ground structures. Emergent macrophytes also exert a strong influence on the transformations and losses of organic matter. They provide an important source of methanogenic substrate, enhance the atmospheric flux of the methane by acting as a conduit for gas transport and aerate sediments allowing for methane consumption by methanotrophic bacteria.

The importance of macrophytes was also evident in wetland foodwebs (through $\delta^{13}C$ and $\delta^{15}N$ analysis) as substrate for biofilms and a source of organic matter for detrital microorganisms.

The annual carbon budget demonstrated that each wetland basin is currently a sink for tens of thousands of kilograms of carbon each year. However, an extensive unvegetated area in Bokarup Swamp created by a fire event was the only habitat that was a source of carbon, contributing over 300 kgC/year to the global carbon budget. This highlights the potential for disturbance events to transform these wetlands from carbon sinks to sources, which may have important local, regional and global consequences.

The development of a simple, descriptive model indicates that short term erosional events such as fire and long term changes to rates of organic matter supply and decay have led to variable rates of organic matter accumulation in the past. Parameters within the model such as run-time and rates of organic matter supply and decay can be altered to simulate accumulation rates under different environmental conditions. The simulations can be used to examine impacts from altered hydrology, changes in organic matter supply and erosional events on organic matter accumulation rates.

DECLARATION

I certify that this thesis does not, to the best of my knowledge and belief:

(i) incorporate without acknowledgment any material previously submitted for a degree or diploma in any institution of higher education,

(ii) contain any material previously published or written by another person except where due reference is made in the text; or

(iii) contain any defamatory material.

Darren Ryder

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Setting the scene

Peat-forming habitats contribute to many of the critical functions of the worlds' ecosystems. They are a major component of the global carbon and hydrological cycles; they form areas of rich biological diversity and contribute to the maintenance of water quality and availability. It has been estimated that the carbon stored in global peat deposits represents one-quarter of the world's soil carbon pool covering around 3% of the earths land surface (Lappalainen 1996). Despite their value, on a global scale, around 50% of these ecosystems have been destroyed or significantly degraded (Mitsch *et al.* 1994). It is estimated that the loss of peat through environmental degradation and exploitation for human use far exceeds rates of peat formation (Moore & Bellamy 1974). However, knowledge of the rates of peat formation and the impact of disturbance on these systems is only available for a limited number peat forming systems and only in the Northern Hemisphere.

Peat forming environments are found throughout the world, occurring in sub arctic and boreal regions of North America, Europe and Asia, in the tropical rainforest regions such as Indonesia, the southern-most tip of South America and in temperate and tropical regions of Australasia. There is a diversity of names to describe peat-forming systems worldwide based on the dominant habitats, species or hydrology involved in peat accumulation. Peat deposits can occur in mires and moors across vast areas of inundated land, in forested landscapes as boreal and forested wetlands, in raised bogs dominated by *Sphagnum* species and in basin wetlands as fens, swamps and marshes. It has been estimated that up to 60% of basin wetlands throughout the world favour peat-forming processes, making them the dominant wetland type on a global scale.

Peat forming ecosystems are exceptional in possessing within themselves a record of their historical development in the form of peat. Peat formation is a very slow process, with accumulation rates between 20 to 80cm per 1000 years typical in Northern Hemisphere peatlands (Moore & Bellamy 1974). Successive generations of largely undecomposed plant material forms layers of peat, in which the low oxygen availability acts as a partial preservative (Barber 1981). Peat often contain recognisable fragments of the vegetation that formed it, providing a mechanism to trace the development of a peat forming system by studying the succession of peat types as well as the microfossil record. Much can be learnt about past vegetation communities, water levels and climate changes from the presence, structure and composition of peat.

The rate at which peat accumulates has been determined for a number of sites in the Northern Hemisphere, predominantly raised *Sphagnum* bogs and boreal wetlands (eg. Wildi 1978; Clymo 1984; Makila 1997; Karofeld 1998). Estimates of peat accumulation rates have been determined using short-term carbon budgets or sediment dating techniques. In Australia, estimates of peat accumulation have been based on sediment dating and palynological data. Direct measurements such as these provide an indication of the average rate of peat accumulation, but they do not further our knowledge of the peat accumulation process itself. While Clymo (1978) and others have incorporated peat characteristics and palaeoecological data to develop an empirical model of peat accumulation in raised *Sphagnum* bogs, a model describing long-term rates of organic matter accumulation has not been developed for Australian peat forming systems.

Rates of peat formation are not uniform throughout time, as they are influenced by factors such as hydroperiod, quality and quantity of organic matter inputs and decomposition rates (Tallis 1983). Alterations to these factors from short-term disturbances such as erosion from fire or mining directly impact on rates of peat accumulation. Equally, a prolonged disturbance such as changes in regional hydrology, leading to extended inundation or drought periods and decreases in water quality through nutrient enrichment and salinisation, impact the rates of peat accumulation.

Within Western Australia, conditions conducive to the accumulation of peat are geographically restricted and generally occur in coastal and/or forested landscapes. The Muir-Unicup region in the far south west of Western Australia contains an extensive system of basin wetlands with deep, highly organic sediments. Current management regimes in this region such as prescription burning, land clearing and artificial drainage have the potential to alter rates of organic matter accumulation in wetland habitats. The impacts of these management regimes on wetland biota, processes and development are unknown, and therefore the sustainability of these ecosystems under current management practices needs to be examined.

This thesis explores the impact of altered environmental conditions on the rates of peat accumulation in basin wetlands with extensive peat deposits in south-western Australia. It focuses on the effects of altered hydrology, water quality and fire regimes on the rates of organic matter inputs and decay. The thesis is organised broadly into four parts. Part I describes the physical and chemical characteristics of the study sites; Part II quantifies organic matter inputs and losses to study wetlands; Part III constructs a carbon budget for each wetland and; Part IV uses carbon budget and palaeoecological data to construct a model of peat accumulation rates.

1.2 What is peat?

Partially decayed organic matter, mainly of plant origin accumulates in aquatic systems under a wide variety of conditions, oxygen deficiency being the most pronounced. Oxygen may not diffuse into the system as rapidly as its consumption by microbial and animal respiration resulting in deoxygenation and reduced decomposition, favouring accumulation of organic matter in the sediments (Plaster 1985). Despite numerous classifications, peat is a cosmopolitan term that is used to describe a variety of soils with high organic contents. Peat is defined by Plaster (1985) as 'undecayed or partially decayed organic soil, formed under saturated conditions where low oxygen conditions inhibit decomposition'. This definition is used in this thesis.

Peat soils are derived from primary production within wetland systems (autochthonous) and from terrestrial sources (allochthonous). Autochthonous sources are usually dominated by emergent macrophyte material, which contains substantial structural material (cellulose, lignin) and occurs in very large particle sizes. These properties make macrophyte tissue relatively resistant to decomposition and prone to accumulation. The result of primary productivity in excess of decomposition is the formation of peat.

Isbell (1996) has used the term 'Organosols' in a recent Australian classification of sediments to describe peat soils. They are the order of soils dominated by organic materials, and have previously been known as neutral to alkaline, and acid peats. Organosols have been classified as either:

(i) having more than 0.4 m of organic materials within the upper 0.8 m and are not regularly inundated by saline tidal waters, or

(ii) having organic materials extending from the surface to a minimum depth of 0.1 m: these either directly overlie rock or other hard layers, partially weathered or decomposed rock, or overlie fragmental material such as gravel in which the interstices are filled with organic material.

These soils are further divided into suborders dependant on the extent of decomposition of the organic materials and are generally representative of depth and age. *Fibric* describes soils with a highly fibrous texture and are common surface peats with recognisable plant components. *Hemic* soils occur as a deeper horizon and represent an intermediate stage of decay, with *Sapric* soils being highly decomposed organic matter with few recognisable plant components usually deep in a soil profile. This thesis will use the terms *Fibric, Hemic* and *Sapric* to describe peat soils in various stages of decay according to the above classification.

Peat soils therefore consist of the following components (after Moore & Bellamy 1974)

- Organic matter in an organised state of preservation and therefore identifiable.
- Organic matter which has undergone considerable breakdown but in which cell structure is still visible.
- Organic matter which has been degraded below the cellular level and often forming a peat matrix.
- Inorganic matter either derived from allochthonous sources (eroded sediments) or from the cells of some plants (eg. diatom frustules).

While peat soils possess a high absorptive capacity, their cohesion and plasticity are low resulting in most peats being very light, porous and loose (Clymo 1983). However, the structure of peat soils is by no means uniform, with both the physical and chemical characteristics determined by the original plant material, biological activity, environmental conditions (particularly temperature and the extent of waterlogging) and more broadly by the characteristics of the peat forming system, such as topography, hydrology, morphology and history of the system (Clymo 1983).

1.3 Peat accumulation in wetland basins

The ecological mechanism of peat accumulation in wetland systems is succession (Tallis 1983). Although the concept of succession is of fundamental importance in ecology, definitions and details of its expression are controversial (see review in Kangas 1990). 'Hydrosere' or 'Hydrach' succession are historically the main terms given to wetland succession (Tallis 1983). The process is a simple linear chain, beginning with an open water system which progresses towards terrestrialisation through the deposition of sediments and organic matter. However, this process is by no means simple or linear, as changes in climate, water levels or organic matter quality and quantity may severely alter the sequence of succession. Plant communities play an important role in wetland development by contributing organic matter, the primary resource of peat, to sediments and by creating a physical resistance to water movement. Regardless of the process, the accumulation of organic matter in excess of degradation is fundamental to the terminal stages of the biotic transition from a wetland system to a landscape (Wetzel 1975).

Peat deposits provide a basis for reconstructing the history of both natural and anthropogenic disturbance, as the understanding and amelioration of present and future environmental problems rests, in part, on knowledge of their origin (Kangas 1990). Estimates of peat accumulation rates have been derived from measurements of height, bulk density and age of peat deposits for raised *Sphagnum* bogs and boreal wetlands in the Northern Hemisphere (eg. Wildi 1978; Clymo 1984; Makila 1997; Karofeld 1998). The most detailed studies have incorporated peat characteristics and sediment dating techniques to develop an empirical model of peat accumulation in raised *Sphagnum* bogs (Clymo 1978; 1984). While direct measurements provide an indication of the average rate of peat accumulation, they cannot provide a contemporary context for the processes involved in organic matter accumulation.

Carbon budgets have also been used to estimate rates of peat accumulation (Ramlal *et al.* 1994; Kelly *et al.* 1997). These studies provide valuable information on contemporary environmental conditions and processes involved in peat formation. However, they provide limited interpretation of accumulation rates as they do not allow for continued *in situ* decomposition or compaction processes, nor use sediment characteristics such as bulk density or dating techniques to quantify long-term accumulation rates. A combination of data on modern processes and palaeoecological studies aids in the interpretation of palaeoecological data and places contemporary data in the context of long-term peat accumulation. By combining such techniques a better understanding of ecosystem function can be gained. This thesis aims to achieve this combination of approaches.

1.4 Disturbances to peat accumulation

The process of peat formation occurs over a large geological time frame and is by no means regular or definite, as changes in climate, water levels or quality and quantity of organic matter inputs and decomposition rates may severely alter the sequence. The classical model of succession implies constant environmental conditions (Tallis 1983). This assumption is seldom justified as many environmental parameters are characterised by considerable variation from factors such as natural and anthropogenic disturbances. Disturbance in aquatic ecosystems has been defined as "an unpredictable, discrete or gradual event (natural or human induced) that disrupts structure or function at the ecosystem, community, or population level" (Sparks *et al.* 1990). Press disturbances inflict sustained changes to ecosystems and can occur at a range or spatial and temporal scales, ranging from altered regional hydrologic or salinity regimes to continued global climate change. In contrast, pulse disturbances result from instantaneous rather than sustained impacts (Yount & Niemi 1990). However, similar to press disturances, pulse disturbances such as fire may also result in a sustained change to ecosystems.

Alteration to the hydrologic regime is the most pronounced form of wetland disturbance as the hydroperiod is the primary factor controlling their structure and function. Survival of dominant emergent macrophytes in Australian temperate wetlands is linked to inundation regime (Froend & McComb 1994). Macrophytes may not survive inundation of more than 1m for prolonged periods, leading to a loss of organic inputs to peat formation. At the other extreme, drought can lead to the aerobic exposure of organic sediments and increase decomposition rates (Mallik & Wein 1986; Freeman *et al.* 1994). Alternate wetting and drying cycles also accelerates the decomposition process in wetland sediments (Reddy & Patrick 1975; Taylor & Parkinson 1988; Ryder & Horwitz 1995a)

Many climate change models predict changes to temperatures and precipitation in continental areas (Hogenbirk & Wein 1991) which may affect the global distribution and development of wetlands with peat soils. The most serious effects for wetlands may arise through an increased frequency of summer drought, which could reduce the persistence of waterlogging and therefore compromise the very factor that characterises wetlands. Warmer and drier postglacial periods have been strongly correlated with increased severity and frequency of drought and fire (Johnson & Larson 1991), with future global warming potentially causing a similar change in drought and fire regimes (Overpeck *et al.* 1990).

As in many ecosystems, fire in wetlands often coincides with drought conditions. Fires become possible when natural or artificial drainage lowers the water table for a sufficient period of time exposing combustible organic matter. Alternatively, severe fires can spread across an inundated wetland by burning aerial portions of emergent macrophytes or littoral tree species. The magnitude of the impact of fire on the physical conditions, biological activity and vegetation recovery of wetlands depends on the timing and intensity of the burn. Eframova and Eframov (1994) identified two types of peat soil fires, (1) open fires that spread over the soil surface on account of ground fire and, (2) underground fires that can burn for many months or years (Ellery *et al.* 1989). In the former, plant communities are rapidly re-established vegetatively from undamaged roots and rhizomes (Timmins 1992). Deeper fires lead to the destruction of above and below plant material and substantial losses of peat (Tallis 1983). Fires have the potential to disrupt the accumulation of peat by the direct loss of organic substrate through combustion and compaction, removal of vegetation contributing to peat accumulation and accelerating decomposition through increased aerobic exposure of peat surfaces.

Although humans start a significant proportion of modern fires (intentionally or unintentionally), a sizeable proportion of fires ignite naturally, principally by lightning. However, the instances of managed prescription fires in wetland systems for reducing the risk of wildfire, maintaining biodiversity and water quality and waterfowl management is increasing worldwide (Kirby *et al.* 1988). Despite the worldwide literature documenting the detrimental impacts of fire to peat forming systems (eg. New Zealand - Clarkson 1997, Timmins 1992; Africa - Ellery *et al.* 1989; Australia - Horwitz *et al.* 1998, Pemberton 1988, Wein 1981; Canada - Hogenbirk & Wein 1991, Kuhry 1994; Russia - Yefremova & Yefremov 1994; Sweden - Segerstrom *et al.* 1996 and Britain - Radley 1965, Maltby 1980, Maltby *et al.* 1990) little or no attention has been paid to them with respect to fire ecology and management. Unlike the literature on fire in terrestrial communities, specific fire prescriptions, knowledge of fire behaviour under different fuel and environmental conditions, and the detailed consequences of fire frequencies, intensities and severities in wetlands are largely unknown (Kirby *et al.* 1988).

1.5 Thesis outline

The development and local distribution of peat soils in Australia have been poorly documented, occurring in geographically restricted regions of the continent (Churchill 1968; Campbell 1983; Flood & Grant 1984; Semeniuk 1987; Pemberton 1988; Isbell 1996; Clark & Martin 1999). Within Western Australia, the conditions conducive to the accumulation of peat soils are restricted to the far south-west, and as such these habitats are relatively rare and geographically isolated. An extensive suite of wetlands with peat soils in Western Australia occurs within the Muir-Unicup region of the south-west. This area is dominated by basin wetlands occurring within a forested landscape. Current management of this region includes the use of management fires to control fuel accumulation, the artificial drainage of sub-catchments, extensive clearing of native forests for agriculture leading to secondary salinisation. These factors have the potential to alter wetland development through altered hydrology, changes in vegetation communities, interruption of aquatic carbon cycles and direct loss of peat. The impacts of these management regimes on wetland biota, processes and development are unknown, and therefore the sustainability of these ecosystems under current management practices needs to be examined. No studies are available providing insights into peat forming processes or rates of accumulation for Australian wetlands.

This thesis investigates the rates and processes involved in peat accumulation in three wetlands with peat deposits in the Muir-Unicup region of south-west Australia. Bokarup Swamp, Kodjinup Swamp and Noobijup Lake are representative of the wetlands occurring in this region. They are shallow (<1m) wetlands dominated by extensive stands of emergent macrophytes (predominantly *Baumea articulata*; jointed twig rush) and contain deep, organic rich soils (up to 3m). Each wetland has a different recent history of disturbance from fire and altered drainage and water quality. Major carbon inputs (autochthonous and allochthonous) and losses (CO_2 and CH_4 ebullition) are quantified to construct an annual carbon budget for each wetland. A descriptive model of rates of peat accumulation is developed using empirical data from the carbon budgets, $^{14}C/^{210}Pb$ dated profiles and peat characteristics such as bulk density and carbon content. This model incorporates both palaeoecological and ecological data and allows the exploration of both short and long-term accumulation rates and the impact of environmental conditions on the accumulation process.

The key objectives of this research program have been as follows:

- Describe the physical, chemical and biological features of wetlands in the Muir-Unicup area including detailed vegetation and bathymetric surveys and monitoring physico-chemical status of three wetlands (Chapter 2).

- Quantify rates of allochthonous and autochthonous inputs of organic matter to each wetland (Chapter 3).

- Quantify organic matter decomposition through the measurement of sediment and macrophyte gas ebullition (CO_2 and CH_4) and peat microbial biomass (Chapter 4).

- Explore the trophic structure of aquatic macroinvertebrate communities within each peatland using C:N ratios and stable carbon and nitrogen isotopes to examine the importance of dominant allochthonous and autochthonous carbon sources to system function (Chapter 5).

- Construct a seasonal and annual carbon budget for each wetland using quantitative data of organic matter inputs and losses (Chapter 6).

- Build a descriptive model of long-term peat accumulation using empirical data from the carbon budgets (Chapter 6), sediment dating and peat characteristics. This model is used to examine the impact of short and long-term changes in environmental conditions on peat accumulation rates.

- Discuss organic matter accumulation rates in a regional and global context and provide recommendations for the future management of these systems and surrounding landscapes (Chapter 8).

CHAPTER 2

WETLANDS OF THE MUIR-UNICUP AREA

Regional Setting and Wetland Characteristics

2.1 INTRODUCTION

An extensive wetland system with peat soils occurs in the Muir-Unicup region of south-west Australia, around 60 km east of Manjimup, which is 300 km south-east of Perth (Figure 2.1). It encompasses the area around Lake Muir and the Tordit-Byenup wetland system in the south to the extensive area of shallow wetlands around Lake Unicup in the north. The system contains a mosaic of wetland types, covering an area of around 40 km north-south and 20 km east-west. There are seventeen named and numerous unnamed wetlands, most occurring within State Nature Reserves interspersed amongst cleared agricultural land and plantation forests. The majority of these wetlands are relatively undisturbed compared to those that have been incorporated within farms and often degraded.

Nature reserves within the Muir-Unicup area are of significant conservation value, containing important wetland and woodland habitats with a diversity of vegetation communities, water quality characteristics and faunal populations. The Nature Reserves are actively managed through the use of prescription burning for organic fuel reduction and constructed drainage systems to divert saline ground and surface water. The wetlands with peat deposits are of high conservation value due to their limited distribution in Western Australia, comparatively fresh waters and few remaining relatively undisturbed examples. The majority of these wetlands are shallow (<1 m), have basins dominated by emergent vegetation (primarily *Baumea articulata*; jointed twig rush) and have deep, highly organic sediments.

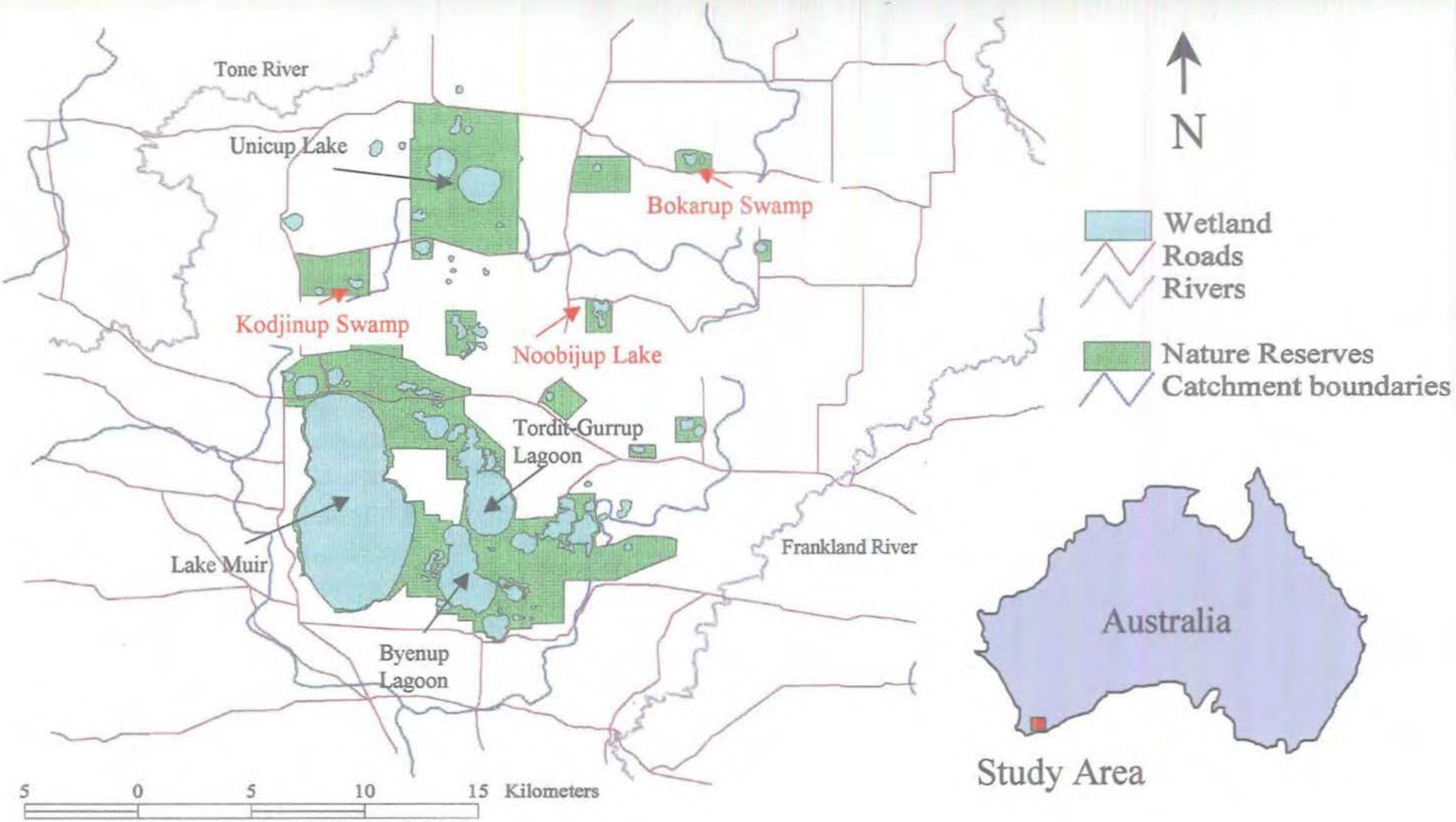


Figure 2.1 The location of the Muir-Unicup wetland system and study sites (in red) in south-western Australia

This chapter provides a regional setting for the project, outlining general catchment characteristics such as climate, geology, hydrology and biota of the Muir-Unicup wetland system. A detailed examination of the three study wetlands follows which identifies wetland factors such as water levels, physico-chemistry, sediment characteristics and vegetation associations.

2.2 THE MUIR-UNICUP WETLAND SYSTEM

2.2.1 Physical environment

The Muir-Unicup wetland system lies within the Darling Plateau and the Ravensthorpe Ramp, which are the two main regional geomorphic units of south-west Western Australia. The geology, through varied rock and sediment types, aquifer properties and Precambrian structures (dykes, faults, sheers and folds) all influence local hydrology. The region is at an elevation of around 220 m Australian Height Datum (AHD) and underlain by Pallinup siltstone. The Eocene would have extended this far inland, and may have covered this Muir-Unicup region to a depth of 30 m (Cockbain 1968).

Two aspects of the geology have an effect on local geomorphology and hydrology. These are the deep weathering of the Precambrian rock to produce saprolite which acts to perch wetlands, and the Manjimup and Pemberton Lineaments which influence deposition and drainage (Semeniuk & Semeniuk 1997). The catchment was divided into three discrete geomorphic units by Semeniuk & Semeniuk (1997): the Old Plateau, the Old Basin and the Young Basin. The 'Old Plateau' (defined by areas >200 m AHD) is an undulating landscape of low relief (circa 20m). Slow drainage rates and local ponding has resulted in the development of basin wetlands within the valleys and beach-ridge wetlands in low relief terrain. The 'Old Basin' (180 to 200 m AHD) has formed by Tertiary age weathering driven by near-watertable conditions, leading to the excavation of a basin into the Old Plateau and similar wetland geomorphic processes of wetland formation to the Old Plateau. The 'Young Basin' forms the boundary of Lake Muir (160 m AHD) and was formed by Quaternary age weathering processes.

As with geology and geomorphology, climate influences regional and local hydrology through precipitation, evaporation, salinity and vegetation distribution. The Muir-Unicup wetland system is located in a region of Mediterranean climate, with high winter rainfall and summer drought. This area experiences a strong north-south rainfall gradient, with average annual rainfall to the north of Lake Unicup around 700 mm, increasing to 900 mm to the south of Lake Muir. Annual evaporation is around 1600 mm, with a much less marked north-south gradient. Mean temperatures range from 12 to 25°C in January and 6 to 14°C in July.

The catchment hydrology consists of three main water types: Main Groundwater, Perched Groundwater and Surface Drainage Water (Semeniuk & Semeniuk 1997). The Main Groundwater is regionally inclined, located at 180 m AHD in the south to 220 m AHD in the north. Lakes Muir and Unicup are surface expressions of this groundwater table. The Perched Groundwater is of various heights and is dependent on the perching mechanism (impermeable saprolite, ferricrete, clay or peat deposits). Surface Drainage is derived from rainfall or emergent and is channelised into creeks and rivers. The permanence or seasonality of wetland water levels is driven by direct precipitation (into clay or peat lined basins), water table rise associated with the unconfined aquifer or surface drainage from local creeks and rivers. Seasonal rainfall is the predominant factor determining wetland water levels and salinity.

2.2.2 Biological characteristics

The Muir-Unicup region is composed of Jarrah (*Eucalyptus marginata*) and Marri (*E.calophylla*) forest on the uplands, with valleys and wetlands lined with *Melaleuca* spp, *E.rudis* (Flooded Gum), *Kunzea* spp. and species of emergent rushes, dominated by the native rush *B.articulata*. The vegetation within wetland basins varies from complete, patchy or peripheral cover of sparse forest and sedgeland. The most typical arrangement of vegetation is concentriform (Semeniuk *et al.* 1990) with a centre of sedgeland (*B.articulata/B.juncea*) and a forested margin (*M.raphiophylla* or *M.preissiana / Banksia littoralis*).

Unlike other regions of south-west Western Australia, the Muir-Unicup suite of wetlands has received little attention regarding their aquatic fauna, with coastal wetland studies dominating the literature (eg. Pusey & Edward 1990a; Davis *et al.* 1993; Storey *et al.* 1993; Edward *et al.* 1994). The earliest study documenting the aquatic fauna in this region was by DeHaan (1987) who intensively sampled southern wetlands prior to peat mining exploration. Other small collections have been made by Harvey (1987; 1996) and Horwitz (1994), with a recent comprehensive survey of 27 wetlands in the Muir-Unicup system finding 219 macroinvertebrate taxa with seven taxa locally endemic (Storey 1998). The majority of species showed a marked salinity tolerance. Seven species of fish were recorded, three with a geographically restricted occurrence in south-west Western Australia and one introduced species (*Gambusia holbrookii*). The Muir-Unicup region is also a significant habitat and breeding ground for waterfowl (Jaensch *et al.* 1988; Wilson 1995). The area is ecologically important for the Australian Shelduck, and periodically is a major drought refuge for waterfowl (Jaensch *et al.* 1988). Five species listed under international treaties and 4 migrant shorebirds have been recorded in the region.

2.2.3 Wetlands of the Muir-Unicup system

The wetlands of the Muir-Unicup area have been recognised as being of national significance and are listed in the Directory of Important Wetlands in Australia and on the Register of the National Estate. The Muir-Unicup region was proposed for listing under the Ramsar Convention in 1990 by CALM. The proposal was declined due to the likelihood of peat mining (CALM 1990).

The wetlands of the Muir-Unicup area form a mosaic, varying in their size, salinity, permanence and vegetation cover. The northern wetlands are generally made up of individual basins, whereas the southern wetlands comprise a continuous spread of wetlands with extensive areas of seasonally inundated flats. Most wetlands occur within Nature Reserves and are surrounded by cleared and partly cleared private property, by land resumed by the Western Australian Water and Rivers Commission (WAWRC), Vacant Crown Land or by Timber Reserves and State Forest.

Lake Muir is by far the largest wetland in the area, approximately 4600 hectares in size and contains brackish surface water for around nine months of the year. Adjacent to the main basin is a series of wetlands in the swales of marginal beach ridges. The surface waters of Lake Muir range from subhaline to hyposaline (2-4 ppt), with much higher concentrations in groundwater (10-96 ppt). Water column pH ranges from mildly acidic to alkaline (pH 6.2-9.7) (Jaensch & Lane 1993). A number of large peat-floored wetlands occur within the Lake Muir Nature Reserve. Tordit-Garrup Lagoon (690 hectares) and Byenup Lagoon (570 hectares) are the largest wetlands, although there are numerous smaller wetlands within the reserve. These wetlands are extensive, relatively undisturbed peat wetlands with predominantly fresh waters (Semeniuk & Semeniuk 1997). These wetlands are thought to be scientifically important in that they record a transition from more arid conditions earlier in the Holocene to relatively more humid conditions (conducive to peat formation) presently experienced (Semeniuk & Semeniuk 1997). Basal peats in Tordit-Gurrup Lagoon have been carbon dated to 5720 ± 320 years BP (Magnet Industries1990).

Salinities in the northern wetlands around Lake Unicup range from fresh to hyposaline (up to 10 ppt) with pH values ranging from 5.8-9.7 (Jaensch & Lane 1993). Geomorphically, wetlands range from open seasonally inundated flats to closed basins. This area is scientifically important in that it provides evidence for wetland developmental processes and hydrological processes in this part of the Muir-Unicup region (Semeniuk & Semeniuk 1997). This range of wetlands represents a geomorphic evolution from creekbeds to broad valley flats which 'clog' to form irregular shaped basins such as Noobijup Lake. During intermittent cycles of inundation and periods of variable wind conditions, sedimentary processes result in the basins becoming excavated, ringed by beach ridges, and finally circular. Wetland water levels vary seasonally by up to one metre with maximum levels in November/December and minimum levels in May/June.

2.2.4 Muir-Unicup wetland management

2.2.4.1 Land clearing

Since European settlement much of south-western Australia has been developed for agricultural production with over 16 million hectares cleared (EPA 1993). The result is changes to catchment hydrology, with rising saline groundwater tables, increased land inundation and waterlogging with enhanced transport of nutrients and salt into wetland basins. Alterations to catchment hydrology in the Western Australian wheatbelt has substantially contributed to the loss of wetland habitat (Froend *et al.* 1987) and the documented extinction of several species of native mammals and ground dwelling birds reliant on wetlands (Sanders 1991). Land in the Muir-Unicup area was taken up for farming in the 1850's due to the availability of water in the area. Land clearing started in the 1920's, with the most extensive clearing occurring in the 1970's. At present farms make up around 50% of the catchment area. Land use consists of tree plantations (*E.globulus* and *Pinus radiata*), mixed grazing or vegetation mixed farming.

Regular monitoring by Agriculture Western Australia (AgWA) indicates increases in both local groundwater levels and salinity. Possible solutions to this problem proposed by AgWA are the strategic planting of vegetation belts on cleared land, grade interceptor banks to divert surface water into creeks and wetlands and diversion of saline waters away from freshwater wetlands into saline creeks and rivers. All of these options will impact on wetland water levels. A complex web of open drains already exists within the catchment which drain water into wetlands and channels saline surface waters.

At present a Draft Management Plan (CALM 1997) is in place for the reserves of the Muir-Unicup area. The Plan states management will maintain and conserve the natural environment and protect, care for and promote the study of indigenous flora and fauna. It acknowledges that the Muir-Unicup wetlands are an important wetland and woodland resource, containing water bodies of low salinity, a feature increasingly uncommon in south-western Australia. The CALM have recognised the paucity of knowledge of the aquatic flora and fauna or ecological processes is recognised for further investigation.

2.2.4.2 Prescription burning

In south-west Australia several tall forest formations are found in regions exceeding 600 mm annual rainfall. The Jarrah (*E. marginata*) forests are the most extensive formation in this region and are managed for multiple use by the Department of Conservation and Land Management (CALM). Within this region fire is a natural phenomenon due to summer drought and lightning storms. Human-induced fires are also common for the regeneration of logged areas and as a fuel reduction, fire suppression strategy (Wardell-Johnson & Nichols 1991). The average frequency of prescription burns ranges from between 5 to 7 years for south-west Jarrah forests (Wardell-Johnson & Nichols 1991).

The Muir-Unicup wetlands within reserves are actively managed by CALM in regard to prescribed burning and firebreak construction. Prescription fires have been used in a number of reserves since 1986. Within the Muir-Unicup area fuel reduction strategies have been developed based on reserve size and habitat sensitivity. Large reserves (>800 ha) are burnt on rotational lengths of 5 to 7 years, in medium sized reserves (250 to 800 ha) only strategic buffers of 50 m width are rotationally burnt to retain low fuel loads, and small reserves (<250) have an opportunistic burning regime (CALM 1997). Management is for a diversity of burn types and fire ages, including no burn sites such as paperbark and rush areas. Despite this, medium sized reserves such as Kodjinup Swamp and Noobijup Lake have areas of paperbark and rushes burnt as a result of prescription burns on more than one occasion.

2.2.4.3 Peat mining

Mining tenements for peat occur over two wetlands on Vacant Crown Land adjacent to Lake Muir Nature Reserve. These wetlands have been actively mined since 1978 for horticultural peat. The wetlands have been channelised and are periodically drained through open drains into adjoining wetlands, and in turn into Lake Muir. Water levels in the adjoining wetlands have increased over one metre since receiving water from the mined wetland, resulting in the loss of large communities of emergent vegetation. The current Draft Management Plan states that future mining operations will not be permitted in 'A' Class Nature Reserves.

2.3 STUDY SITES

Three wetlands with peat soils representative of those found in the Muir-Unicup system were comprehensively studied: Bokarup Swamp, Kodjinup Swamp and Noobijup Lake. All are located within 'A' Class Nature Reserves vested in the National Parks and Nature Conservation Authority (NPNCA) for the protection of water quality and the conservation of flora and fauna. They are typically small wetlands in Nature Reserves not much larger than the wetland boundaries. Wetland water levels are seasonally offset and range from around 1 m depth to no surface water. The emergent vegetation is dominated by the native rush, *Baumea articulata* (jointed twig rush) a large emergent macrophyte growing to 2.5 m in height (Froend & McComb 1994). Wetland basins contain peat deposits up to 3 m deep and the overlying waters have high concentrations of Dissolved Organic Matter (DOM) (up to 60 mg/L). Each wetland possesses different environmental characteristics, such as recent fire histories, degree of salinisation and alterations to local catchment hydrology.

2.3.1 Bokarup Swamp

Bokarup Swamp Nature Reserve (Plate 2.1a) covers an area of 146 hectares and is the most northern of the study sites. The wetland has no surface drainage channels into the wetland, and therefore derives its water predominantly from the groundwater and direct rainfall. An outlet channel on the western side regulates wetland water levels to a maximum of around 1 m. Forestry records indicate Bokarup Swamp Reserve has not experienced wildfire or prescription fires for at least 27 years, a comparatively long time in south-west Western Australia. However, there are extensive areas of the wetland basin that have been exposed to fire. A large proportion of the aerial extent of the emergent vegetation and up to one metre of peat have been lost in 40% of the wetland as a result of one or more fire events (unvegetated area in Plate 2.1b). It is assumed that this event(s) occurred prior to 1973. Basin vegetation is dominated by uniform stands of *B.articulata* (Plate 2.1c) with a large area of open water at the northern end (Plate 2.1d). Surrounding vegetation is Jarrah/Marri forest with a ring of *Melaleuca* spp. at the wetland margin.

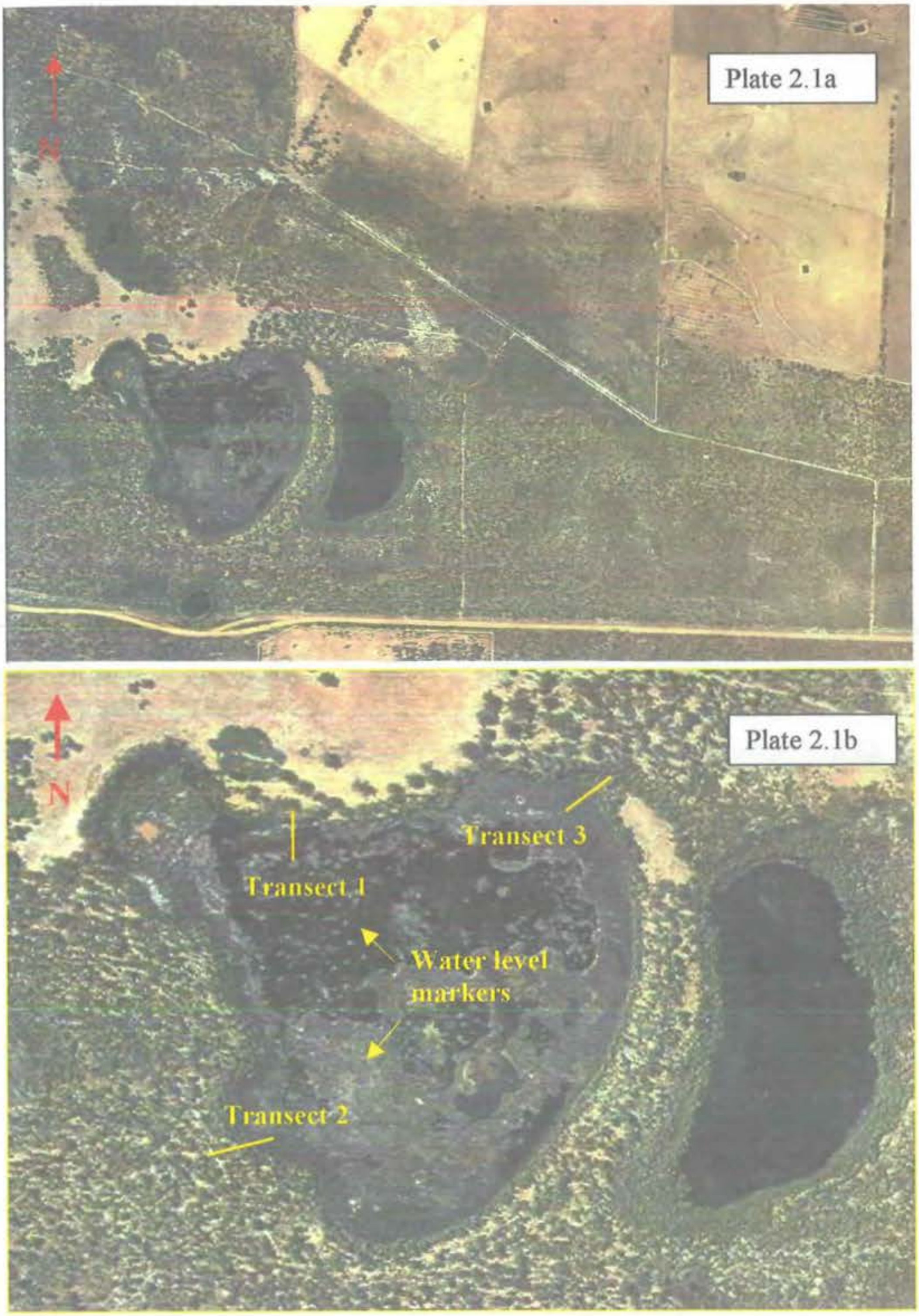


Plate 2.1 Aerial photographs of (a) boundaries of Bokarup Swamp Nature Reserve and (b) Bokarup Swamp (western most wetland) indicating the location of the two water level markers and bathymetry and vegetation tramsects (Source AgWA Photo 1126 25/01/91).

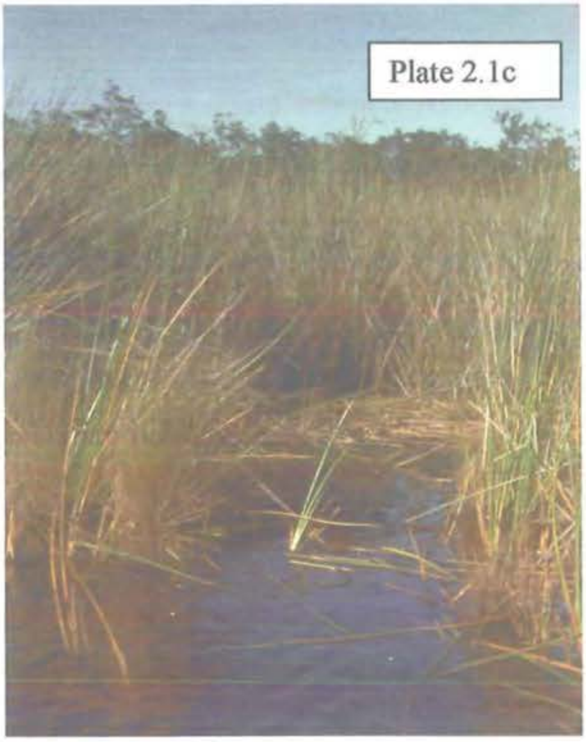


Plate 2.1 (c) Stands of *Baumea articulata* (jointed twig rush) in Bokarup Swamp and (d) a large expanse of open water and littoral macrophytes and *Melaleuca raphiophylla* at the northern end of Bokarup Swamp. (Source D.Ryder)

2.3.2 Kodjinup Swamp

Kodjinup Swamp Nature Reserve (Plate 2.2a) covers an area of 625 ha. The reserve is one of the western-most wetlands in the Muir-Unicup region, located on the boundary between the Lake Muir and Tone River catchments. The reserve contains two wetlands, east and west Kodjinup Swamps. This research examined east Kodjinup Swamp. Water levels are influenced by surface water inputs from surface water flow and from groundwater, with water levels ranging from a depth of 1.1 m to no surface water. In 1994 a series of open drains were constructed through the north-west of the reserve, designed to divert saline surface water flow away from the wetland basin and into the Tone River. This has reduced the surface water catchment of Kodjinup Swamp by two thirds, resulting in the wetland drying completely in 1995 for the first time on record. Kodjinup Swamp has been subjected to Spring prescription burns in 1986 and 1993. There is evidence of burnt layers of peat, emergent vegetation and fringing *Melaleucas* on the south and west sides of the wetland (Plate 2.2b). Basin vegetation is dominated by less dense stands of *B.articulata* with surrounding vegetation of Jarrah/Marri forest with a ring of *Melaleuca* spp. at the wetland margin (Plate 2.2c).

2.3.3 Noobijup Lake

Noobijup Lake Nature Reserve (Plate 2.3a) covers an area of 183 ha and is the southern most study site. The area immediately surrounding Noobijup Lake has been substantially altered by road construction along the northern boundary, the extensive clearing of native vegetation and planting of annual crops on all sides. A salt seep has developed on the western side of the reserve as a result of locally increased groundwater levels and is encroaching on the western margins of the wetland basin. There is an inlet channel at the southern end of the wetland that drains large areas of cleared catchment into Noobijup Lake (Plate 2.3b). Water levels vary from 1.2 m to 0.5 m and are less seasonal than the other study sites. A Gley/saprolite lining around 1.5 m below the peat surface indicates this wetland may be perched. Noobijup Lake was prescription burnt in late spring 1986 and has not subsequently been burnt by management or wild fires.

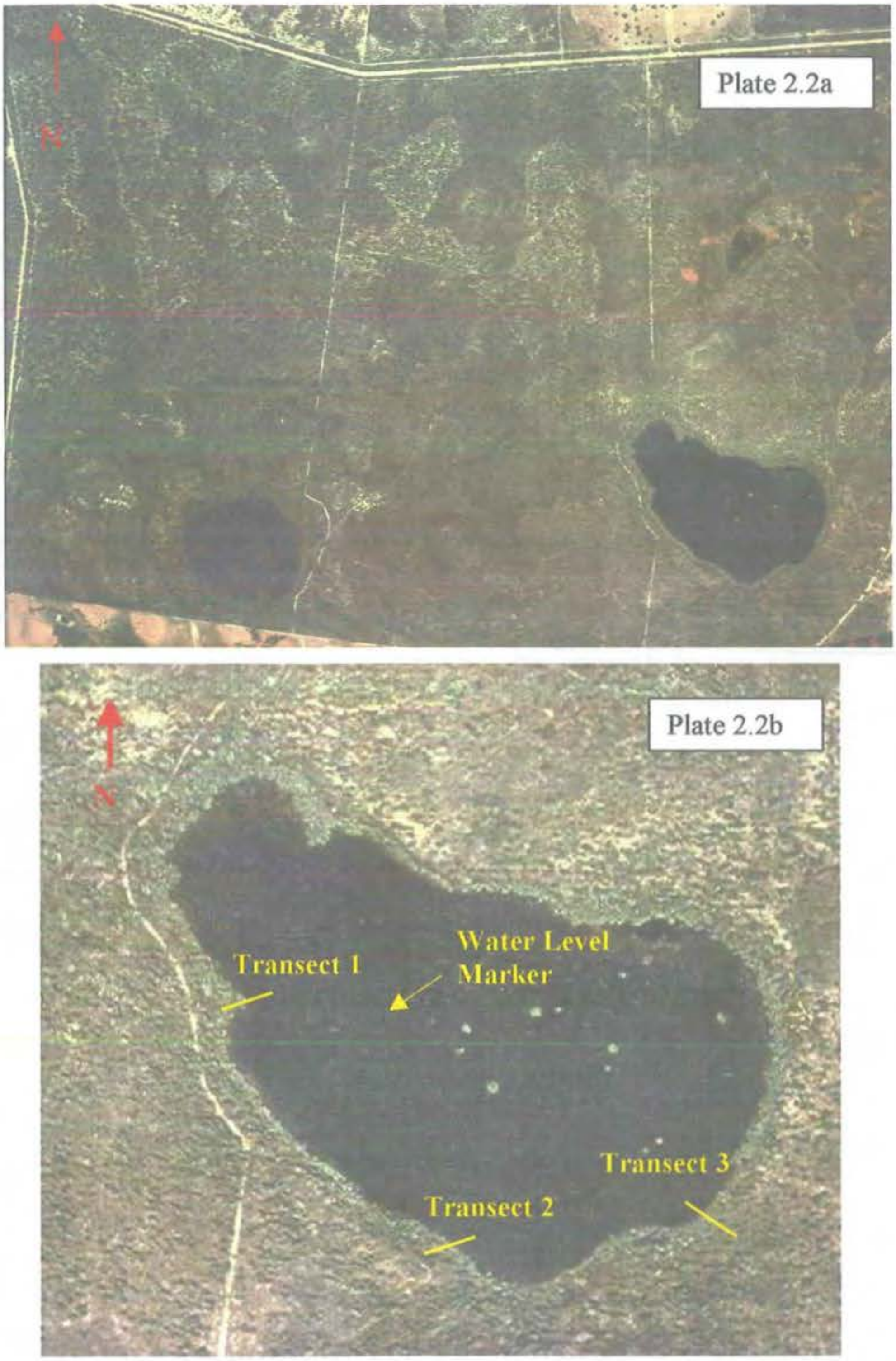


Plate 2.2 Aerial photographs of (a) boundaries of Kodjinup Swamp Nature Reserve and (b) Kodjinup Swamp indicating the locations of the water level marker and the vegetation distribution transects (Source AgWA Photo 2063 25/01/91).

Plate 2.2c. Uniform stands of *B.articulata* in the basin of Kodjinup Swamp with surrounding *Melaleuca* and Jarrah/Marri forest in the background (Source D.Ryder).

Plate 2.3 (a) Noobijup Lake Nature Reserve (Source AgWA Photo 0280 25/01/91).

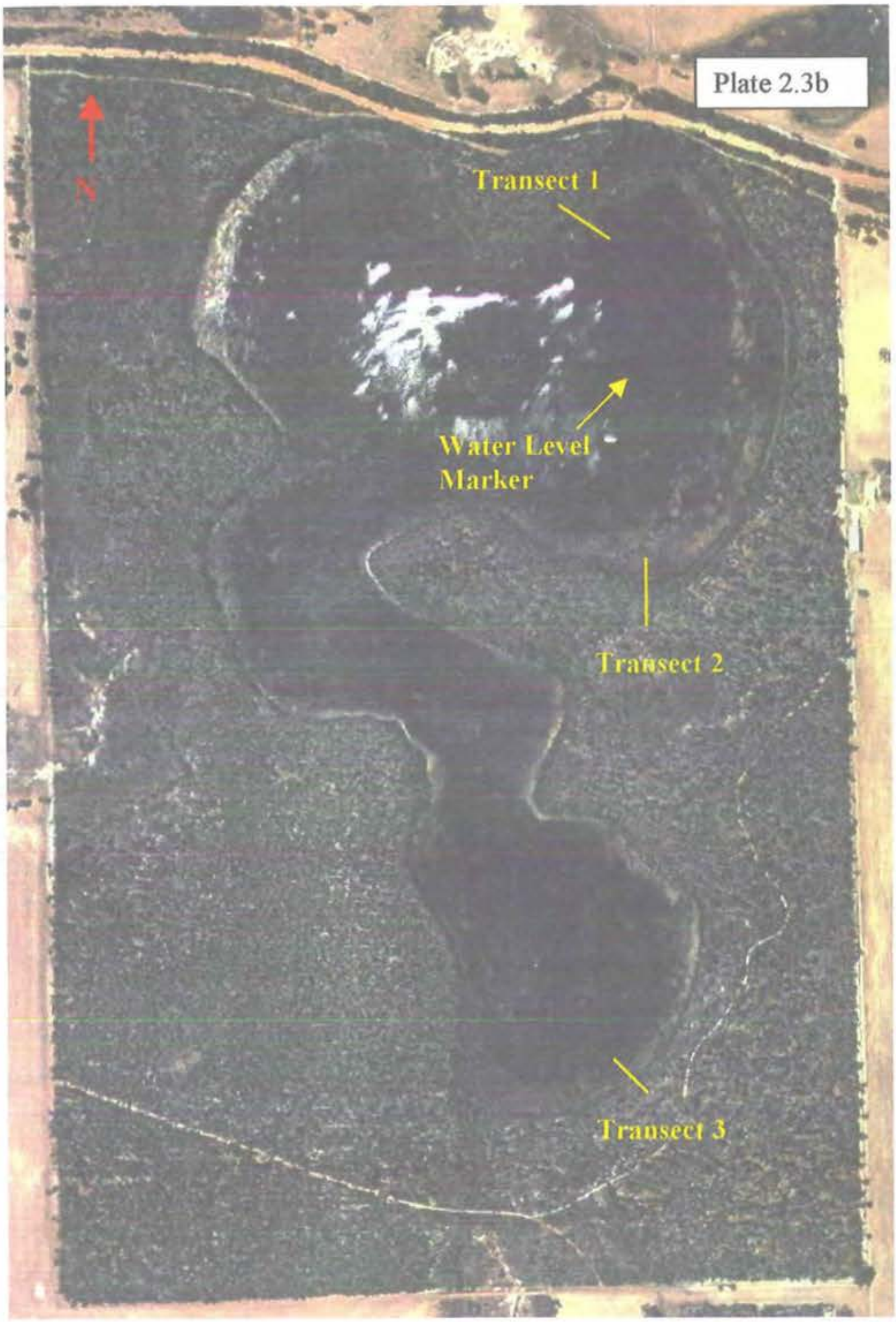


Plate 2.3b Aerial photograph of Noobijup Lake indicating the locations of the water level marker and vegetation distribution transects (Source AgWA Photo 0280 25/01/91)

Basin vegetation is dominated by stands of sedges (predominantly *B.articulata*) with surrounding vegetation of Jarrah/Marri forest with a ring of *Melaleuca* at the wetland margin (Plate 2.3c)

Plate 2.3c. Stands of *B.articulata* and other sedges in the basin of Noobijup Lake with surrounding *Melaleuca* and Jarrah/Marri forest in the background (Source D.Ryder).

2.4 SAMPLING REGIME

The three study wetlands in the Muir-Unicup region were sampled on nine occasions from July 1995 to May 1997. To aid in the presentation and discussion of water column profile data, sampling dates have been classified into seasons. The exact dates of the each visit and the season in which they fall are shown in Table 2.1.

Table 2.1 Field sampling dates and seasonal classifications of dates.

Year	Month	Dates	Seasonal classification
1995	July	18th – 26th	Winter
	September	18th – 24th	Spring
	December	5th – 12th	Summer
1996	February	5th – 12th	Summer
	April	8th – 15th	Autumn
	July	9th – 16th	Winter
	October	10th – 17th	Spring
1997	January	5th – 15th	Summer
	May	8th – 13th	Autumn

2.5 METHODS

2.5.1 Wetland water levels

Water levels in each wetland were measured on each sampling occasion from a graduated wooden stake in a fixed location. Measurements were recorded to the nearest centimetre, with the base of the water column defined as the sediment-water interface. Two major habitats were defined in Bokarup Swamp (vegetated and unvegetated) which have different hydrologic regimes; therefore measurements were recorded from each habitat. Locations of the stakes in each wetland are shown on Plates 2.1b, 2.2b and 2.3b.

2.5.2 Sediment profile analysis

Three cores were taken from each wetland in May 1997. Cores were sampled using a D-section corer (50 mm diameter) to a depth beyond which the corer could no longer penetrate. A D-section corer was used as it does not compress samples. The corer was inserted into the sediment to depths of 50 cm, turned 180 degrees and removed with an intact sediment core inside. Sediment horizons were identified and representative samples from each horizon were removed from the corer, wrapped in aluminium foil to retain their structure and frozen. Sub-samples from each sediment horizon were analysed for the following parameters: electrical conductivity and pH, organic matter and particle size.

2.5.2.1 Electrical conductivity and pH

Electrical conductivity and pH were quantified using the methods of McDonald *et al.* (1990) on three replicates from each subsample from each core as outlined below.

- Ten grams wet weight of sediment was placed into a 100 ml plastic vial.
- Fifty ml of distilled water was added to each sample.
- Samples were placed on a stirring block for 30 minutes.
- The solution was allowed to stand for 30 minutes (0.5 ml of 1M $CaCl_2$ added for pH samples).

- Soil conductivity was measured using a calibrated WTW portable conductivity meter LF 95/set 1 using a tetracon 96 probe (results recorded in µS/cm standardised to 20°C).
- Measurements of soil pH were made with a calibrated WTW portable microprocessor pH meter - pH 95 / set 1 using a pH probe.

2.5.2.2 Organic matter

Sediment organic matter was quantified using the methods of McDonald *et al.* (1990) on three replicates from each subsample from each core as outlined below.

- Pre - weigh all crucibles.
- Ten grams wet weight of sediment was added to each crucible and oven dried in a Series 5 Contherm drying oven for 48 hours at 105°C.
- Samples were cooled in a desiccator and weighed in grams to four decimal places on a OHAUS analytical balance.
- Crucibles were placed in a Furnace Brand muffle furnace for 4 hours at 550°C.
- Samples were cooled in a desiccator and reweighed.
- Organic matter (OM) Loss on Ignition (LOI) was calculated using the following formula:

$$\frac{\text{OM\% (LOI)} = 100 \times (\text{mass of oven dry sediment} - \text{mass of ignited sediment})}{\text{mass of oven dry sediment}}$$

2.5.2.3 Particle size analysis

Sediment particle size was quantified using the methods of McDonald *et al.* (1990) on three replicates from each subsample from each core as outlined below.

- Ten grams of oven dried sediment was placed in a 500 ml beaker. Sixty ml of distilled water was added and boiled down to 30 ml.
- One hundred ml of 6% hydrogen peroxide (H_2O_2) was added to the beaker and boiled to reduce the liquid to 50 ml.
- The solution was transferred to a 500 ml plastic vial, made up to 250 ml with distilled water and 10 ml of sodium hexametaphosphate and sodium carbonate and placed on a stirrer for 15 minutes.

- The solution was added to a 500 ml graduated cylinder and made up to 500 ml with distilled water. The solution was stirred for one minute and allowed to stand.
- Exactly 40 seconds after stirring, a bouycous hydrometer reading was taken to the nearest 0.1 g and the temperature of the solution taken. This represented the silt and clay fraction.
- Two hours later another bouycous hydrometer and temperature reading were taken. This represented only the clay fraction.
- A blank hydrometer reading was obtained using the same procedure on a solution of distilled water and 10 ml of sodium hexametaphosphate and sodium carbonate.

Calculations :

W_1 = initial weight of oven dried samples (g)

A = temperature corrected 40 second reading (g/L)

B = temperature corrected two hour reading (g/L)

C = temperature corrected blank reading (g/L)

Percent Sand :

Silt and Clay (W_2) = (A - C) x volume (L)

Sand % = $[(W_1 - W_2)/W_1] \times 100$

Percent Clay :

Clay (W_3) = (B - C) x volume (L)

Clay % = $(W_3 - W_1) \times 100$

Percent Silt :

Silt % = 100 - (% sand + % clay)

2.5.3 Wetland physico-chemistry

Dissolved oxygen (DO) in % saturation and mg/L, pH, conductivity (mS/cm), redox potential (millivolts) and temperature (°C) were measured *in situ* at 10 cm intervals through the water column, from the water surface to immediately above the sediment water interface using the following equipment (all meters were regularly calibrated):

- Dissolved Oxygen (% and mg/L) and temperature (°C) - *Wissenshaftlich Technishe Werkstatten* (WTW) portable microprocessor Oximeter, Oxi 96 / EO 96 probe.

- pH - WTW portable microprocessor pH meter - pH 95 / set 1 using a pH probe.
- Redox - WTW portable microprocessor pH meter - pH 95 / set 1 using a redox Ingold Electrode Pt 4805-57.
- Conductivity - WTW portable conductivity meter LF 95 / set 1 using a tetracon 96 probe (converted to K_{20} values using Wetzel 1975).

Profiles were recorded at five random locations within each wetland on each sampling occasion. Readings were taken from a dinghy so as not to disturb the water column. However, the disturbance of emergent vegetation was often unavoidable so a minimum of 10 minutes was allowed for the water column to settle before readings were taken. Where water levels were insufficient for the dinghy to be used, readings were taken by wading to each sample location with minimal possible disturbance to both sediment and water column and placing the probes around one metre in front. As some of the lakes dried in late summer and autumn, water column profiles could not be taken. Where surface water was absent, holes were carefully dug at each of the five random locations and allowed to fill with pore water, given a minimum of 10 minutes to settle and a single reading taken. These data have been summarised into representative profiles for each wetland in each of the season classifications (Section 2.4) to ease the interpretation of results.

Diurnal variations in water column profiles were examined as readings for water column profiles could not be standardised by time. Parameters were measured over a 24-hour period at 4 hour intervals at one location within each wetland. Readings were taken in January 1997, representing a period that may experience maximum variation in many of the parameters being measured. Weather conditions were relatively calm and consistent during the 4 day period the three wetlands were sampled.

Water samples for organic and inorganic nutrients were taken from five random locations in each wetland on each sampling occasion. An integrated water column sample was taken using a 2 cm diameter polyethylene tube. The tube was lowered through the water column to immediately above the sediment-water interface, capped and bought to the surface. Samples for inorganic nutrients (PO_4, NO_2/NO_3, NH_3) were passed through a filter tower under vacuum using a Whatman GF/C filter paper with an effective pore size of 0.45 µm. The filtrate was placed in acid washed 30 ml polyethylene vials for each nutrient and placed on ice in the dark. All samples were frozen within 4 hours of collection. Organic nutrient samples were unfiltered and stored as above.

In the laboratory, samples were defrosted in a 4°C fridge and analysed on a Skalar san-system segmented flow autoanalyser housed at Edith Cowan University Joondalup using the following methods :

- Orthophosphate (PO_4) - ascorbic acid method (APHA 1989).
- Ammonia (NH_3) - Modified berthalot reaction using salicylate and dichloroisocyanurate (APHA 1989).
- Nitrate/Nitrite (NO_2/NO_3) - cadmium reduction method (APHA 1989).
- Total Phosphorus - Perchloric acid digestion (APHA 1989) followed by orthophosphate analysis as described above.

Total phosphorus analysis of leaves, roots and rhizomes of the dominant emergent macrophyte *B.articulata* was taken from plant material collected during the April and September 1995 biomass harvests (Section 2.5.6). Subsamples of green leaves, root sections and rhizomes were randomly taken from five plant parts from each wetland on each sampling occasion. Each subsample was air dried and homogenised using a mortar and pestle. Samples were analysed for total phosphorus using a Perchloric acid digestion (APHA 1989) followed by orthophosphate analysis described above.

2.5.4 Wetland habitat classification

The distribution of major habitat types within each wetland basin was mapped by overlying sketches on 1:5000 true colour aerial photographs. The geographical location of each wetland was determined using the Australian Map Grid (AMG) using 1:50000 topographic map (Department of Conservation and Land Management, Unicup Sheet) and topographical characters from aerial photographs. These points were digitised using Microstation™ PC v5 to place each wetland accurately in the landscape, with an error less than 0.4%. Digitised images were ground-truthed and habitat boundaries or classifications were corrected where necessary. Digitised images were exported to ARC-INFO™ and calculations of the areal coverage of each habitat were compiled in ArcView 4.0™.

2.5.5 Vegetation transects and wetland bathymetry

Three belt transects were conducted in random locations within each wetland to examine the distribution of upland plants and emergent and submerged vegetation. All transects were conducted in October 1996, when water levels were maximal and most vegetation would be in flower. Transects were 3m wide and 60m in length, 30m in each direction from the water's edge. Transect locations are shown in Plates 2.1b, 2.2b and 2.3b. Wetland bathymetry (depth increment) was measured at one metre intervals along the 30m submerged section of the transect. The height increment upland from the high water level was measured using an in line level suspended on a line of string between two wooden stakes. Elevation was calculated from the height lost between the two stakes, with the horizontal distance covered recorded. Results were calculated using Microsoft Excel™ and plotted using Aldus Superpaint™.

Vegetation data were recorded at one metre intervals along each belt transect. The occurrence of each species was recorded as presence/absence data. Major vegetation associations based on dominant species were identified in the field and plotted on each transect. Each delineated vegetation association was given a letter (A to E) for each wetland and the species occurring in that association listed in Appendix 1. Taxa that could not be identified in the field were collected, labelled and stored in a plant press for later identification. In the laboratory each sample was identified to the lowest possible taxonomic level using Grieve & Blackall (1982), Marchant *et al.* (1987) and Bennett (1988). Results were overlain on bathymetric maps to produce maps of vegetation associations relative to the wetland water level.

2.5.6 Emergent macrophyte harvest

Above and below ground biomass of emergent macrophytes was quantified for each wetland by harvesting 5, $1m^2$ quadrats randomly located in each wetland. Two harvests were conducted, September 1995 and April 1996, corresponding to the periods of maximum and minimum leaf growth respectively (Froend & McComb 1994).

Within each quadrat all above ground vegetation was removed at the sediment-water interface and sealed in plastic bags. The following information was recorded for each quadrat and for each species.

- Number of ramets,
- Number of leaves/ramet,
- Percentage of live, dead and senescent leaves,
- Number of flowering leaves.

Below ground biomass was estimated from 10 cores to 30cm depth within each of the $1m^2$ quadrats using the D-section corer. The cores were combined on site into a pooled sample and sealed in a plastic bag.

In the laboratory the above ground biomass samples for each quadrat were separated into live, dead and senescent leaves, placed into paper bags and dried in a Series 5 Contherm drying oven at 90°C for 48 hours. Samples were then weighed in grams to 2 decimal places immediately after removal from the oven. Pooled below ground biomass samples from each quadrat were passed through a series of wet sieves (2 mm, 1 mm and 0.5 mm) to remove sediment. Roots and rhizomes retained by the sieves were separated, placed in paper bags, dried and weighed as above.

2.6 RESULTS

2.6.1 Local climate data and wetland water levels

Monthly rainfall and maximum and minimum temperatures followed a predictable cycle associated with a Mediterranean type climate (Figure 2.2). Maximum temperatures varied from around 30°C between January and March to around 15°C in winter of each year. Minimum temperatures ranged from around 15°C in summer to 6°C in winter. Differences between maximum and minimum temperatures were most pronounced during the summer months. Rainfall peaked in July of each year, with July 1996 being the wettest month during the study period with 289 mm. Rainfall during 1996 was well above average at 1092.4 mm, substantially wetter than the first year of the project at 930.8 mm.

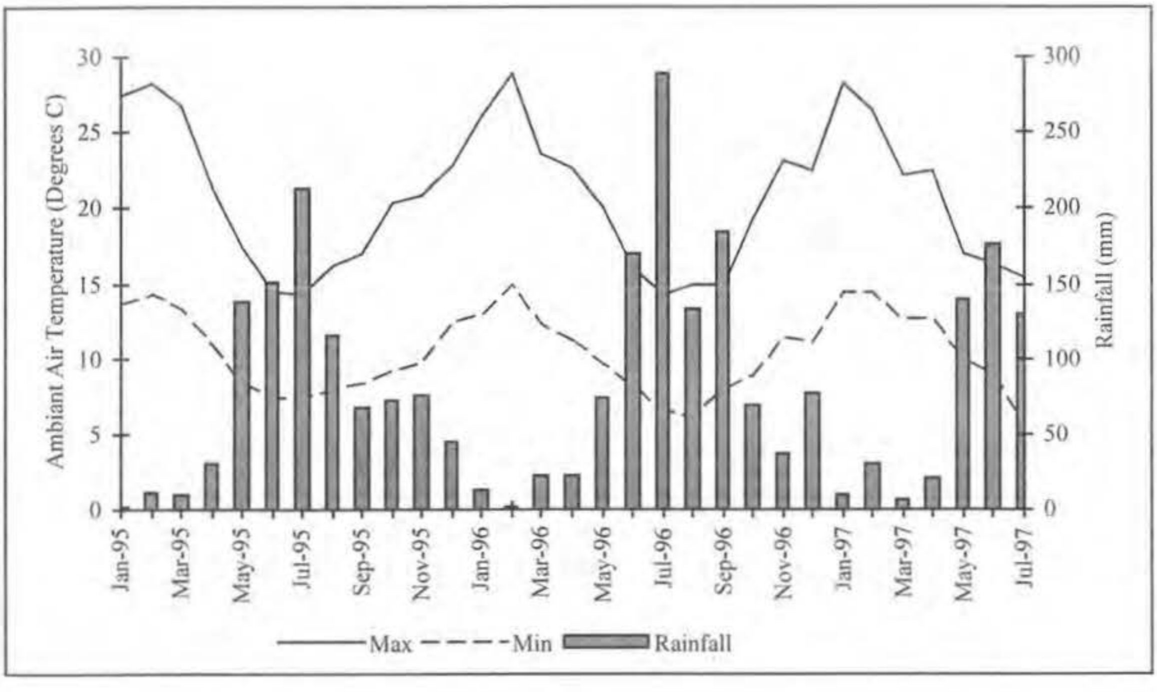


Figure 2.2 Monthly rainfall (mm) and daily maximum and minimum temperatures (°C) taken from Rocky Gully weather station (25km south-east of Noobijup Lake: Lat 34°15'19" S, Long 116°08'32" E)

All wetlands displayed marked seasonal fluctuations in their water levels with maximum levels between October and January and lowest levels between April and July (Figure 2.3). Water levels exhibited approximately a six month lag between maximum rainfall and maximum water levels. Noobijup Lake displayed the least seasonality in its water level variations.

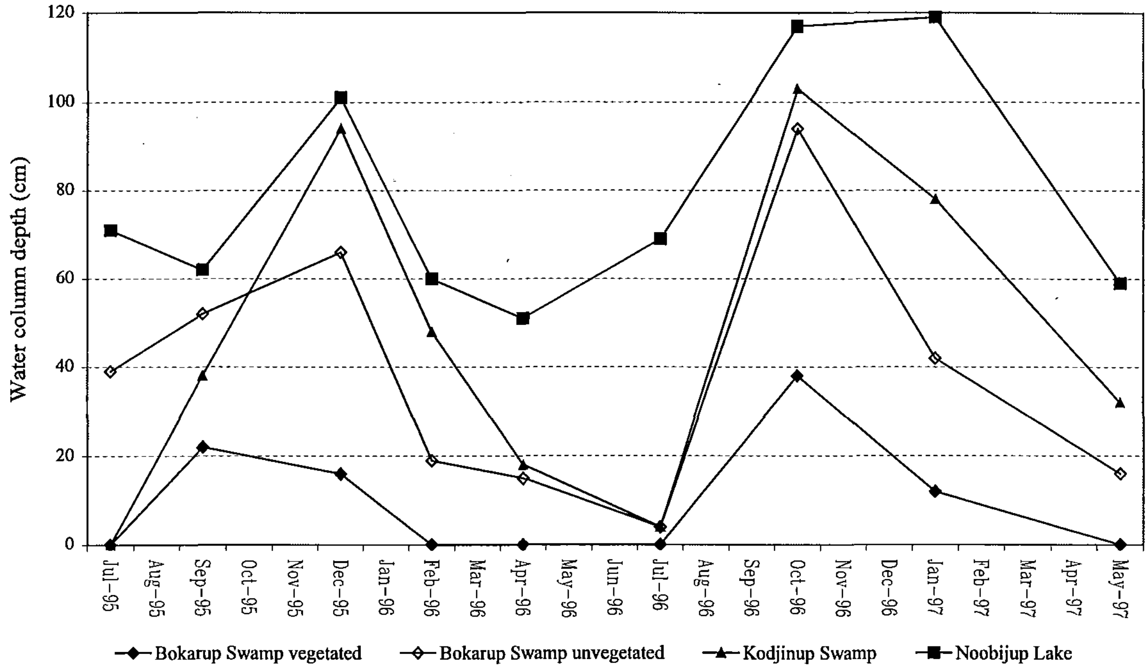


Figure 2.3. Wetland water levels in Bokarup Swamp (vegetated and unvegetated habitats), Kodjinup Swamp and Noobijup Lake from July 1995 to May 1997.

During 1995 water levels peaked in December, whereas in the second year levels peaked earlier in the year. Noobijup Lake consistently had the highest water levels, with the other study wetlands having no surface water at some stage. Water levels in Noobijup Lake increased from April to July 1996, whereas levels in the other wetlands continued to decline until July 1996, when levels rose dramatically, increasing by almost one metre in the 3 months to September. Kodjinup Swamp had no surface water in July 1995 at the first sampling occasion but retained water for the rest of the sampling period, although the water level was only 5cm in April 1996. Bokarup Swamp had two major habitats with different hydrologic regimes. The unvegetated area of open water retained surface water throughout the study, with the more elevated *B.articulata* habitat having consistently lower water levels, with no surface water evident between February and July of each year.

2.6.2 Sediment profile analysis

Sediment profiles varied greatly between wetlands both in their structure and chemistry. Despite this there are trends that are apparent in all profiles. Each wetland has highly organic sediments of differing depths, with Bokarup Swamp having the deepest organic sediments in excess of 2.76 m. The other wetlands have similar shallower organic soils to around 1.5 m. Each wetland had trends of decreasing pH and increasing conductivity with depth (Tables 2.2, 2.3, 2.4). Conductivity readings were similar in Bokarup and Kodjinup Swamps from around 1000 µS/cm in surface sediments to 1500 µS/cm at the base of the profile, with Noobijup Lake displaying the least saline sediments. In the general trend of increasing conductivity with depth there is a spike of high conductivity readings at the second interval in each sediment profile. Within the profile this is the point where a defined, solid sediment surface begins. Above this point the substrate is unconsolidated, consisting of non-decomposed plant remains. The pH values are similar in all wetlands throughout the profile, from around 6.5 in surface sediments to 5.7 at the base of the profile. These values are consistent in each wetland despite the differing depths, with Bokarup Swamp having sediments over 1.2 m deeper than the other wetlands.

Noobijup Lake stands out from the other wetlands in its particle size, organic content and colour. Bokarup and Kodjinup Swamps both have consistent black sediments throughout the profile. Noobijup Lake has the same black surface sediments but at the base of the profile has a horizon of grey/black sediment at 120 cm followed by a horizon of green/grey Gley that was impenetrable to the corer. Noobijup Lake also had the least organic sediment and a decreasing organic content with depth. Both Bokarup and Kodjinup Swamps have organic contents ranging between 70% and 90% increasing with depth. The surface sediments at Noobijup Lake have an organic content of 63.4%, but this rapidly fell to 26.3% at the base of the water column. These data correspond to the marked increase in the clay content at the base of the profile.

Both Bokarup and Kodjinup Swamps had a percentage of sand throughout their profiles, and an increasing silt composition with depth. Noobijup Lake had sand in the profile in the two surface horizons, with a clay content that increased from 34% to 71% at the base of the profile. Each wetland also displayed the trend of an increased percentage of sand at the second interval, again the point where consolidated sediments were found in each wetland.

Table 2.2. Sediment particle size, colour and average (± SE) OM%, pH and conductivity for peat profiles taken from Bokarup Swamp.

Depth (cm)	Particle size	Colour	% OM	pH	Cond. (μS/cm)
0	4% sand 62% silt 34% clay	10YR/2/1	78.4 ± 7.8	6.47 ± 0.59	1117 ± 4
42	13% sand 49% silt 38% clay	10YR/2/1	72.7 ± 4.6	6.34 ± 0.44	1224 ± 7
100	7% sand 55% silt 38% clay	10YR/2/1	81.3 ± 8.3	6.04 ± 0.71	1155 ± 4
170	4% sand 61% silt 35% clay	10YR/2/1	80.4 ± 5.5	5.76 ± 0.34	1178 ± 12
220	3% sand 61% silt 36% clay	10YR/2/1	83.3 ± 2.9	5.82 ± 0.43	1403 ± 9
276	3% sand 69% silt 28% clay	10YR/2/1	91.4 ± 5.1	5.80 ± 0.27	1506 ± 14

Table 2.3. Sediment particle size, colour and average (± SE) OM%, pH and conductivity for peat profiles taken from Kodjinup Swamp.

Depth (cm)	Particle size	Colour	% OM	pH	Cond. (µS/cm)
0	8% sand 76% silt 16% clay	10YR/2/1	71.3 ± 9.7	6.47 ± 0.38	980 ± 11
25	26% sand 54% silt 20% clay	10YR/2/1	66.3 ± 10.8	5.88 ± 0.46	1297 ± 18
60	23% sand 59% silt 18% clay	10YR/2/1	68.7 ± 8.8	5.88 ± 0.29	1057 ± 9
90	19% sand 58% silt 23% clay	10YR/2/1	73.5 ± 9.2	5.82 ± 0.35	1302 ± 13
128	13% sand 60% silt 27% clay	10YR/2/1	86.3 ± 7.7	5.74 ± 0.32	1470 ± 16

Table 2.4. Sediment particle size, colour and average (± SE) OM%, pH and conductivity for peat profiles taken from Noobijup Lake.

Depth (cm)	Particle size	Colour	% OM	pH	Cond. (µS/cm)
0	3% sand 63% silt 34% clay	10YR/2/1	63.4 ± 5.9	6.58 ± 0.42	662 ± 21
15	5% sand 54% silt 41% clay	10YR/2/1	61.5 ± 8.6	6.46 ± 0.25	899 ± 16
40	0% sand 56% silt 44% clay	10YR/2/1	49.3 ± 11.3	6.46 ± 0.36	699 ± 12
70	0% sand 51% silt 49% clay	10YR/2/1	44.6 ± 9.1	6.42 ± 0.09	733 ± 9
120	0% sand 43% silt 57% clay	10YR/10/1	38.4 ± 5.8	6.33 ± 0.41	783 ± 12
154	0% sand 29% silt 71% clay	Gley N2.5	26.3 ± 3.9	5.64 ± 0.33	1053 ± 31

2.6.3 Wetland physico-chemistry

2.6.3.1 Water column profiles

All wetlands displayed thermal and oxygen stratification, both being most pronounced in spring and summer when ambient air temperatures and water depths were highest. Dissolved Oxygen (DO) levels in Bokarup Swamp were lowest in summer (2.51 mg/L surface and 0.29 mg/L epibenthic) with stratification in the 40cm water column most pronounced in spring (6.99 mg/L surface and 0.25 mg/L epibenthic) (Figure 2.4a). Increased DO levels were found in autumn and winter associated with low water levels. Surface water temperature was typically highest in summer at 25.5°C and lowest in winter at 10.4°C. Temperature stratification was also evident in spring and summer with differences between the surface and epibenthos of 6°C and 5.1°C respectively (Figure 2.4b). Conductivity varied enormously from 1.93 mS/cm in spring to 8.59 mS/cm in autumn, corresponding to highest and lowest water levels (Figure 2.4c). Water column pH varied from mildly acidic (6.34) in autumn to mildly alkaline (7.50) in winter (Figure 2.4d). A slight increase in acidity with depth was evident in spring and summer.

Dissolved Oxygen levels in Kodjinup Swamp were lowest in winter at 4.45 mg/L. Stratification in the 100cm deep water column was most pronounced in summer with DO concentrations of 6.17 mg/L at the surface and 0.35 mg/L at the epibenthos (Figure 2.5a). Surface water temperature was typically highest in summer at 29.3°C and lowest in winter at 9.9°C. Temperature stratification was also evident in spring and summer with differences between the surface and epibenthos of 7.4°C and 6.9°C respectively (Figure 2.5b). As with Bokarup Swamp, conductivity varied enormously between seasons ranging from 2.25 mS/cm in spring to 7.31 mS/cm in autumn, corresponding to highest and lowest water levels (Figure 2.5c). Water column pH varied from an acidic 6.57 in autumn to an alkaline 7.4 in spring (Figure 2.5d). A slight increase in acidity with depth was evident in spring and summer.

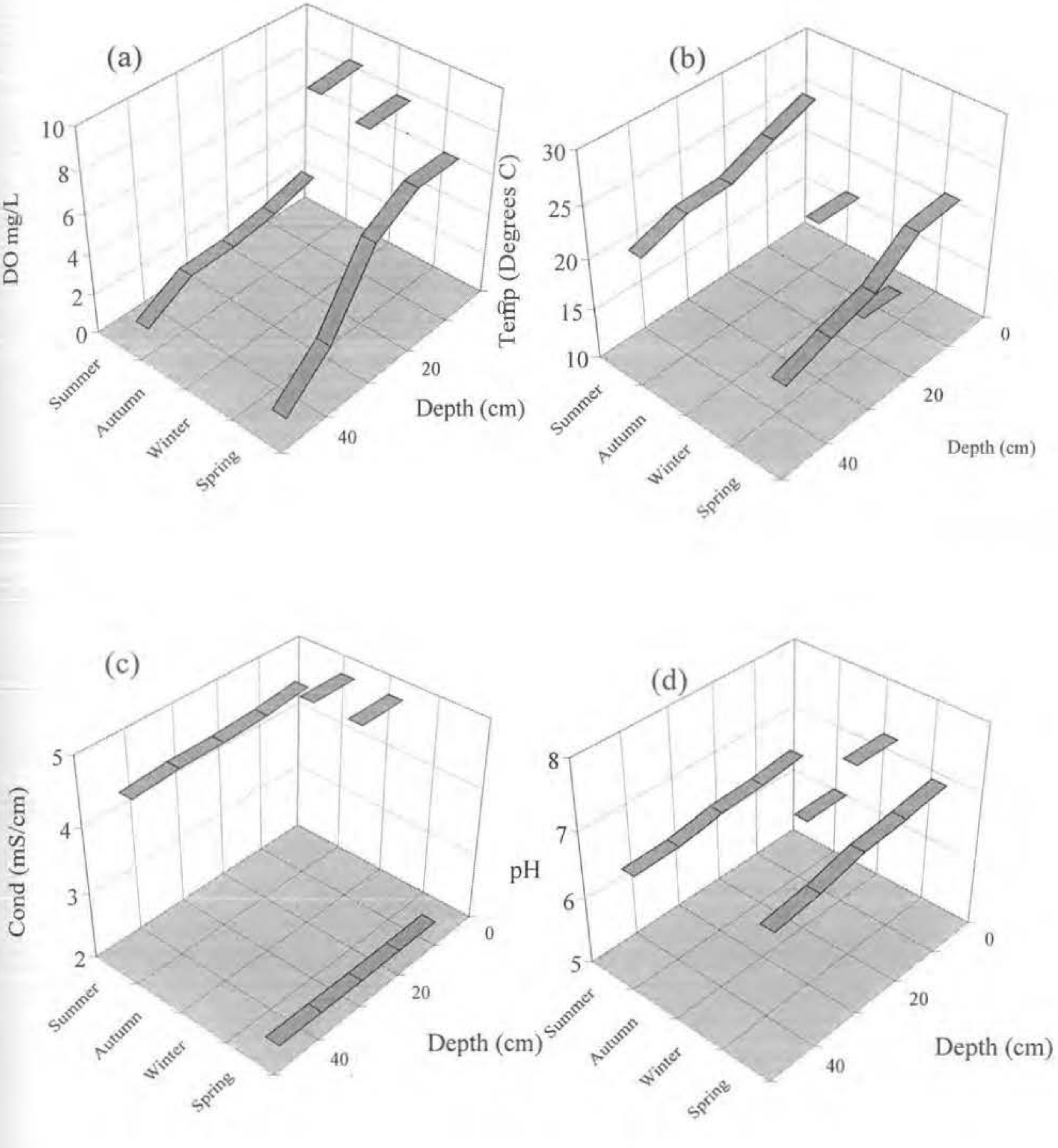


Figure 2.4. Dissolved Oxygen mg/L (a), temperature °C (b), conductivity (mS/cm) (c) and pH (d) profiles at 10 cm intervals from surface to epibenthos for each season in Bokarup Swamp. All values are means of readings taken from five replicate profiles.

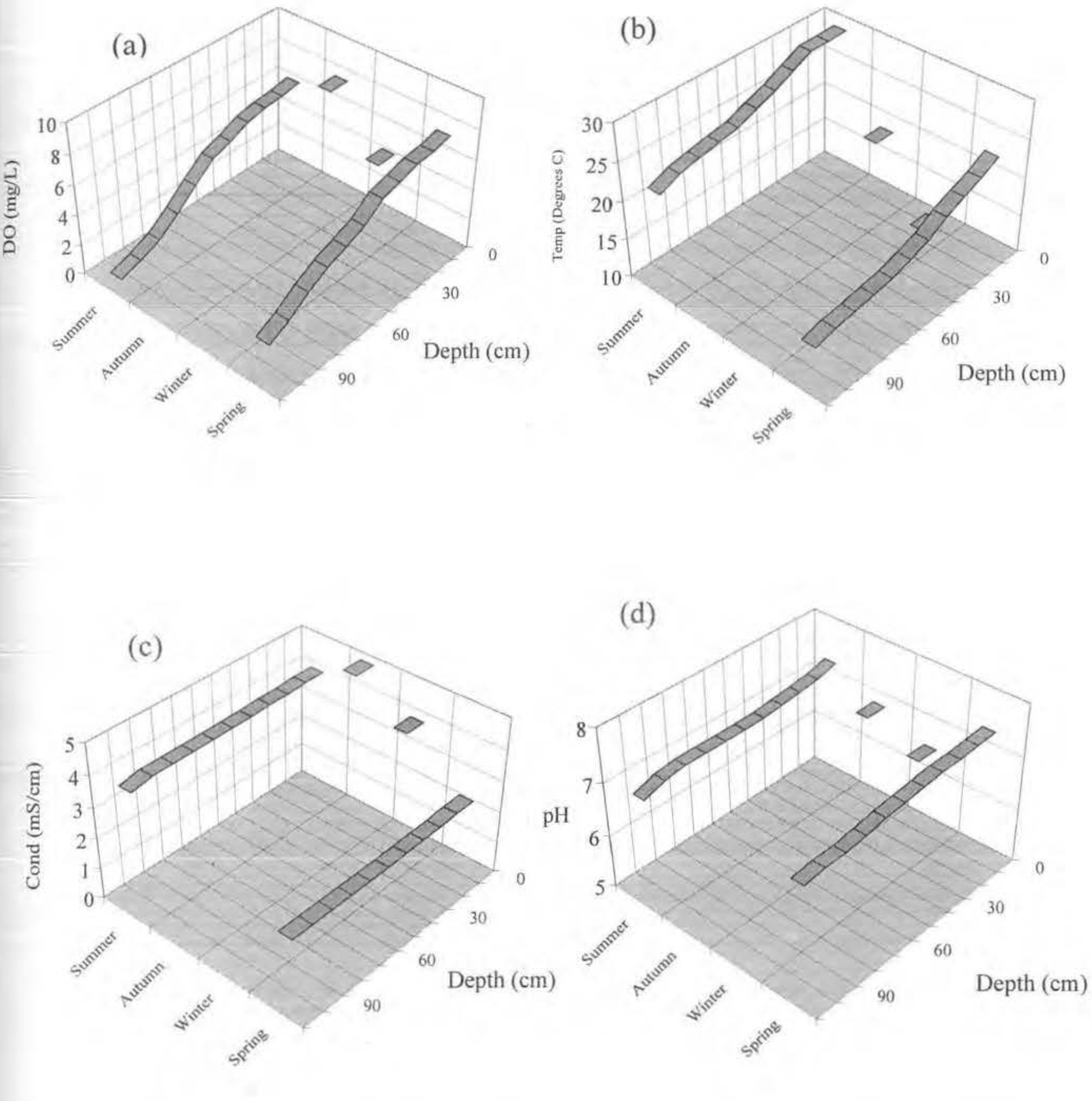


Figure 2.5. Dissolved Oxygen mg/L (a), temperature °C (b), conductivity (mS/cm) (c) and pH (d) profiles at 10 cm intervals from surface to epibenthos for each season in Kodjinup Swamp. All values are means of readings taken from five replicate profiles.

Noobijup Lake differed from the other wetlands, displaying less seasonal variation in water depth, ranging from 50 cm in autumn to 120 cm in spring. Similar to Bokarup Swamp, DO levels were lowest in summer when stratification was most pronounced (5.64 mg/L surface and 0.28 mg/L epibenthic) (Figure 2.6a). Noobijup Lake consistently had the highest DO concentrations of all wetlands, reaching 11.43 mg/L at the surface in spring. The DO profiles in spring and summer also exhibited an increase in concentration at 30 cm and 60 cm respectively. Water temperature was again typically highest in summer at 29°C at the surface and lowest in winter at 10.8°C. Temperature stratification was also evident in spring, summer and autumn with differences between the surface and epibenthos of 7.6°C, 8.6°C and 5.2°C respectively (Figure 2.6b). During winter, an increase in temperature of 2.5°C was evident in the profile. This trend is also evident in the winter conductivity profile with an increase of 2.64 mS/cm with depth. Conductivity varied less than the other wetlands from 2.25 mS/cm in spring to 6.48 mS/cm in autumn, corresponding to highest and lowest water levels (Figure 2.6c). Water column pH was consistently alkaline, surface values ranging from 7.85 in winter to 7.39 in spring (Figure 2.6d). Noobijup Lake also had the most pronounced pH stratification with an increase in acidity with depth in summer.

2.6.3.2 Diurnal dissolved oxygen and temperature profiles

Water depth in Bokarup Swamp was only 30 cm at the time of sampling, however, both DO and temperature stratification were evident. Dissolved Oxygen concentrations were consistently less than 1 mg/L at the epibenthos throughout the 24 hour period, falling as low as 0.13 mg/L at the first 16:00 hour reading (Figure 2.7a). Surface concentrations varied little, from 5.39 mg/L at midday to 3.55 mg/L at midnight. Temperature stratification was not permanent, with the thermocline breaking down at night. A maximum temperature difference of 6.1°C between the surface and epibenthos was recorded at the second 1600 hour reading, with surface waters reaching 33.1°C (Figure 2.7b).

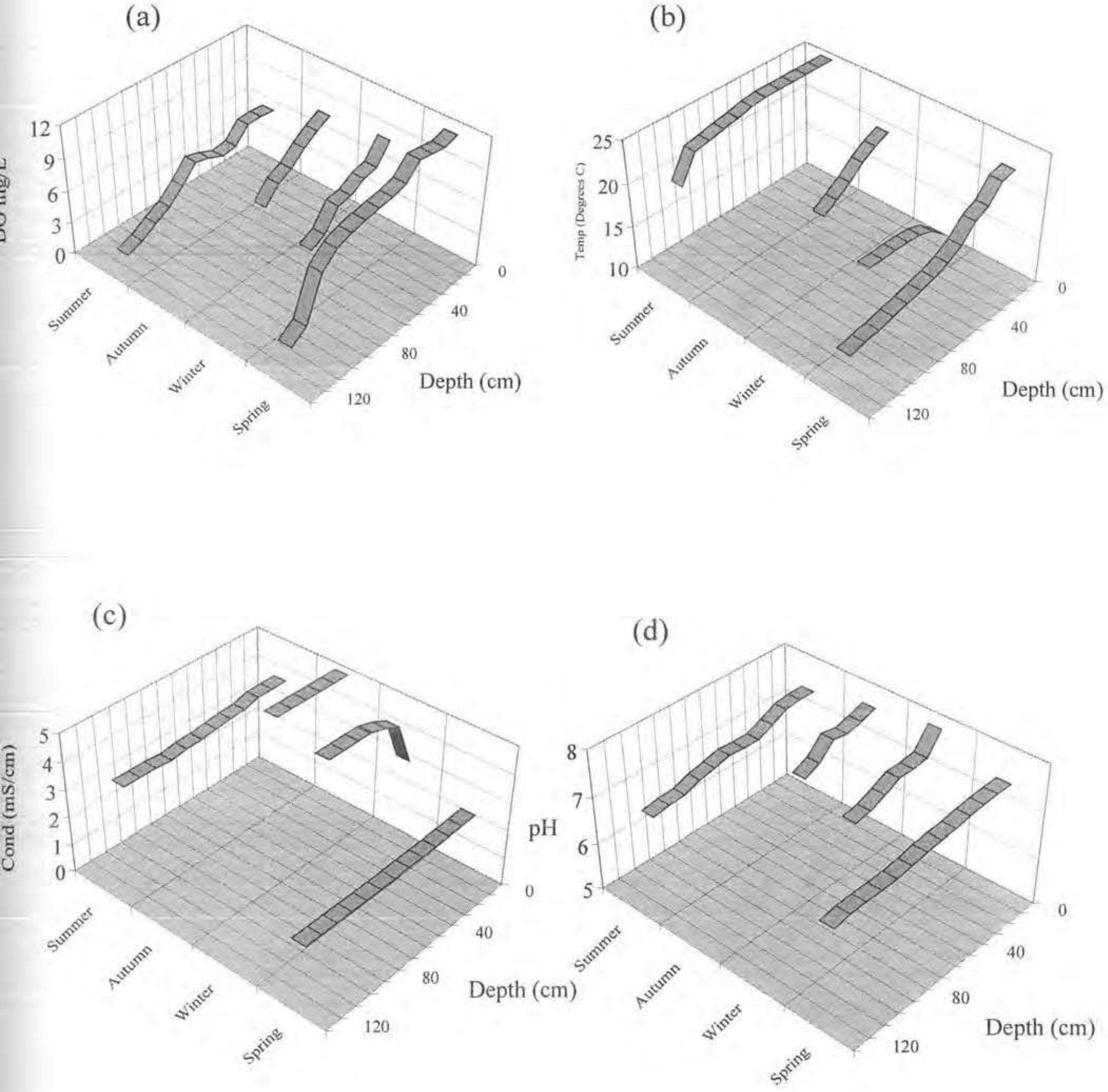
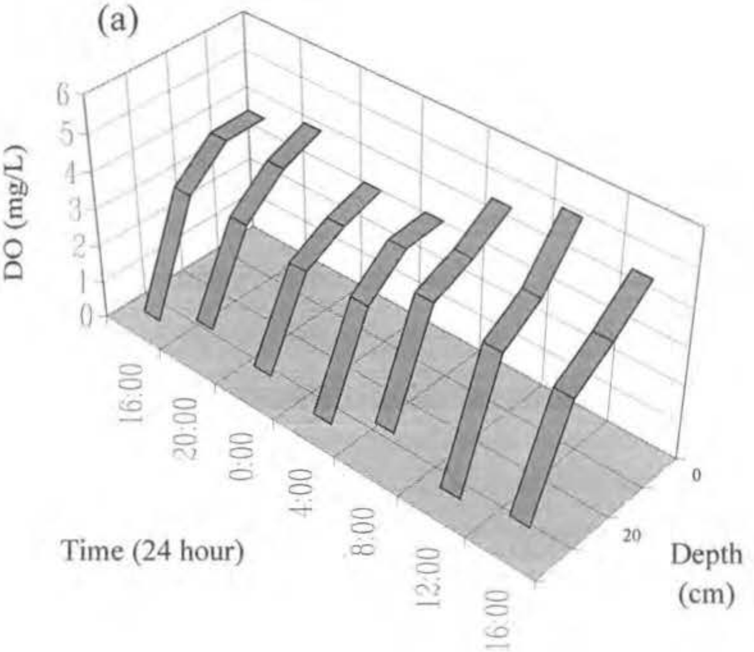


Figure 2.6. Dissolved Oxygen mg/L(a), temperature °C (b), conductivity (mS/cm) (c) and pH (d) profiles at 10cm intervals from surface to epibenthos for each season in Noobijup Lake. All values are means of readings taken from five replicate profiles.



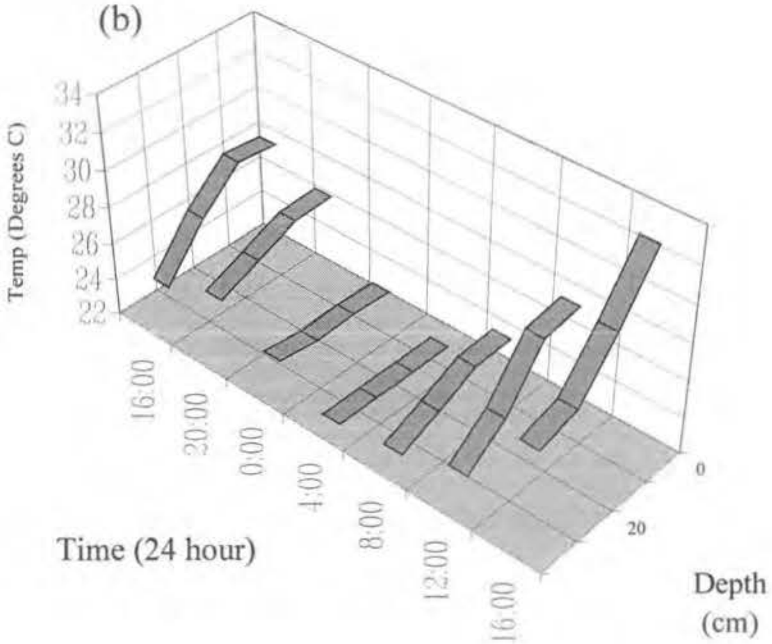


Figure 2.7. Diurnal variations in Dissolved Oxygen mg/L (a) and temperature °C (b) profiles at 4 hourly intervals at 10 cm intervals from surface to epibenthos in Bokarup Swamp.

Water depth in Kodjinup Swamp was 80cm at the time of sampling with both DO and temperature stratification evident. Dissolved Oxygen concentrations were consistently less than 1 mg/L at the epibenthos throughout the 24 hour period, falling as low as 0.18 mg/L at 20:00 hours (Figure 2.8a). Surface concentrations varied from 6.84 mg/L at 16:00 hours to 3.33 mg/L at 0400 hours. As with Bokarup Swamp, temperature stratification was not permanent, with the thermocline broken down at night. A maximum temperature difference of 11.6°C between the surface and epibenthos was recorded at the 1600 hour reading, with surface water temperatures reaching 34.3°C (Figure 2.8b).

As with the other two wetlands, both DO and temperature stratification were evident in Noobijup Lake, with the thermocline broken down at night. Dissolved oxygen concentrations were consistently less than 1 mg/L at the epibenthos throughout the 24 hour period, falling as low as 0.06 mg/L at the second 16:00 hour reading (Figure 2.9a). Surface concentrations varied from 6.99 mg/L at 0400 hours to 3.67 mg/L at 0800 hours. A maximum temperature difference of 8.6°C between the surface and epibenthos was recorded at 1600 hours, with surface water temperatures reaching 29.3°C (Figure 2.9b).

2.6.3.3 Nutrients

Orthophosphate concentrations showed little variability within and between wetlands, with concentrations consistently less then 10 µg/L (Figure 2.10a). A sharp increase in orthophosphate concentrations was apparent in all wetlands in July 1996, peaking at 9.54 ± 1.38 µg/L in Bokarup Swamp. Total phosphorus concentrations were also low in all wetlands, consistently below 20 µg/L (Figure 2.10b). Bokarup Swamp and Noobijup Lake had a trend of low summer and higher autumn/winter concentrations, with Kodjinup Swamp displaying the reverse trend. In contrast, total phosphorus concentrations in emergent macrophyte material were consistently higher than the water column (Figures 2.11a and 2.11b). Total phosphorus concentrations were also slightly higher in April in all wetlands. Bokarup Swamp stands have the highest concentrations in *B.articulata* leaves, roots and rhizomes in both sampling periods. Total Phosphorus in *B.articulata* leaves were consistently higher than in other plant parts, 805.45 ± 65.06 and 820.83 ± 85.05 µg/L in April and September respectively.

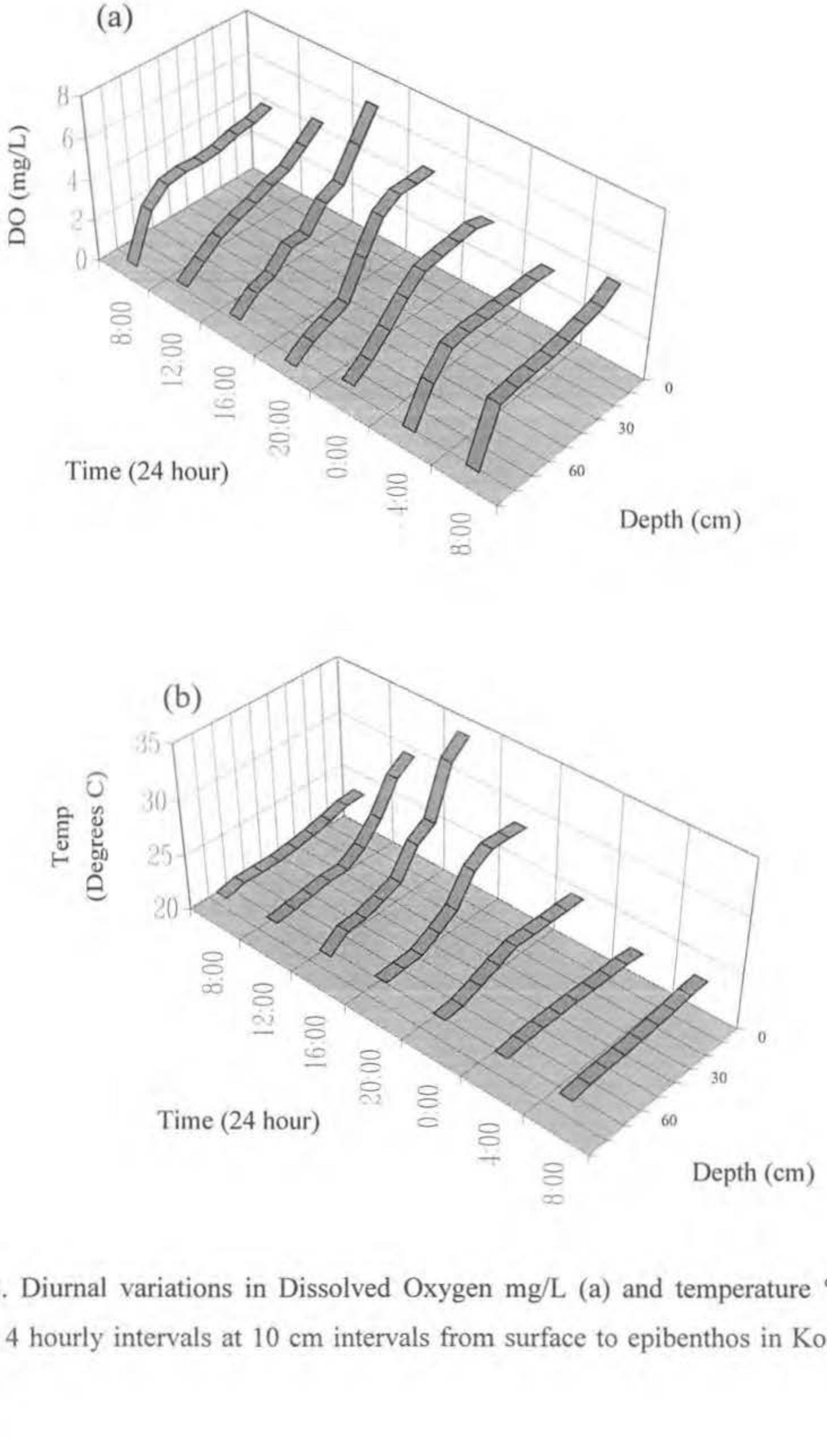
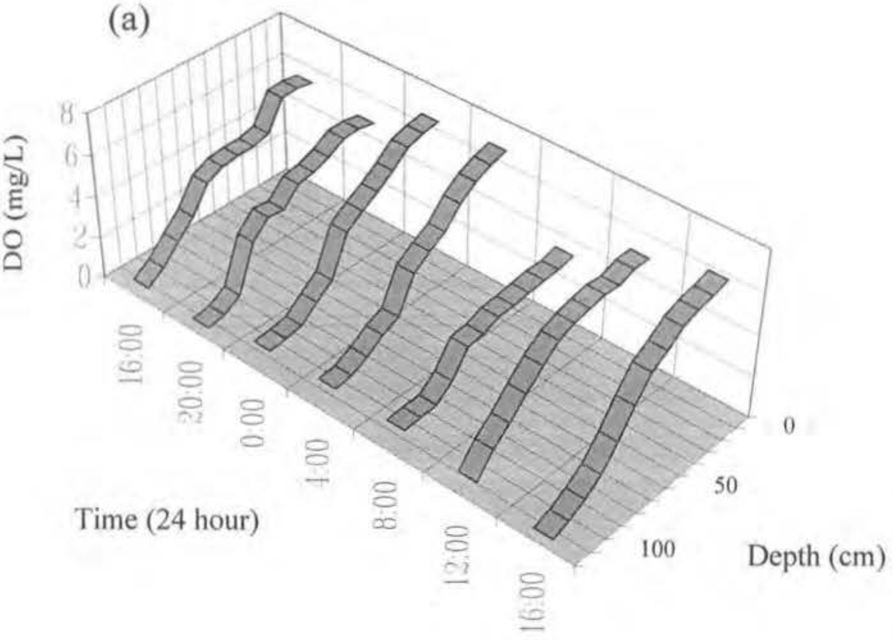


Figure 2.8. Diurnal variations in Dissolved Oxygen mg/L (a) and temperature °C (b) profiles at 4 hourly intervals at 10 cm intervals from surface to epibenthos in Kodjinup Swamp.



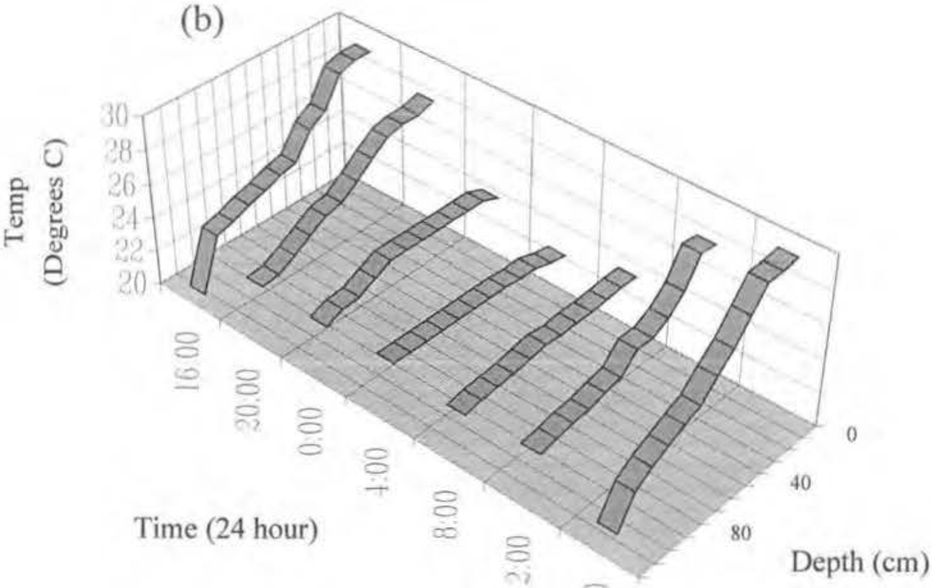


Figure 2.9. Diurnal variations in Dissolved Oxygen mg/L (a) and temperature °C (b) profiles at 4 hourly intervals at 10 cm intervals from surface to epibenthos in Noobijup Lake.

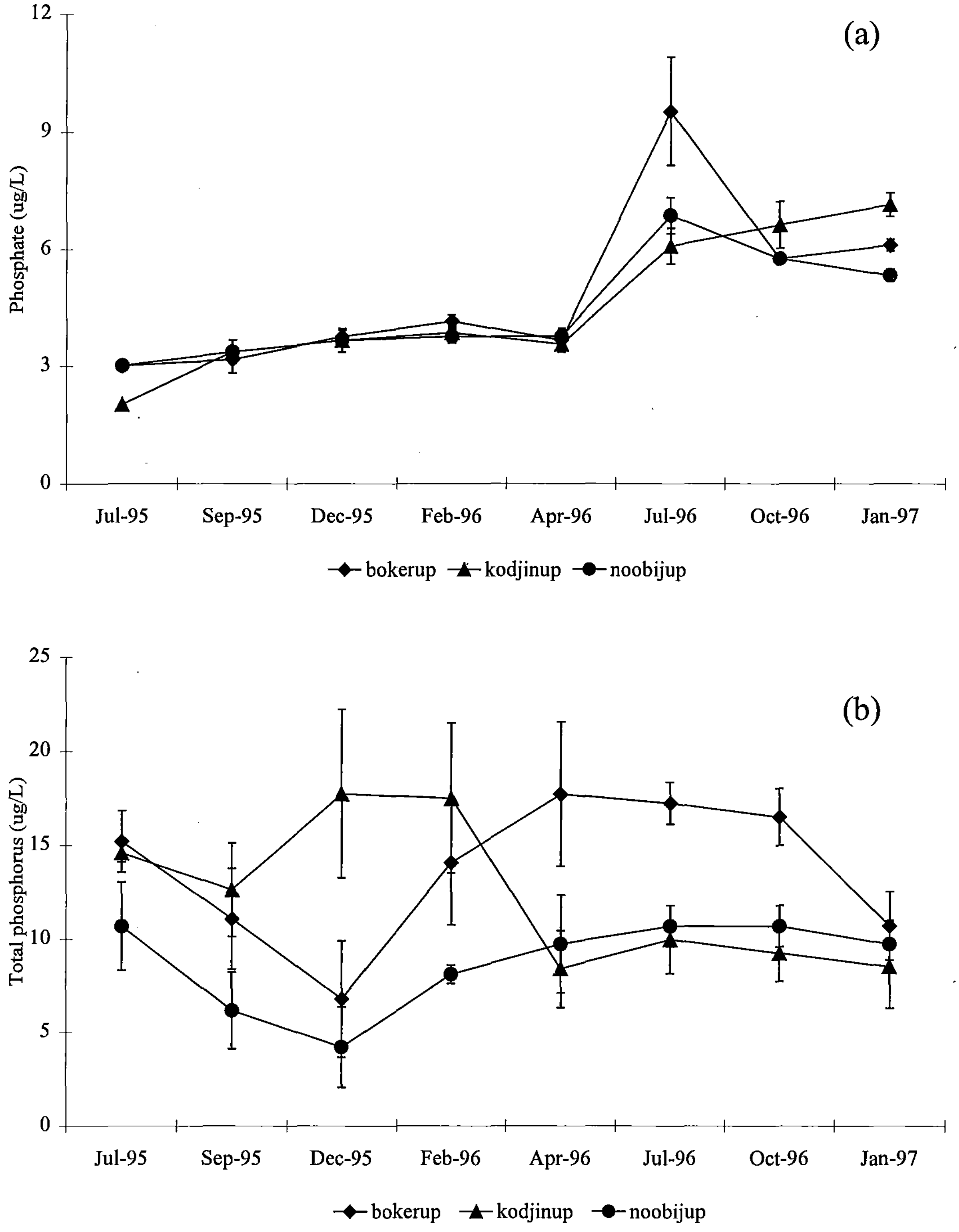


Figure 2.10 Mean (±SE) water column concentrations of (a) orthophosphate µg/L and (b) Total Phosphorus µg/L in each wetland from July 1995 to January 1997.

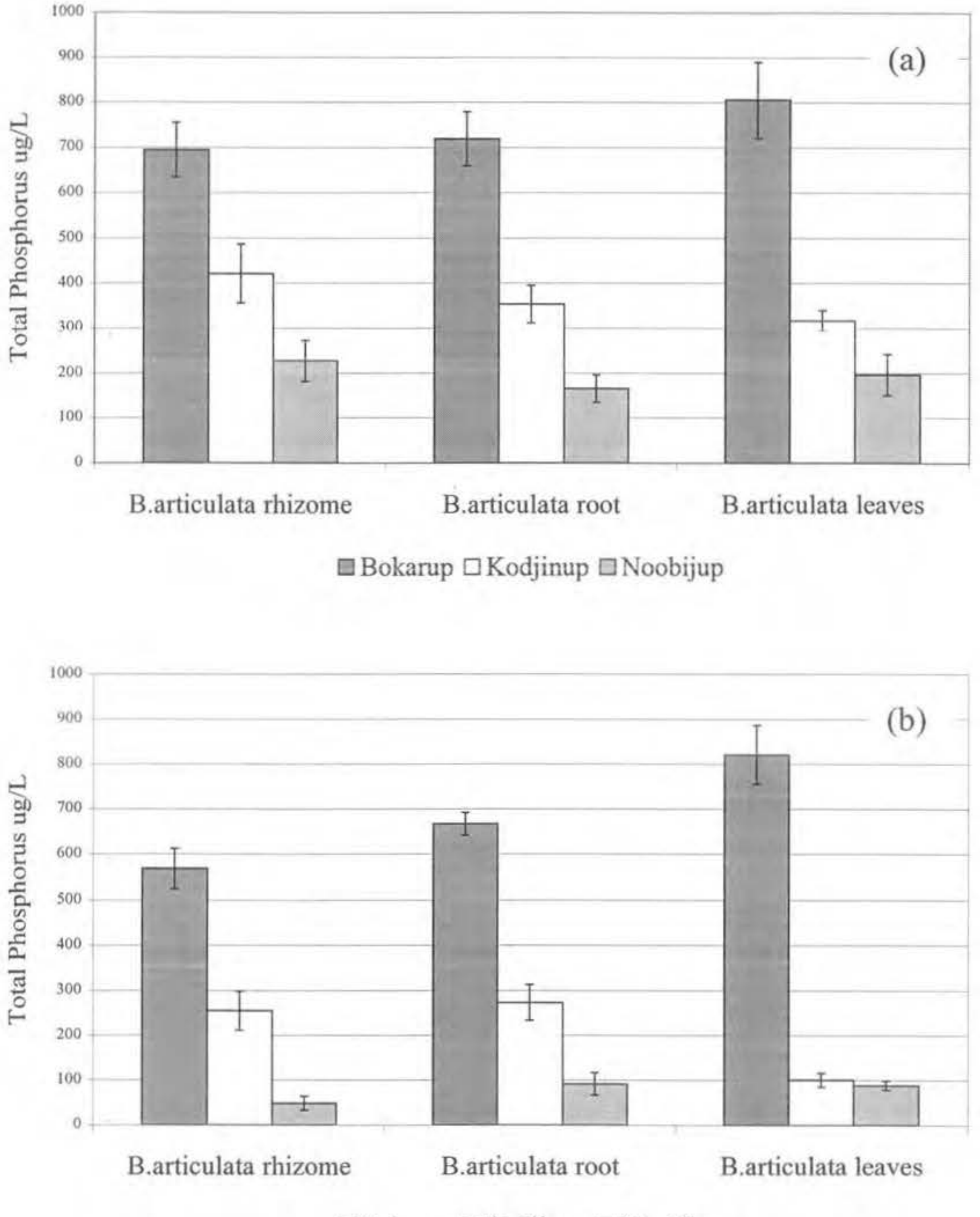


Figure 2.11 Mean (±SE) concentrations of Total Phosphorus µg/L in (a) April and (b) September from *B.articulata* rhizomes, roots and leaves from each wetland.

Concentrations of total phosphorus decreased in all plant parts from April to September in Kodjinup Swamp and Noobijup Lake, most apparent in rhizomes and leaves.

In comparison, concentrations of ammonia showed marked differences between wetlands and seasons (Figure 2.12a). Bokarup Swamp showed a distinct seasonal cycle of high summer (2011.00 ± 112.37 μg/L) and low winter (264 ± 9.08 μg/L) concentrations. Seasonal changes in ammonia concentrations were less distinct in Kodjinup Swamp, peaking at 944.92 ± 108.22 μg/L in July 1996. Noobijup Lake had comparatively low concentrations, peaking at 125.00 ± 13.69 μg/L in April 1996.

Nitrate/nitrite concentrations were generally low, peaking at less than 30 μg/L in all wetlands in the summer/autumn period (Figure 2.12b). Kodjinup and Bokarup Swamps showed a dramatic decline in nitrate/nitrite concentrations following their peaks in February and April 1996 respectively. These values were lower than those at the same time in the preceding year.

2.6.4 Wetland habitat classification

Emergent vegetation was the dominant habitat in each wetland, occurring as either as a monospecific stand of *B.articulata* or mixed *B.articulata* and other emergent species (Table 2.5). This habitat ranged from around 54% in Bokarup Swamp to almost 90% in the other two wetlands. Despite the differences in the size of wetland perimeters, *Melaleuca* was consistently around 10% of the total wetland area. Bokarup Swamp had the only significant area of open water, covering nearly 40% of the wetland basin. Wetland vegetation cover in Kodjinup Swamp and Noobijup Lake can be classified as concentriform and Bokarup Swamp as Gradiform (after Semeniuk *et al.* 1990).

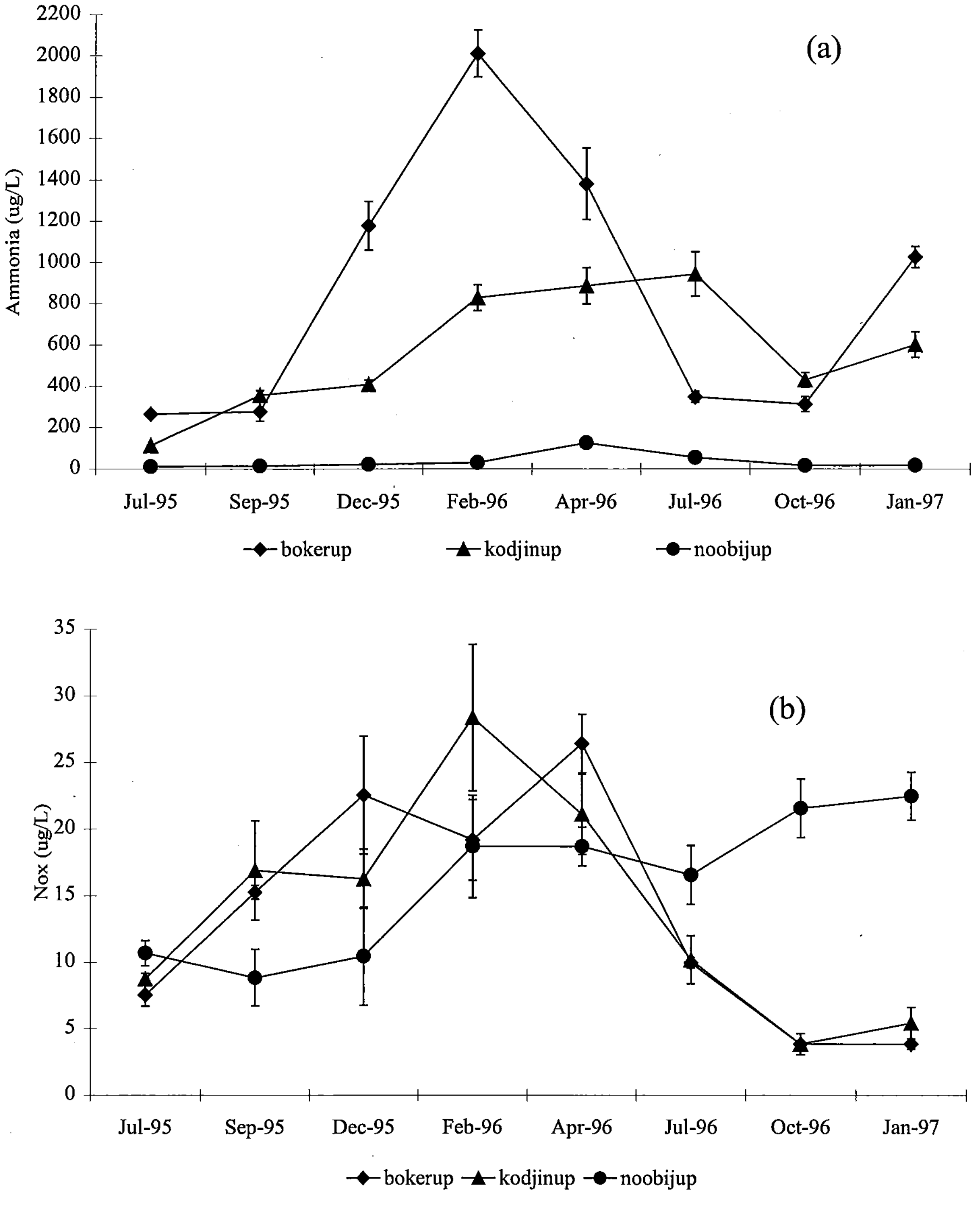


Figure 2.12 Mean (±SE) water column concentrations of (a) ammonia µg/L and (b) nitrate/nitrite in each wetland from July 1995 to January 1997.

Table 2.5. Areas (hectares) of wetland basins and major habitat types for Bokarup Swamp, Kodjinup Swamp and Noobijup Lake.

Wetland	Habitat	Area (ha)
Bokarup Swamp	*Melaleuca spp.*	2.87
	Open Water	12.42
	B.articulata	18.11
Total		33.40
Kodjinup Swamp	*Melaleuca spp.*	3.58
	Open Water	0.14
	B.articulata	21.99
Total		25.71
Noobijup Lake	*B.articulata*	13.37
	Mixed sedges	43.87
Total		65.04

2.6.5 Vegetation transects and wetland bathymetry

A total of 62 aquatic and riparian plants were found from the three wetlands. Noobijup Lake had the highest species richness of 39 taxa, followed by Bokarup Swamp with 34 taxa and Kodjinup Swamp with only 26 taxa (Table 2.6). Appendix 1 contains a complete taxonomic list for each transect and wetland. Noobijup Lake also had the highest number of unique taxa (16), followed by Bokarup Swamp (11) and Kodjinup Swamp (7). The unique taxa of Noobijup Lake are predominantly perennial shrub plants including *Hibbertia amplexicaulis*, *Hypocalymma angustifilium*, *Boronia spathulata* and two species of *Hakea*. This wetland also has one species of emergent macrophyte, *Baumea arthrophylla*, not found in the other wetlands.

Table 2.6 Species richness of wetland plants along each transect and within each defined vegetation association (A, B, C & D/E) in Bokarup Swamp, Kodjinup Swamp and Noobijup Lake.

	Transect 1				Transect 2			Transect 3				Species Richness
	A	B	C	D/E	A	B	C	A	B	C	D	
Bokarup Swamp	2	3	0		27	5	6	22	5	5		34
Kodjinup Swamp	13	4	6	4	1	18	6	3	18	4	3	26
Noobijup Lake	28	14	5	2	23	19	6	25	10	4	2	39

Similarly, species unique to Bokarup Swamp are smaller perennial shrubs such as *Hibbertia hypercoides*, *Davesia sp.*, and *Bossiaea linofolia* with two species of larger understorey plants also found only here, *Acacia extensa* and a species of *Hypocalymma*. Kodjinup Swamp was the only wetland where *Pteridium esculentum* was found, a fern species known to recolonise after fire. All of the species only occurring at Kodjinup were the larger understorey plants such as *Acacia saligna* and *Hypocalymma sp.*

Dominant vegetation types within each transect were categorised into vegetation associations. Eucalypt woodland, *Melaleuca* woodland and emergent vegetation were common to all wetlands. Open Eucalypt woodland was consistently the upland vegetation, *Melaleuca* woodland occurred around the seasonally inundated zone and areas of emergent macrophytes (dense or sparse) dominated by *B.articulata* were found in the inundated zones (Figures 2.13, 2.14 and 2.15). Transect one at Bokarup Swamp differs in that it does not possess understorey species, *Melaleuca* woodland or extensive areas of emergent vegetation. Dense stands of emergent vegetation are

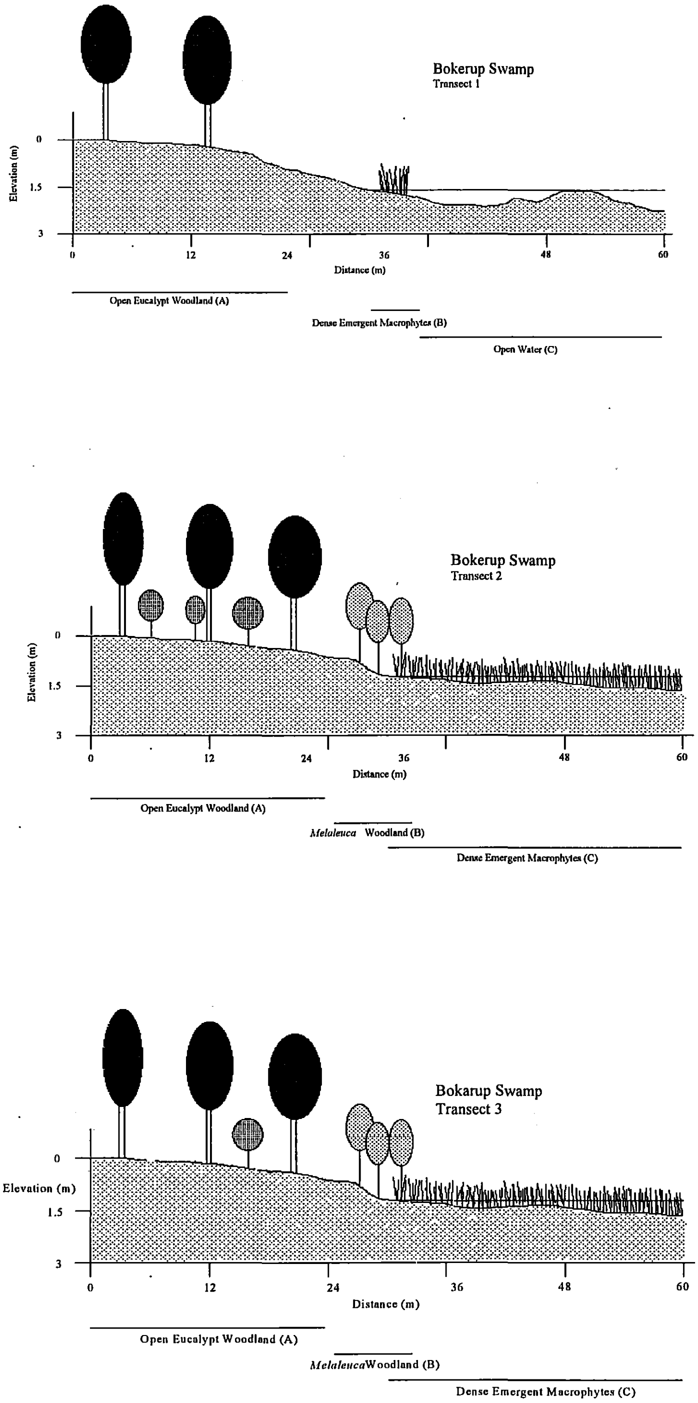


Figure 2.13 Stylised diagrams of belt transects showing major vegetation associations and wetland bathymetry in Bokarup Swamp. Taxonomic lists for vegetation associations A, B and C are in Appendix 1.

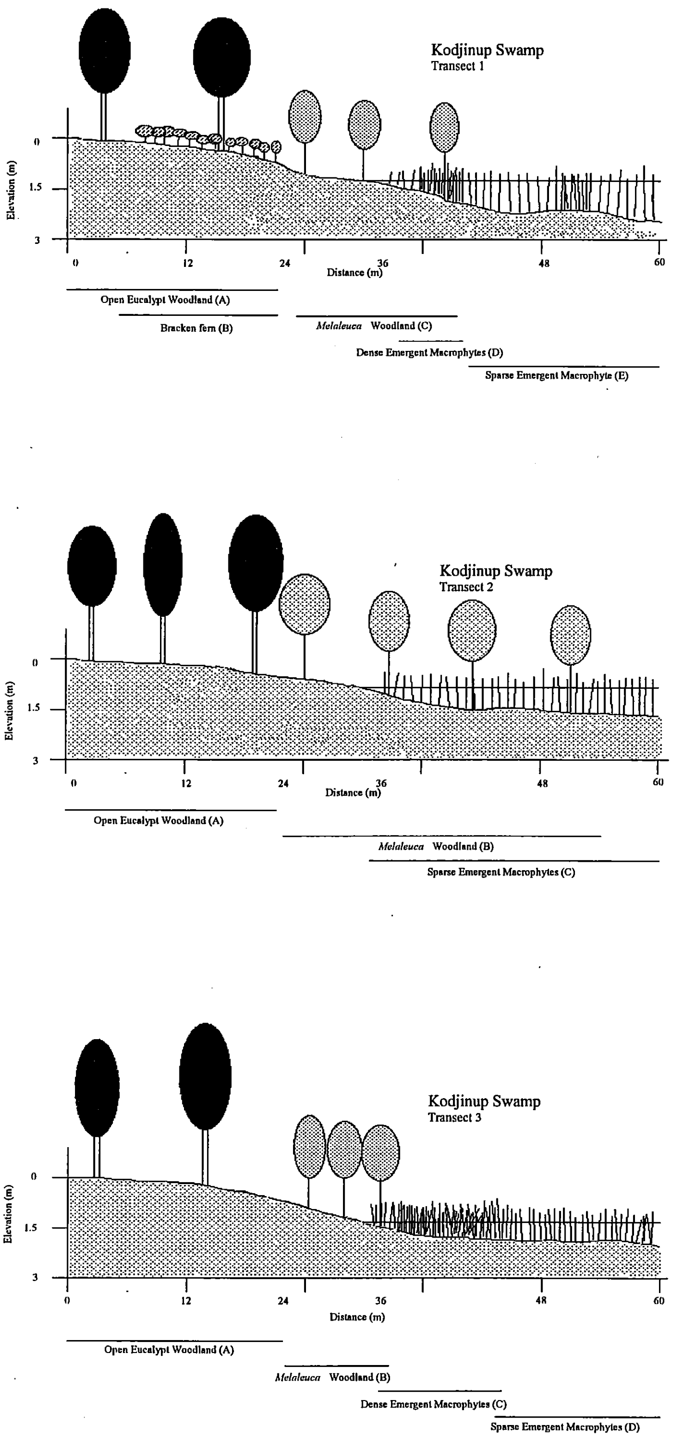


Figure 2.14 Stylised diagrams of belt transects showing major vegetation associations and wetland bathymetry in Kodjinup Swamp. Taxonomic lists for vegetation associations A, B, C, D and E are in Appendix 1.

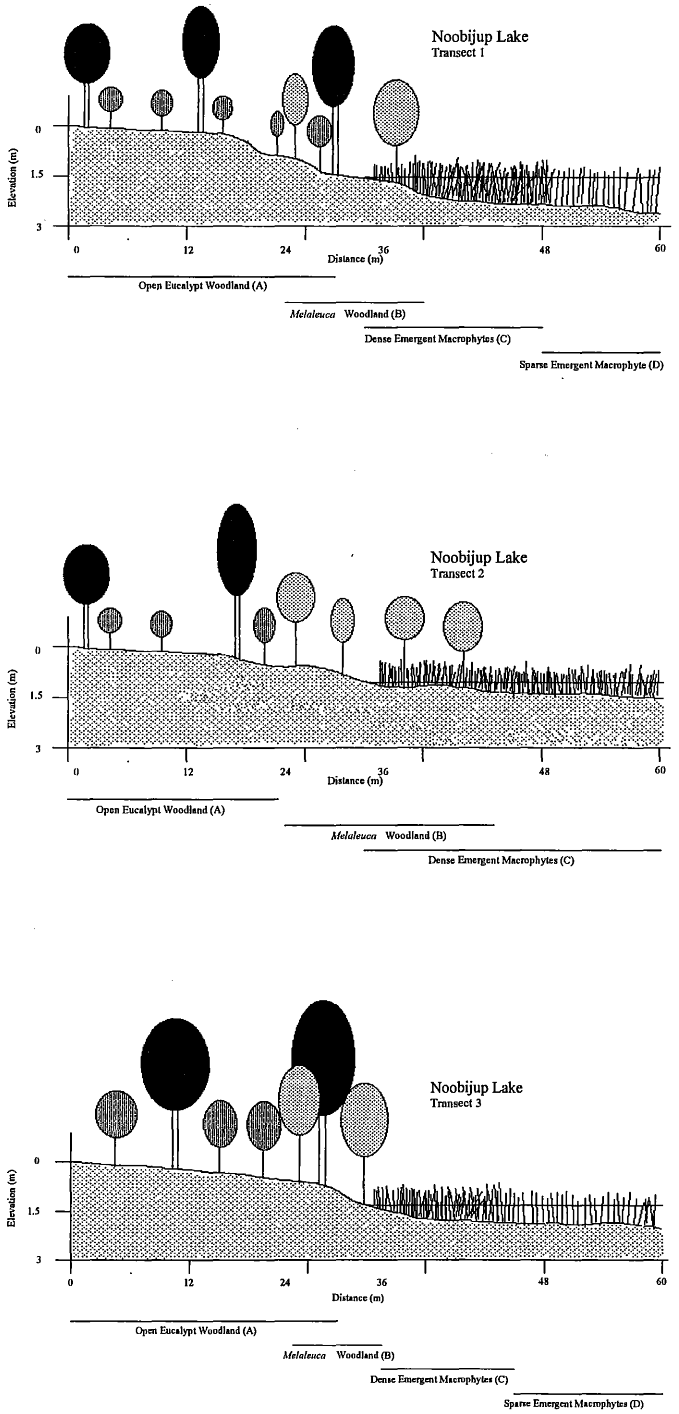


Figure 2.15 Stylised diagrams of belt transects showing major vegetation associations and wetland bathymetry in Noobijup Lake. Taxonomic lists for vegetation associations A, B, C and D are in Appendix 1.

associated with water levels less than one metre, except in transect one where the bathymetry shows an island of organic sediment around 50m along the transect. Transect one at Kodjinup Swamp again differed from the others in that it had a dense band of *Pteridium esculentum* around 15m wide and has the deepest water column of the three transects. Again dense stands of emergent macrophytes are associated with water less than one metre deep, substantially thinning when water levels increase above this level. Noobijup Lake had a well defined wetland basin, with the water column rapidly exceeding one metre. A dense band of emergent macrophytes was present in the seasonally inundated zone of transects one and two, whereas transect three was a much shallower habitat.

2.6.6 Emergent macrophyte harvest

Bokarup Swamp had the largest total above ground biomass of emergent vegetation in both seasons, remaining relatively constant at an average of over 900 g/m^2 (Tables 2.7 and 2.8). The above ground biomass in Kodjinup Swamp increased by 74.3 g/m^2 between September and April. The total above ground biomass in Noobijup Lake also increased between September and April by around 120g/m^2. These data reflect the number of *B.articulata* leaves per square metre, with Bokarup Swamp consistently having the highest density of stems.

Structural differences of vegetation associations in each wetland was evident in the species present and their life history stage for each season sampled. Kodjinup Swamp was the only wetland with monospecific stands of *B.articulata*, with the other wetlands having two or more species of emergent or submerged macrophytes increasing their above ground biomass. Within each wetland, the percentage of live leaves of *B.articulata* was around 50% of the total above ground in September, dropping by an average of 15% in April. This corresponds to a marked increase in the biomass of dead and senescent leaves in all wetlands during this period.

Kodjinup Swamp had the largest total below ground biomass in both seasons, despite a large decrease in the biomass of almost 200g/0.5m^3 between September and April (Table

2.7 and 2.8). Bokarup Swamp and Noobijup Lake also recorded a small decline in biomass between sampling periods. The differences in total below ground biomass result from differences in the root biomass, with the biomass of rhizomes remaining relatively constant between wetlands and season.

Table 2.7. The average total above and below ground biomass of emergent and submerged macrophytes for Bokarup Swamp, Kodjinup Swamp and Noobijup Lake in September 1995, incorporating biomass of individual species and different life stages of *B.articulata*.

	Bokarup Swamp		**Kodjinup Swamp**		**Noobijup Lake**	
	Mean	SE	Mean	SE	Mean	SE
B.articulata Ramets m^{-2}	6.60	0.9	5.40	0.5	5.60	1.1
B.articulata Leaves m^{-2}	33.20	4.3	19.00	2.3	23.40	4.5
Avg *B.articulata* leaves/ramet	5.06	0.5	3.55	0.7	4.23	0.6
live *B.articulata* leaves gDW m^{-2}	299.77	25.1	334.81	44.7	201.81	23.8
dead *B.articulata* leaves gDW m^{-2}	251.60	50.1	223.23	38.5	127.86	18.7
senescent *B.articulata* leaves gDW m^{-2}	125.60	27.8	100.78	20.9	79.25	13.4
Restionaceae sp. leaves gDW m^{-2}	90.42	24.1	0	0	24.35	9.6
B.juncea leaves gDW m^{-2}	136.76	34.1	0	0	0	0
Triglochin sp. gDW m^{-2}	9.83	3.0	0	0	6.52	1.5
B.arthrophylla leaves m^{-2}	0	0	0	0	72.87	8.6
Total Above Ground gDW m^{-2}	913.98	50.8	658.83	65.4	512.66	51.3
Root gDW $0.5m^{-3}$	320.71	37.7	493.45	112.5	164.03	21.5
Rhizome gDW $0.5m^{-3}$	48.05	16.5	45.99	17.8	65.28	9.7
Total Below Ground gDW m^{-3}	368.76	51.6	539.43	124.9	229.31	19.2

Table 2.8. The average total above and below ground biomass of emergent and submerged macrophytes for Bokarup Swamp, Kodjinup Swamp and Noobijup Lake in April 1996, incorporating biomass of individual species and different life stages of *B.articulata*.

	Bokarup Swamp		**Kodjinup Swamp**		**Noobijup Lake**	
	Average	SE	Average	SE	Average	SE
B.articulata Ramets m^{-2}	6.00	1.0	3.60	1.1	4.60	0.9
B.articulata Leaves m^{-2}	30.00	4.7	15.60	3.6	21.80	3.1
Avg *B.articulata* leaves/ramet	5.08	0.9	4.45	0.5	4.88	1.1
live *B.articulata* leaves gDW m^{-2}	269.52	30.4	309.93	33.4	242.33	12.5
dead *B.articulata* leaves gDW m^{-2}	181.79	16.8	173.25	23.7	119.73	22.6
senescent *B.articulata* leaves gDW m^{-2}	248.30	41.2	249.94	22.8	144.47	17.4
Restionaceae sp. leaves gDW m^{-2}	83.66	11.4	0	0	21.34	5.5
B.juncea leaves gDW m^{-2}	137.94	20.1	0	0	0	0
Triglochin sp. gDW m^{-2}	0	0	0	0	1.40	1.9
B.arthrophylla leaves m^{-2}	0	0	0	0	102.03	14.9
Total Above Ground gDW m^{-2}	921.21	31.5	733.12	24.7	631.30	27.6
Root gDW 0.5m^{-3}	240.80	21.4	288.32	45.2	137.98	24.8
Rhizome gDW 0.5m^{-3}	63.58	10.2	41.82	0.3	28.78	17.9
Total Below Ground gDW m^{-3}	304.38	19.8	330.14	45.2	166.76	12.3

2.7 SYNTHESIS AND DISCUSSION

2.7.1 Wetland water levels and chemistry

This chapter examined many general characteristics of the Muir-Unicup region such as climate, geology, hydrology and biota. A detailed examination of three wetlands, Bokarup Swamp, Kodjinup Swamp and Noobijup Lake quantified factors such as water levels, physico-chemistry, sediment characteristics and vegetation associations. All wetlands displayed marked seasonality in their water levels, with late spring/summer maxima and autumn/winter minima. There was approximately a six-month lag (taking into account the sampling interval) between maximum rainfall and maximum water levels. This is significantly longer than the lag time noted in Swan Coastal Plain wetlands that were connected to the unconfined groundwater aquifer (Townley *et al.* 1993). This indicates that these wetlands, particularly Bokarup and Kodjinup Swamps may be reliant on groundwater sources that move very slowly through the unconfined aquifer and not surface water flow. The result is a suite of wetlands with highly seasonal water levels that are deepest in the warmer summer periods, an uncommon feature in south-west Australian wetlands. The timing and duration of this hydrological cycle will have pronounced effects on water column and sediment processes and their biota.

Bokarup and Kodjinup Swamps both had periods when there was no surface water in all or part of their basins. Kodjinup Swamp has an altered catchment through surface water drainage to divert saline, overland catchment flow away from the wetland basin and into the Tone River. Drainage began in 1994 and in the first summer proceeding this the wetland dried completely for the first time on record. Large plantations of *Eucalyptus globulus* and *Pinus radiata* (reliant on groundwater for survival) surround the reserve, adding to the alteration of local hydrology. Within Bokarup Swamp, the vegetated and unvegetated habitats showed distinctly different hydrographs. The area of emergent vegetation had no surface water for up to five months of the year and the open area had surface water present throughout the study. The area of open water appears to have been created by the removal of organic sediments and emergent plants by a recent fire event, with the remnants of burnt macrophytes clearly evident. The water regime in this habitat is therefore somewhat artificial. This type of mass removal of peat by fire and the creation of large areas free of vegetation has been demonstrated in other south-west Australian wetlands (Horwitz *et al.* 1998). It was hypothesised that these areas were no longer in net gain of carbon due to the removal of the dominant carbon sources and the increased exposure of peat to aerobic processes through extensive cracking. However, the data from Bokarup Swamp indicate that if the wetland still had pre impact peat depths and emergent vegetation communities, the wetland would have dried out in its entirety for several months each year. This would also exposed surface sediments to increased aerobic processes which may result in similar consequences to peat accumulation as disturbances from fire.

Noobijup Lake had water level fluctuations quite distinct from the other two wetlands, showing the least seasonality and increases in levels between April and July 1996, three months before the other wetlands. Sediment profiles revealed that Noobijup Lake has a clay-lined basin around 1.5 m below the sediment surface, which may perch water levels. This indicates that Noobijup Lake may be receiving water predominantly from surface runoff, which is prevented from being exchanged with the groundwater by the clay layer. Aspects of wetland physico-chemistry support this hypothesis, with Bokarup and Kodjinup Swamps having similar sediment conductivities that increased with depth and Noobijup Lake did not, indicating that Noobijup Lake is perched and the other two wetlands are predominantly groundwater fed.

One of the primary factors controlling peat formation is the suppression of the aerobic decay of plant material. All wetlands displayed DO concentrations at the soil-water interface less than 1 mg/L during spring and summer periods when water levels were greater than 10 cm. Diurnal measurements highlighted the persistence of water column deoxygenation. Pronounced thermal stratification was also found in each wetland during spring and summer, with differences of up to 11.6°C between the surface and the epibenthos (the surface water temperature at Kodjinup Swamp reached 34.3°C at 1600 hours). However, the stratification did not persist with a mixed water column evident during the night in each wetland. The lack of persistent stratification throughout the diurnal cycle is supported by Ryder and Horwitz (1995b) who found a coloured wetland (high in Dissolved Organic Carbon) on the Swan Coastal Plain was thermally stratified during the day and mixed at night. The presence of a thermally mixed water column at night but consistently low epibenthic DO concentrations throughout a diurnal cycle in each wetland indicates that the low DO levels are driven by a high benthic oxygen demand, not reduced surface diffusion (Ryder & Horwitz 1995b). Microbial communities utilising the highly organic sediments as substrate for respiration drive this high benthic oxygen demand. The maintenance of wetland physico-chemistry such as sufficient water levels to maintain anoxic sediments and the supply of organic substrates for microbial communities are important for creating the conditions conducive to peat accumulation (Plaster 1985).

All wetlands displayed marked seasonality in salinity concentrations, following a trend of lower salinity in Spring during maximum water levels, and highest salinity in autumn/winter during low water levels. Salinity levels ranged from fresh to brackish in spring to hypersaline in winter. This seasonally driven evapoconcentration of salts in wetland basins is a well documented occurrence in south-west Australian wetlands (eg. Balla & Davis 1993; Davis *et al.* 1993; Edward *et al.* 1994; Storey 1998). However, as these wetlands contain deep peat deposits, they have the potential to retain moisture throughout the year in their organic soils which may increase the surface evaporation of salts. This is most important for Bokarup and Kodjinup Swamps that have distict dry phases. The different water regime in Noobijup Lake resulted in a conductivity profile that displayed a marked decrease with water depth of around 2.64 mS/cm in winter. This phenomenon occurred in winter immediately following a major rainfall event, and may represent an overlying layer of fresh surface water. This further supports the hypothesis that Noobijup Lake is perched.

Water column profiles for pH showed that during high water levels, pH values were generally above 7 and low water levels produced a mildly acidic pH as low as 6.34. These are within the range of values found in organic rich wetlands in south western

Australia (Pusey & Edward 1990b; Storey *et al.* 1993; Edward *et al.* 1994), but are less acidic that many Northern Hemisphere peatlands (Clymo 1984). Gradients of increasing acidity with depth were present in each wetland during high water levels, and is consistent with an increased degree of humification of organic material occurring at the sediment surface (Wetzel 1992). The release of fulvic and humic acids from decomposing organic matter in the sediments contribute to the decreasing pH, and are an important regulator of the role of water column productivity in wetland carbon cylcles

All wetlands contained very low concentrations of available phosphorus, however elevated nitrogen concentrations indicate that the wetlands could be classified as eutrophic to hyper-eutrophic. DeHaan (1987) also noted elevated nitrogen levels in the Muir-Unicup wetlands, and suggested this was due to the release of nitrogen from decomposing peat. However, wetlands in this study did not behave as eutrophic systems (eg. extensive algal blooms were not observed). The absence of algal blooms and the fact that phosphorus levels were very low indicates that the wetlands may be phosphorus-limited. The potential therefore exists for substantial algal growth if phosphorus levels become elevated (eg. as a result of agricultural run-off). The effects of nutrient enrichment in agricultural wetlands have been demonstrated in Lake Towerrinning (Froend & McComb 1991) and Lake Powell (Edward *et al.* 1994) in south-western Australia which have become eutrophic as a result of human activities. The presence of substantially higher concentrations of organic phosphorus in emergent vegetation than in the water column indicates much of the phosphorus entering each wetland is biologically bound in plant material. Changes in water levels or chemistry affecting the presence and distribution of emergent vegetation also have the potential to increase available phosphorus in the water column which may lead to algal blooms.

Peat depths varied greatly between wetlands, with Bokarup Swamp having the deepest deposits at 2.78 m. Kodjinup Swamp and Noobijup Lake had shallower peat at around 1.5 m. Despite differences in depth there were consistencies in peat structure and chemistry between wetlands. Each wetland possessed an unconsolidated layer of fibric peat in the surface horizon. This was most evident in Bokarup Swamp where an organic slurry dominated the surface 10 to 20 cm. During the course of the study the depth of the slurry changed considerably at fixed sites. During low water conditions in the autumn/winter months, extensive banks of this unconsolidated slurry would form. The continued wind and water erosion of the exposed sediments in the area of open water may be the source of the slurry material. At the point where the sediment formed a consolidated sapric peat there was a spike in the conductivity and also in the percentage sand found in the sample. This may be the point where permanent layers of organic sediments are formed (Clymo 1984). The layer of unconsolidated material may provide a medium by which organic and inorganic particulates (such as sand) can settle.

Semeniuk & Semeniuk (1997) hypothesised that irregular shaped basins are formed through the geomorphic degradation of creeks to become broad valley flats which in turn cease to flow. During intermittent cycles of inundation and variable wind conditions, sedimentary processes result in the basins becoming excavated, ringed by beach ridges and finally circular. Both Bokarup and Kodjinup Swamps, are roughly circular wetlands, suggesting that these circular wetlands are older geomorphic forms than the irregularly shaped Noobijup Lake. Elevated levels of the sand fraction within the two circular wetlands, and its absence from Noobijup Lake indicate that these wetlands may have been formed through these evolutionary processes. Bokarup Swamp had the deepest organic sediments, however, this does not necessarily mean that it is the oldest wetlands, as it may just accumulate organic material in the sediment at a faster rate than the other wetlands.

2.7.2 Wetland vegetation

Noobijup Lake had the highest species richness of aquatic and riparian vegetation, with 39 taxa of which 16 were unique to that wetland. Bokarup Swamp had 34 taxa and Kodjinup Swamp had 26 taxa of which only 7 were unique to that wetland. The differences in unique taxa are quite large considering the similarity of upland soil types and the close proximity of the three wetlands to each other. Fire regime is one factor that differs between the wetlands. Noobijup Lake was prescription burnt in Spring 1986 and has remained unburnt since. Kodjinup Swamp was prescription burnt in 1986 and 1993, and Bokarup Swamp has been unburnt for more than 24 years. In south west jarrah forests, fire exclusion for more than 15 years reduced species richness, with greatest richness found two to five years following fire (Bell & Koch 1980). This does not concur with this study with the lowest species richness found in the most recently and most frequently burnt wetland and much higher species richness in the longer unburnt wetlands. Kodjinup Swamp also had the lowest number of unique species, two of which are species promoted by fire, *Acacia saligna* and *Pteridium esculentum* (Bracken Fern). Bracken have formed dense monospecific stands up to 20 m across and hundreds of metres in length around the edge of the wetland, resulting in the exclusion of other shrub species which are common to the other wetlands. Bokarup Swamp has not only been influenced by fire, but past grazing of surrounding land by stock would have influenced the taxa that are present.

The distribution of emergent macrophytes, particularly *B.articulata*, along the water gradient supports the findings of Froend & McComb (1994), who found this species is tolerant of inundation up to one metre, with productivity reduced by prolonged inundation. The distribution of the large, dense stands of *B.articulata* in each wetland corresponds to each of their seasonally inundated zones. Neill (1990) found seasonal water regimes of flooding and drying increased productivity in emergent macrophytes, with the release of nutrients from seasonally inundated sediments thought to be the mechanism responsible for the increased productivity (Armstrong 1989). Bokarup Swamp concurs with these hypotheses, as it had the most variable water levels and the highest above ground biomass. If periodic exposure and inundation of sediments is contributing to increased macrophyte productivity in the Muir-Unicup wetlands, then the maintenance of these hydrologic regimes is important for sustaining macrophyte communities as a carbon source contributing to peat accumulation.

Differences in the above and below ground biomass were found between wetlands and may result from numerous factors including water regime, nutrient status, substrate type and interspecific and intraspecific competition (Hogeland & Killingbeck 1985; Neill 1990; Froend & McComb 1994; Feijoo *et al.* 1996). All wetlands displayed an increase in above ground biomass from September to April, a time when *B.articulata* scenesces and begins to produce new leaves (Froend & McComb 1994). Other species of emergent macrophytes have been shown to exhibit distinct peaks in biomass in early Summer (eg. Hogeland & Killingbeck 1985; Shamsudin & Sleigh 1995) due to the contribution from new leaf growth. This was not evident in the study wetlands, with a decrease in live mature stems and an increase in biomass of senescent and dead stems during this period. Below ground biomass also displayed differences between wetlands and seasons, with all wetlands having a lower biomass in April. This change is a result of decreased root biomass, with rhizome biomass remaining relatively constant. This reflects the change in the above ground structure, with the senescing of existing leaves corresponding to a reduction in root production. It appears that this species of emergent macrophyte does not have a distinct pattern of leaf fall, with increased seasonal biomass coming from senescing existing leaves which remain attached for extended periods and the concurrent production of new leaves.

Long-term changes in the condition of emergent vegetation in these wetlands may also be a result of changes in salinity regime over the last few decades since clearing for agriculture in the early 1970's. Vegetation assemblages may be reflecting prolonged stress due to increased salinities. Each of the wetlands had periods where their waters were brackish to saline, particularly in autumn and winter. These wetlands may be showing elevated salinities either because they are receiving saline run-off from cleared catchments, or they are showing long-term accumulation of salt as a result of progressive effects of evaporation and concentration. The decline in water quality from increased salinity is occurring across the Muir-Unicup wetlands with salt seeps appearing in the margins of many wetlands (AgWA unpublished data). The decline of *B. articulata* in Lake Towerrinning in south-west Australia was attributed to increased salinities (Froend & McComb 1991). Similar impacts of salinisation on macrophyte communities in the Miur-Unicup region will have major impacts on the rates of peat formation by substantially reducing the input of organic matter from this source.

2.7.3 Summary

Water levels were highly seasonal in Bokarup and Kodjinup Swamps ranging from around 1m deep to no surface water. The lack of surface water in these wetlands has important implications for peat accumulation by exposing organic substrata to aerobic decomposition processes. Water levels were less seasonal in Noobijup Lake. The presence of peak water levels in summer (around 6 months after peak rainfall) may also play an important role in peat accumulation. During this period, thermal stratification and persistent deoxygenation of the water column provide conditions conducive to the accumulation of peat. The water quality in each wetland is closely linked to hydrology, with marked increases in conductivity and pH with decreases in water levels. Conductivity levels approached 5 mS/cm in all wetlands during this study, which may impact on the long-term productivity of vegetation communities in wetland basins. The presence of very high benthic DO demands, a thermally stratified water column and the distribution of emergent vegetation restricted by water levels highlight the need for wetland management to encompass the maintenance of conditions conducive to peat formation.

CHAPTER 3

ORGANIC MATTER SOURCES

Allochthonous and autochthonous inputs

3.1 INTRODUCTION

Peat accumulation not only relies on conducive physical and chemical conditions, but also on the supply of organic matter in excess of its decomposition. Organic carbon in aquatic ecosystems is derived from two principal sources: material contributed externally by the surrounding terrestrial environment (allochthonous carbon) or material synthesised within the system (autochthonous carbon). Coarse particulate organic matter (CPOM) dominates allochthonous resources in lentic systems occurring as leaves, wood and reproductive structures from fringing and littoral tree and shrub species. Autochthonous sources of organic carbon can be contributed directly from emergent and submergent vegetation, biofilms and phytoplankton within the water column, and indirectly from the release of Dissolved Organic Matter (DOM) from these sources and peat soils. Determining the quantities, rates of supply and origin of organic material contributing to peat formation is essential in examining the effects of wetland management on the process of peat formation over the short term.

This chapter reviews the current status of knowledge of organic matter inputs into wetland systems and then quantifies the rates of allochthonous and autochthonous (macrophytes, algae and DOM) inputs of organic matter that contribute to the accumulation of peat in Bokarup Swamp, Kodjinup Swamp and Noobijup Lake.

3.1.1 Allochthonous inputs

The primary resources of peat are the various types of litter entering the system. Allochthonous plant material can be an important part of any aquatic detrital carbon pool when appropriate fringing vegetation, litter dispersal mechanisms and contrasting riparian and terrestrial detritus production exist (Briggs & Maher 1983). Riparian vegetation has been shown to contribute substantial quantities of organic matter as litterfall to Australia riverine systems (eg. Bunn 1986; Bunn 1998; Thomas *et al.* 1992; Herbohn & Congdon 1993; Campbell & Fuchshuber 1994; Treadwell *et al.* 1997). By comparison there have been relatively few attempts to quantify allochthonous inputs into lentic systems.

Wetland hydroperiod was the dominant influence on litterfall from River Red Gums (*Eucalyptus camaldulensis*) into floodplain wetlands in south-eastern Australia (Briggs & Maher 1983). High leaf litterfall and low rates of decomposition were found in a south-eastern Australian *Melaleuca quinquenervia* wetland, suggesting the sediments could act as organic matter and nutrient sinks (Greenway 1994). This was experimentally tested with *M.quinquenervia* contributing three times the organic material to wetland sediments and storing almost twice the nutrients than other riparian species (Bolton & Greenway 1999). Sediments of coastal *Casuarina glauca* dominated wetlands also accumulated litter rapidly, acting as an organic matter and nutrient sink between flood events (Clarke & Allaway 1996). Congdon (1979) examined leaf litterfall rates of *Melaleuca cuticularis* in south-west Australian wetlands to estimate the role of this species in organic matter cycling in estuarine systems. All these studies have examined the input of organic matter to wetlands in isolation from other carbon sources and processes. Briggs *et al.* (1993) provide a rare example of a study of the role of particulate organic matter (POM) in wetland carbon cycles in south-east Australian billabongs.

3.1.2 Macrophytes

Rates of inputs of above ground litter to freshwater detrital systems are well known (Polunin 1984), especially where litterfall occurs at a single, predictable time of year.

Littoral emergent vegetation are amongst the most productive zones within wetlands, with production by macrophytes and associated algal communities often orders of magnitude higher than pelagic phytoplankton (Kairesalo *et al.* 1992). Most of this organic matter remains ungrazed with the majority of the biomass entering the detrital system. The stems of emergent vegetation are characterised by containing substantial structural material (cellulose, lignin) occurring in very large particle sizes relative to plankton (Godshalk & Wetzel 1978). These properties make macrophyte tissue relatively resistant to decomposition and prone to accumulation. The routes by which emergent vegetation contributes to the detrital pool are numerous, varying spatially and temporally in their structure, metabolism and chemical constituents (Godshalk & Wetzel 1978).

Macrophytes can be important contributors to aquatic metabolism, playing key ecosystem roles such as nutrient cycling and amelioration of anoxia through rhizosphere oxidation. Numerous studies are available on the processes of organic inputs from emergent macrophytes and their role in the detrital pathway (eg. Godshalk & Wetzel 1978; Polunin 1984; Jones & Muthuri 1997). More recently the importance of macrophytes and other organic matter sources in aquatic systems has been examined using stable carbon and nitrogen isotopes (see review in Chapter 5). Despite the documented importance of macrophytes in aquatic processes, few studies quantify the contribution of emergent macrophytes as POM to wetland carbon budgets (eg. Hocking 1989; Gessner *et al.* 1996; Kuehn & Suberkropp 1998).

3.1.3 Algae

The main types of algae that occur in wetland systems are phytoplankton and macroalgae (entrained in the water column) and attached algae (biofilms). Despite numerous studies, it is difficult to quantify the contribution of algae to wetland carbon cycles, as few studies have been sufficiently inclusive to measure all potential producers (Goldsborough & Robinson 1996). Algae are easily assimilated into wetland food webs due to their single cell or small cluster nature (Lamberti 1996). Although relatively low in biomass compared with aquatic macrophytes, the high turnover rate of algae is significant in their rate of production (Goldsborough & Robinson 1996). Algae can provide both POM and

DOM to aquatic carbon cycles (Wootton & Power 1993). Photosynthetic production by algae provides both a source of DOM through algal exudates, and a sink for DOM within the cells during periods of respiration (Goldsborough & Robinson 1996).

Algal taxonomic composition and productivity are the result of multiple interactions between hydrological, chemical and biotic factors. Environmental variables influencing algal communities such as light, water chemistry and grazing pressure can covary on both temporal and spatial scales (Lowe 1996). Changes to water chemistry include oxygenation of the water column (Hillebrand 1983; Browder *et al.* 1994), increases in pH, decreases in CO_2 and bicarbonate concentrations (Browder *et al.* 1994) and influence wetland nutrient cycles (Briggs *et al.* 1993). Due to the labile nature of algae, the fate of the majority of algal material is primarily rapid conversion to carbon dioxide with a small amount of the more refractory compounds remaining in dissolved and particulate form (Godshalk & Wetzel 1978).

3.1.4 Dissolved organic matter (DOM)

High amounts of organic matter entering wetland systems or the presence of peat soils often result in wetland water columns becoming heavily stained. The colour is imparted by high concentrations of dissolved organic matter (DOM) released from organic matter during decomposition. DOM is defined as the fraction of total organic matter which passes through a 0.45μm filter (APHA 1989). DOM consists of a soluble labile component (fulvic acid), a soluble refractory component (humic acid) and an insoluble component (humin). Humic and fulvic acids are amorphous, yellow brown or black and hydrophilic, resulting in the yellow brown colouration of many aquatic systems (Wetzel 1992). Humic substances in aquatic systems have been collectively termed 'gilvin' (Kirk 1976) or *Gelbstoffe* (Kalle 1966), describing those yellow substances occurring in water bodies at concentrations sufficient to effect the attenuation of photosynthetically available radiation (PAR). Wetlands with these attributes are referred to as 'dystrophic', characterised by their low pelagic primary productivity (Wetzel 1975).

The direct contribution of DOM to peat formation is minimal, however, numerous studies have described the impact of DOM on the functioning and structure of aquatic ecosystems (eg. Davies-Colley 1992; Wetzel 1992; El Sayed *et al.* 1993). DOM in Australian systems has also received considerable attention (eg. Bowling 1988; Croome & Tyler 1988; Carpenter *et al.* 1991; Briggs *et al.* 1993; Lund & Ryder 1997). High concentrations of DOM can influence food webs by altering the physical or chemical environment, modifying autotrophic primary production or by acting as a direct carbon source (Jones 1992). The lability and abundance of DOM and the chemistry of the water column determine as to whether it stimulates or inhibits biological activity seems to depend on its , .

3.1.5 Aim

There is a dearth of literature concerning the quantities of allochthonous and autochthonous litter entering wetland systems, particularly those in forested landscapes. The development of peat deposits is dependent on the supply of organic matter and determining peat accumulation rates is reliant on quantifying these inputs. This chapter aims to quantify the input of allochthonous and autochthonous organic matter to the three study wetlands. Allochthonous litter fall is separated into aquatic and riparian taxa and individual plant components such as leaves, stems and reproductive parts. Emergent macrophyte leaf litter fall, algae (phytoplankton and biofilm), and DOM are quantified as major autochthonous sources of organic matter contributing to carbon dynamics of these wetlands.

3.2 METHODS

3.2.1 Allochthonous litter traps

Allochthonous litter traps were constructed from large, robust plastic soak wells (0.8 m inner diameter). The base of the litter trap was made from 500 µm mesh to allow for litter to accumulate while rainwater could pass through. Each trap was attached to three wooden stakes and placed with the base around one meter above the sediment surface (modified from Turnbull & Madden 1983). The habitat mapping exercise (Section 2.6.4) identified a vegetation association dominated by *Melaleuca* fringing the wetland margin. In a desktop exercise, this zone was delineated and a grid overlain. A random number generator was used to determine the location of the six litter traps within this area in each wetland. The locations of the litter traps are shown in Plates 3.1a, 3.1b and 3.1c for Bokarup Swamp, Kodjinup Swamp and Noobijup Lake respectively. There were no preliminary studies conducted to examine spatial variability.

Litter traps were emptied at each field sampling occasion and the contents of the trap represent the total litter accumulation since the last collection. Upon collection the base of each trap was removed and the contents brushed into labelled, sealable bags. In the laboratory, each bag was sorted into the following components for each species; leaves, bark, stem, flowering parts and insects/other. Once separated, each component was dried in a Series 5 Contherm drying oven at 90^0C for 48 hours, removed, cooled in a desiccator and weighed in grams to 4 decimal places using an OHAUS analytical balance. Data were converted to input in gDW/m^2/day.

3.2.2 Emergent litter traps

Litter traps were designed and constructed to quantify the input of organic matter from emergent macrophyte leaf litter. Each litter trap consisted of a 1 m^2 frame constructed from 50 mm polypropylene tubing filled with polystyrene foam to ensure the traps would float. Polyethylene mesh with a 50 mm mesh size was placed across each trap and

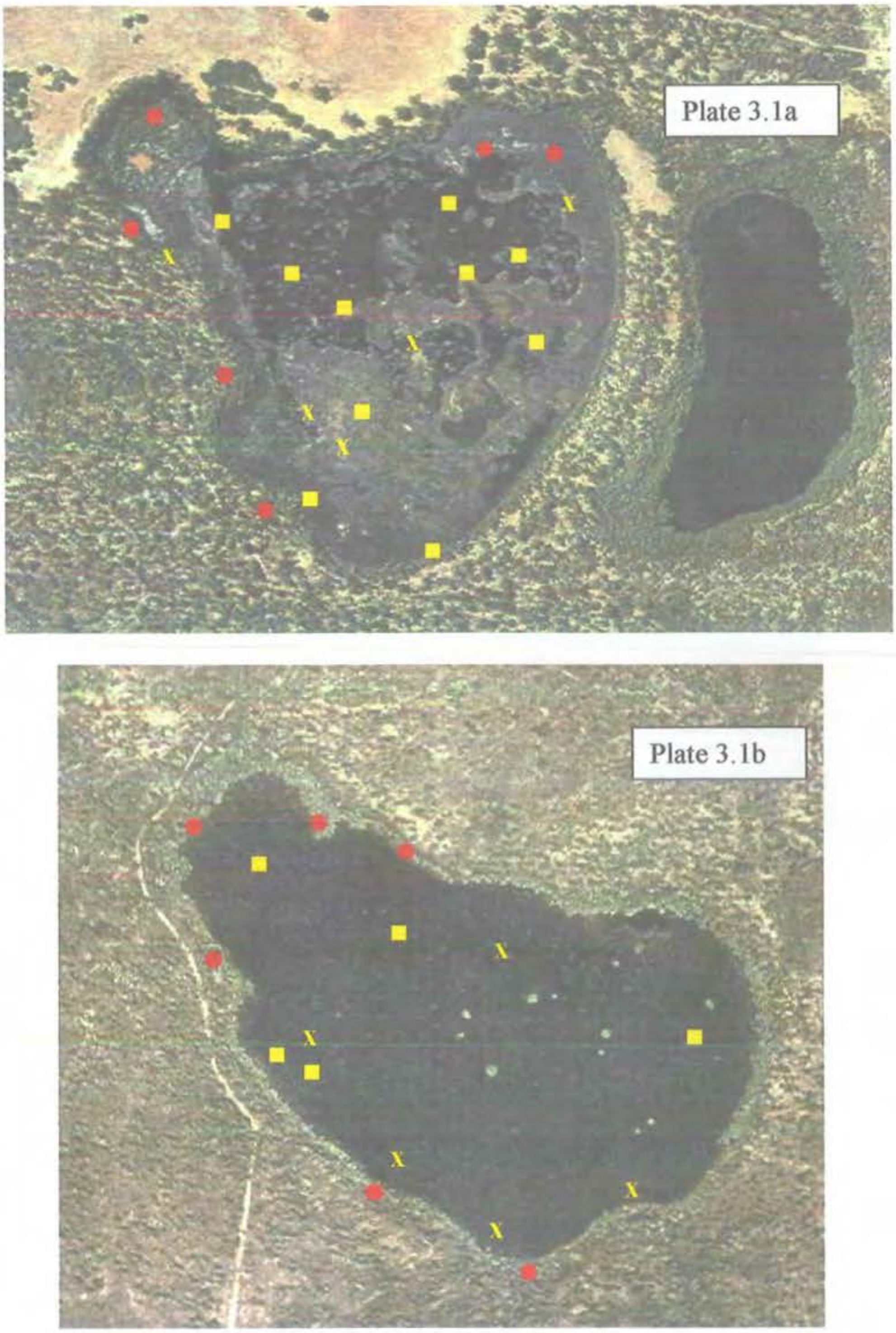


Plate 3.1. Approximate locations of allochthonous litter traps (●), macrophyte litter traps (x) and biofilm slide racks (■) in (a) Bokarup Swamp and (b) Kodjinup Swamp.

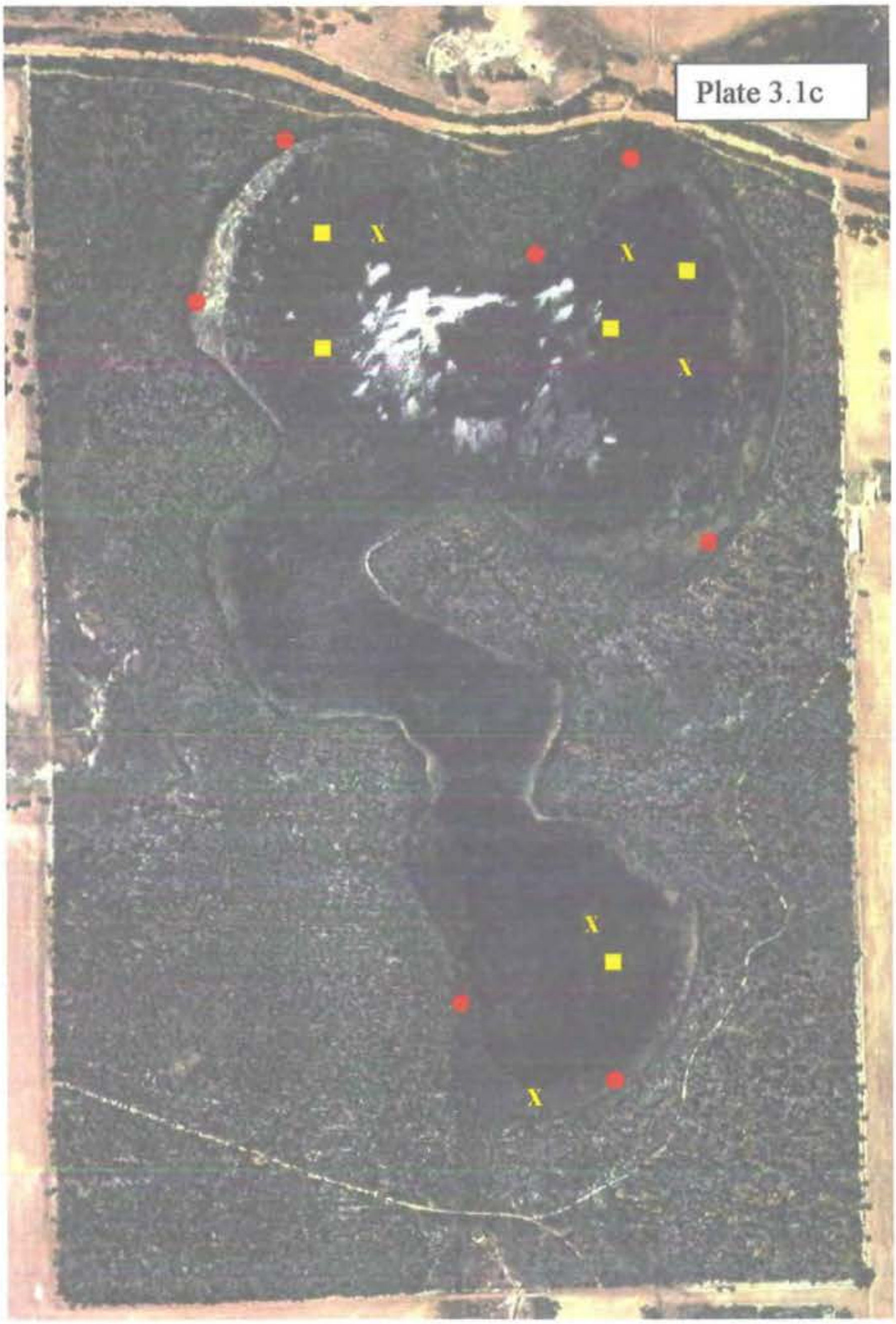


Plate 3.1c. Approximate locations of allochthonous litter traps (●), macrophyte litter traps (X) and biofilm slide racks (■) in Noobijup Lake.

fastened to the edges using cable ties. The mesh trapped fallen emergent vegetation while still allowing new leaves to emerge through the trap.

The habitat mapping exercise (Section 2.6.4) identified major assemblages of emergent macrophytes within each wetland basin. In a desktop exercise, the area of emergent macrophytes was delineated and a grid overlain. A random number generator was used to determine the location of the five litter traps within this area in each wetland. There were no preliminary studies conducted to examine spatial variability. The traps were placed without influencing the emergent macrophyte assemblages, by lowering them over the emergent vegetation from a boat. Existing vegetation was able to protrude through the mesh until the trap floated evenly on the water surface. The locations of litter traps are shown in Plates 3.1a, 3.1b and 3.1c for Bokarup Swamp, Kodjinup Swamp and Noobijup Lake respectively.

Litter traps were emptied at each field sampling occasion and the contents represent the total litter accumulation since the last collection. Litter was only removed from within the 1 m^2 quadrat, and was cut if a leaf protruded beyond the edge of the quadrat, and placed in sealed plastic bags. Samples were returned to the laboratory, dried in a Series 5 Contherm drying oven at 90 ^{0}C for 48 hours, removed, cooled in a desiccator and weighed in grams to 2 decimal places using an OHAUS analytical balance. Data were converted to organic matter input in $gDW/m^2/day$.

3.2.3 Phytoplankton biomass

Chlorophyll *a* was analysed using the trichromatic method (APHA 1989) from replicate samples taken from integrated water samples from 5 random locations within in each wetland basin on each sampling occasion. Two litres of water was passed through a Whatman GF/C filter paper, the filter paper folded in half, wrapped in aluminium foil, placed on ice in the dark and frozen within 5 hours of collection.

In the laboratory, filter papers were defrosted in a 4°C fridge and replicates placed in individual 10 ml polyethylene centrifuge tubes. Four ml of 90% aqueous acetone

(C_3H_6O) was added to each tube, and the filter papers homogenised with a glass rod. A further 6 ml of 90% aqueous acetone was added to each sample, the centrifuge tube wrapped in aluminium foil and placed in a 4°C fridge for 2 hours to extract. The samples were then centrifuged for 10 minutes at 2500 rpm. Three ml of supernatant was decanted into a quartz cuvette and its absorbance at 750 nm, 664 nm, 647 nm and 630 nm was recorded using a Shimadzu UV-1201 spectrophotometer using 90% aqueous acetone as a blank. The 750 nm reading is used as a correction factor for turbidity and spectrophotometric properties of the acetone solution. To determine the optical densities for each wavelength, the 750 nm value was subtracted from the other readings. The following calculation was used to calculate chlorophyll *a* :

$$\text{Chl a } \mu\text{g/ml acetone (A)} = 11.85_{(OD664)} - 1.54_{(OD647)} - 0.08_{(OD630)}.$$

$$\text{Chl a } \mu\text{g/L} = \frac{[(\text{A}) / \text{cell pathlength}] \times \text{vol of extract (ml)}}{\text{Volume of filtered water (L)}}$$

3.2.4 Biofilms

A preliminary experiment examined the temporal scales required to accumulate sufficient biofilm for biomass and chlorophyll analysis. In July 1995, 20 500 mm x 200 mm ($0.2m^2$) slides (glass louvres) were randomly placed in four locations Noobijup Lake. Slides were attached to a floated rope tied between two wooden stakes and suspended 5 cm below the water surface. This design minimised the effect of shading from the wooden stakes and ensured a constant water depth. Ten slides were harvested after 14 days and the remaining 10 slides after 28 days. Individual slides were scraped into vials using a razor blade and rubber policeman, labelled, wrapped in aluminium foil, placed on ice in the dark and frozen within 5 hours of collection. The efficiency of this method is outlined in Cattaneo & Amireault (1992) and Morin & Cattaneo (1992). After 14 days in the field the biofilm had accrued 11.0 ± 2.5 $\mu g/m^2$/day after 14 days and 7.3 ± 1.5 $\mu g/m^2$/day after 28 days. The decrease in biomass and presence of invertebrate grazers on the slides indicated grazing or sloughing was affecting biomass by 28 days.

Macroinvertebrate grazers (aquatic snails) were removed from the slides and not included in the biomass.

Five slides from each collection were used for the determination of biomass and 5 for chlorophyll a. In the laboratory samples were defrosted in a 4°C fridge, the contents of the vials transferred to a centrifuge tube, filled with 10ml of 90% aqueous acetone, wrapped in aluminium foil and placed in a 4°C fridge to extract for 2 hours. The samples were then analysed for chlorophyll *a* using the methods described above and converted to chlorophyll *a* $\mu g/m^2$/day using the following formula:

Chl a $\mu g/m^2$/day = (A) x vol. extract / surface area scraped/ number of days exposed.

The remaining samples were placed in preweighed crucibles and dried in a Contherm series 5 oven for 48 hours at 105°C. Samples were removed from the oven, placed in a desiccator to cool and weighed to 4 decimal places using an OHAUS analytical balance. Crucibles were then placed in a Furnace Brand muffle furnace for 1 hour at 540°C, removed and cooled in a desiccator and weighed in grams to 4 decimal places. These data were converted to mgAFDW/m^2/day.

Following the preliminary trials, a 14 day exposure time was chosen to represent an accumulation rates that was not influenced by grazers or sloughing of particulates. The habitat mapping exercise (Section 2.6.4) identified major assemblages of emergent macrophytes within each wetland basin. A random number generator was used to determine the location of the 5 biofilm racks (each holding 2 slides) in each wetland. The locations of biofilm racks are shown in Plates 3.1a, 3.1b and 3.1c for Bokarup Swamp, Kodjinup Swamp and Noobijup Lake respectively. At each sampling period the 10 biofilm slides were placed in each rack and harvested 14 days later. One slide from each rack was used for chlorophyll and the other used for biomass determination. Slides were collected, stored, processed and analysed as previously described. 3.2.4.1. Biofilms: natural vs. artificial substrata

In January 1997, biofilms from natural substrates was examined over the same 14 day period as growth on the artificial substrates. Ten intact, green attached *B.articulata* leaves were cleaned below the water line using a sponge to remove all biofilm material and marked so they could be relocated. Upon collection the leaves were cut at the sediment surface and the water surface. The length of the leaf and its diameter at each end were measured to calculate the surface of the leaf sampled. The biofilm was removed from macrophyte stems using a rubber policeman, stored, processed and analysed for chlorophyll *a* and biomass as previously described.

3.2.5 Dissolved organic matter (DOM)

The Walkley - Black DOM method was used to determine DOM concentrations (Nelson & Sommers 1982). The method was devised for freshwater samples of 100 - 200 ml with 5 - 30 gC/L. Because of low concentrations of DOM, the standard method was modified, to employ a lower quantity of potassium dichromate and a more dilute solution of ferrous sulfate than the standard, and repeated 3 times per sample to increase volumes.

Measures of DOM were obtained from integrated water samples taken from 5 random locations within each wetland on each sampling occasion. Samples were taken with a 15 mm polyethylene tubing from the surface to the epibenthos and immediately filtered through a prewashed, preashed Whatman GF/F filter paper with an effective pore size of 0.2 µm. Where water levels were insufficient to allow sampling of surface water, pore water samples were used as described in Section 2.5.3. The filtrate was placed in a 200ml vial, stored on ice in the dark and frozen within 5 hours of collection.

In the laboratory, samples were defrosted in a 4°C fridge, thoroughly homogenised and 150 ml of sample placed into a 250 ml Erlenmeyer flask, recording the sample mass (m) to the nearest 0.01 g. The flask was placed in a Contherm Series 5 drying oven and the solution evaporated at 110°C. DOM concentrations were determined using :

- 2 ml 0.1667M Potassium dichromate solution was added to the evaporated sample and also into a clean Erlenmeyer flask as a control.

- 4 ml concentrated H_2SO_4 was added, swirling the sample until the evaporate was rinsed off the sides of the flask.

- 40 ml distilled water was added followed by 2 ml 1M orthophosphoric acid.

- 1 ml Sodium diphenylamine-sulphonate indicator solution was added

- Ferrous sulfate was titrated from the burette, swirling the contents of the flask until the solution changes from dark brown, through blue to green.

- The volume of ferrous sulphate used to the nearest 0.01 ml to titrate the control b(V_1) and the sample (V_2) was noted.

- The total volume (V) in ml of potassium dichromate used to oxidise the carbon was calculated from : $V = 2(1-V_2/V_1)$.

- The concentration of DOM in mg C/L of the sample was calculated by :

DOM = 3886 x V/m.

3.2.6 Data analysis

Differences in mean numbers of values for each data set were compared by analysis of variance (ANOVA). Prior to analysis, the variances of sets of replicate samples were tested for homogeneity with Cochran's test. If variances of raw data were unequal, values were $\log_{10}$ transformed or $\log_{10} + 1$ transformed and retested. Significance levels for ANOVA's were set at $\alpha = 0.05$. Anova models were constructed for each hypothesis using Underwood (1995). For simple one-way and two-way Anova's with orthogonal designs and fixed factors, the mean squares (MS) error value is the residual and common to all effects and interactions. For models that incorporate a random factor, such as Sampling Event, the MS error for each effect and interaction has been calculated using the 'table of multipliers' procedure outlined in Underwood (1995). The following models analysed using Statistica (Statistica 1995).

Allochthonous and autochthonous litterfall

Null Hypothesis: there is no difference in the total litterfall from allochthonous or autochthonous sources between wetlands and sampling occasions.

ANOVA Model Design: (Repeated measures ANOVA: 1 within-1 between)

Wetland - fixed factor with 3 levels

Sampling occasion - random factor with 7 levels

Chlorophyll *a*

Null Hypothesis: there is no difference in the water column concentrations of chlorophyll *a* between wetlands and sampling occasions.

ANOVA Model Design: (2 factor ANOVA)

Wetland - fixed factor with 3 levels

Sampling occasion - random factor with 8 levels

DOM

Null Hypothesis: there is no difference in water column DOM concentrations between wetlands and sampling occasions.

ANOVA Model Design: (2 factor ANOVA)

Wetland - fixed factor with 3 levels

Sampling occasions - random factor with 8 levels

Biofilm field samples (Chlorophyll *a* and biomass)

Null Hypothesis: there is no difference in biofilm chlorophyll *a*/biomass between wetlands and sampling occasions. The open water area of Bokarup Swamp is not included in the analysis.

ANOVA Model Design: (2 factor ANOVA)

Wetland - fixed factor with 3 levels

Sampling occasion - random factor with 6 levels

Biofilm artificial vs. natural substrata

Null Hypothesis: there is no difference in biofilm chlorophyll *a*/biomass between natural and artificial substrata in any of the wetlands.

ANOVA Model Design: (2 factor ANOVA)

Wetland - fixed factor with 3 levels

Substrate - random factor with 2 levels

Tukey-Kramer post hoc tests were used to further examine the data set where significant differences were found within single factor analyses. Where significant differences were found in multiple interactions, the percent of total sum of squares of each factor was used to explore sources of variation (after Zar 1984).

3.3 RESULTS

3.3.1 Allochthonous litter traps

Allochthonous litterfall displayed consistent differences between wetlands and a distinct seasonal pattern of litter input (Figure 3.1). Total annual allochthonous inputs ranged from 925 gDW/m^2, 542 gDW/m^2 and 198 gDW/m^2 in Bokarup Swamp, Kodjinup Swamp and Noobijup Lake respectively. A significant difference ($P<0.0001$) was found between wetlands (Table 3.1), with Bokarup Swamp receiving substantially more allochthonous organic matter (peaking at 3.6785 ± 0.558 gDW/m^2/day in December 1995 to Feb 1996) than the other wetlands. Conversely, Noobijup Lake had very low inputs from allochthonous sources, falling to 0.2027 ± 0.106 gDW/m^2/day in July to Oct 1996. A significant difference ($P<0.0001$) was also found between seasons with a defined summer/autumn maxima in each wetland. Organic inputs also showed interannual variability with higher inputs in the 1995/96 summer period than in this period the following year. Inputs in Bokarup and Kodjinup Swamps were dominated by *M.raphiophylla* plant components, ranging between 88 and 99% of total litterfall, with leaves being the predominant source (Table 3.2). The composition of allochthonous litter was markedly different in Noobijup Lake, receiving a large quantity of litter from *E.rudis* and *B.littoralis* (Table 3.2).

A significant interaction between wetland and season ($P<0.0256$) indicates that these parameters are not acting independently (Table 3.1). Overall seasonal trends of summer/autumn maxima and winter lows were evident in all wetlands, however, relative changes in wetlands' inputs were not consistent. For example, mean litter input to Kodjinup Swamp was low in the September to December 1995 period from low inputs of *M.raphiophylla* leaves. Similarly, lower mean litter inputs were found at Noobijup Lake in April to October 1996 compared with the other wetlands.

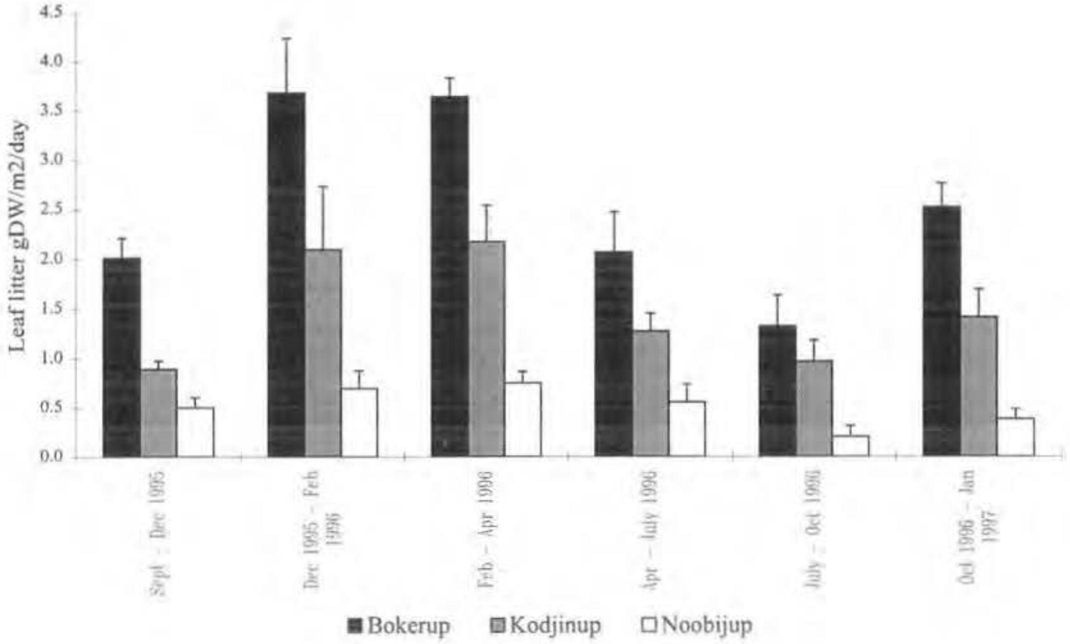


Figure 3.1. Average total allochthonous organic matter input (±SE) gDW/m^2/day in each sampling period for each wetland from September 1995 to January 1997.

Table 3.1. Two-way repeated measures ANOVA (Wetland by Sampling Event) results for allochthonous leaf litter traps.

Source	Df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	9.59	4.79	298.83	0.0001
Sampling Event	5	2.73	0.54	59.16	0.0001
Wetland x Sampling Event	10	0.42	0.04	4.62	0.02

Table 3.2. Average total contribution (gDW/m^2) of individual taxa and plant components (leaf, stem, reproductive, bark) to total allochthonous litterfall in each sampling period for each wetland.

	M.raphiophylla				*E.marginata*	*E.rudis*			*B.littoralis*	
	leaf	Bark	reproductive	Stem	Leaf	Leaf	Bark	reproductive	leaf	stem
Bokarup Swamp										
Sept - Dec 1995	91.5895	2.1315	31.9520	25.5156	0.0000	2.0165	0.0000	-1.5698	0.0000	0.0000
Dec 1995 - Feb 1996	169.2800	0.3295	14.4149	34.2576	0.0000	5.0907	0.0000	1.0182	0.0000	0.0000
Feb - Apr 1996	181.7855	0.3224	9.9003	35.3054	0.0000	6.0069	0.0000	0.0000	0.0000	0.0000
Apr - July 1996	142.9074	0.3384	6.3287	34.2132	0.0000	6.0620	0.0000	0.0000	0.0000	0.0000
July - Oct 1996	110.7657	0.9332	1.5942	9.1362	0.0000	0.2461	0.4368	0.0000	0.0000	0.0000
Oct 1996 - Jan 1997	171.2731	4.3833	22.1565	19.3835	0.0000	0.0816	0.0000	0.0183	0.0000	0.0000
Kodjinup Swamp										
Sept - Dec 1995	41.9562	2.5752	4.5660	11.3798	0.0000	7.8880	0.0000	0.0000	0.0000	0.0000
Dec 1995 - Feb 1996	104.2843	2.8778	5.9197	7.4106	1.1125	5.1652	0.1637	0.6478	0.0000	0.0000
Feb - Apr 1996	115.1437	3.5885	4.4590	7.4667	1.8653	6.6084	0.0000	0.0000	0.0000	0.0000
Apr - July 1996	95.5764	3.5012	4.5205	7.4667	1.1942	4.6142	0.0000	0.0000	0.0000	0.0000
July - Oct 1996	81.4460	3.2126	0.3795	2.7803	0.0557	0.3072	1.5310	0.0194	0.0000	0.0000
Oct 1996 - Jan 1997	102.3318	3.9980	3.2873	4.7066	0.0000	6.3591	0.5647	0.0000	0.0000	0.0000
Noobijup Lake										
Sept - Dec 1995	14.3787	0.4198	3.2765	0.9692	0.0000	2.7349	0.0000	0.3943	3.7901	12.4489
Dec 1995 - Feb 1996	13.9235	1.5184	1.5114	1.4922	0.0000	3.5415	4.4586	3.5179	12.5737	0.0000
Feb - Apr 1996	14.2413	1.7939	1.4448	5.3833	0.0000	7.0117	2.2569	1.7120	14.1261	0.0000
Apr - July 1996	15.7669	9.7450	1.0893	5.6236	0.0000	6.0486	0.3104	0.2204	12.1148	0.0000
July - Oct 1996	8.4442	4.4969	0.0688	2.1940	0.0000	0.9540	0.0000	0.0000	0.5100	2.1794
Oct 1996 - Jan 1997	16.7043	1.4248	1.6940	1.2381	0.0000	1.6893	0.6720	0.6102	4.8340	4.0165

3.3.2 Emergent macrophyte leaf litter traps

Leaf litterfall from emergent macrophytes followed similar trends to that of the allochthonous inputs with a distinct seasonal cycle of summer/autumn maxima and winter/spring minima (Figure 3.2). This was supported in a significant difference ($P<0.0001$) between seasons (Table 3.3). A significant difference ($P<0.0001$) was also found between wetlands with Kodjinup Swamp consistently receiving the highest amount of organic matter from emergent macrophytes, peaking at 0.98 ± 0.1 gDW/m^2/day in the December 1995 to February 1996 period. As with allochthonous litter, Noobijup Lake had the lowest inputs from emergent macrophytes, falling to 0.11 ± 0.1 gDW/m^2/day in September to December 1996 period. Macrophyte inputs also showed interannual variability with higher inputs in the 1995/96 summer period than in this period the following year. The two-way repeated measures ANOVA produced a non-significant *P* value of 0.0542 (Table 3.3).

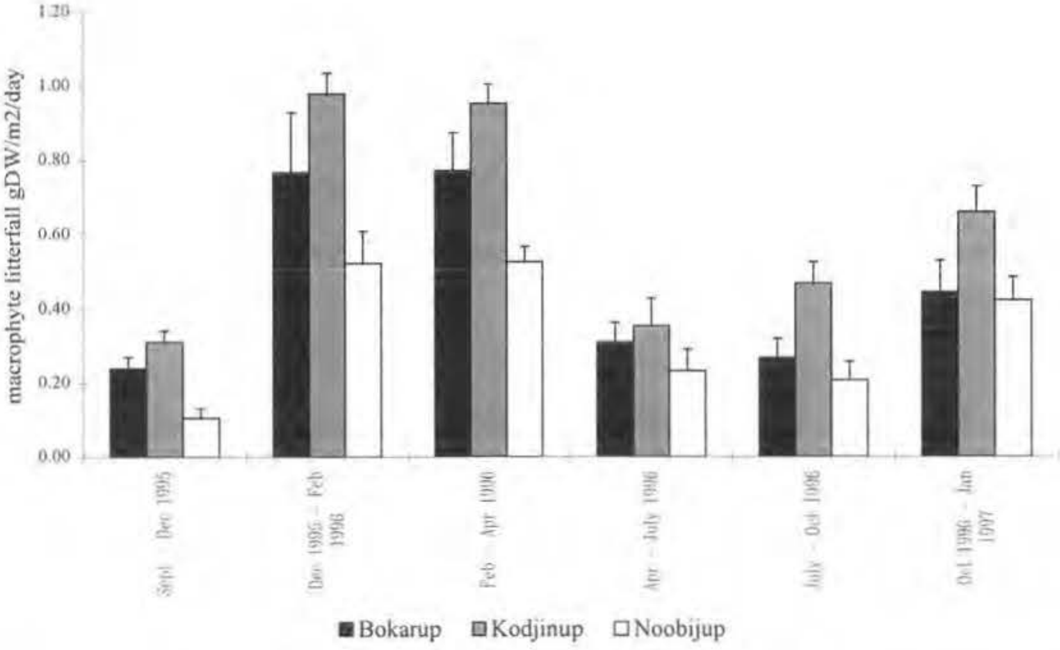


Figure 3.2 Average total input (±SE) gDW/m^2/day from emergent macrophyte leaf litter in each sampling period for each wetland from September 1995 to January 1997.

Table 3.3 Two-way repeated measures ANOVA (Wetland by Sampling Event) results for emergent macrophyte leaf litter traps.

Source	df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	0.72	0.36	75.32	0.0001
Sampling Event	5	2.51	0.50	100.39	0.0001
Wetland x Sampling Event	10	0.16	0.016	3.19	0.0542

3.3.3 Water column Chlorophyll *a*

Concentrations of chlorophyll *a* in all wetlands were very low, with the highest value of 8.87 ± 0.2 μg/L recorded at Noobijup Lake in January (Figure 3.3). Significant differences were found in chlorophyll *a* concentrations between wetlands ($P<0.0001$) and seasons ($P<0.0001$) with the strong seasonal cycle of summer maxima and winter lows again evident (Table 3.4). Bokarup Swamp and Noobijup Lake had similar concentrations throughout the study. Kodjinup Swamp consistently had the lowest concentrations, with no values obtained from this wetland in July of each year as surface water levels were insufficient to sample. A significant interaction between wetland and season ($P<0.0034$) was found in the two way ANOVA. Season contributes over 90% to the total sum of squares indicating its dominant contribution to the interaction. This may be due to zero readings from Kodjinup Swamp during periods of no surface water or the decrease in chlorophyll *a* concentrations at Bokarup Swamp relative to Noobijup Lake in the last three sampling rounds.

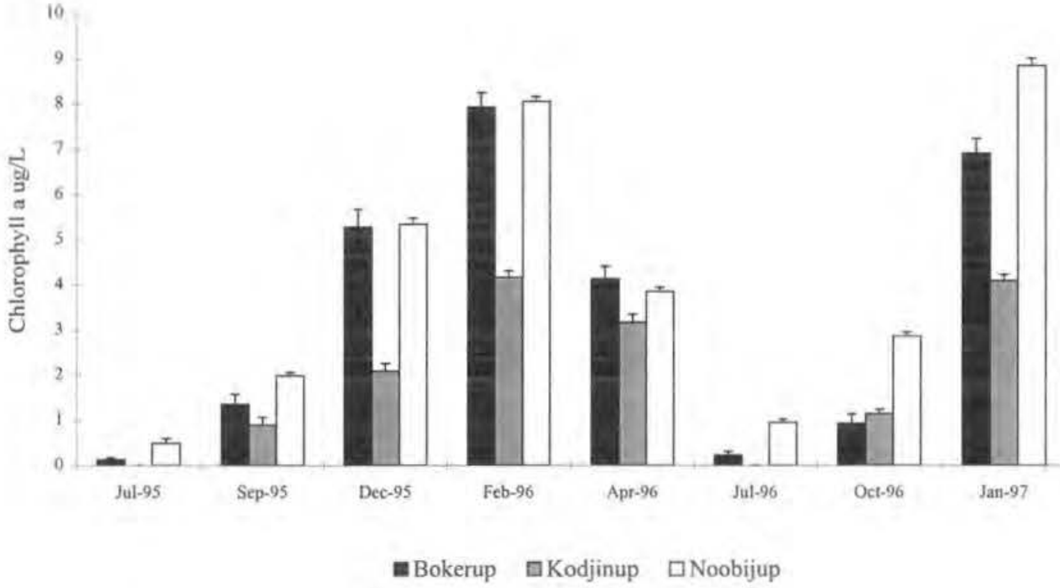


Figure 3.3. Average water column chlorophyll *a* (±SE) μg/L in each sampling occasion for each wetland from July 1995 to January 1997. An absence of data indicates insufficient water levels for chlorophyll *a* sampling.

Table 3.4. Two-way ANOVA (Wetland by Sampling Event) results for water column chlorophyll *a*.

Source	Df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	1.06	0.53	1049.00	0.0001
Sampling Event	7	10.37	1.48	2925.00	0.0001
Wetland x Sampling Event	14	0.37	0.026	52.04	0.0034

3.3.4 Biofilms

3.3.4.1 Chlorophyll *a*

Consistent with other sources of organic matter, biofilm chlorophyll *a* concentrations showed significant differences between wetlands ($P<0.0001$) and seasons ($P<0.0018$) (Table 3.5). A strong seasonal cycle was evident with higher chlorophyll concentrations in the warmer, summer months (Figure 3.4). Concentrations in Kodjinup Swamp and Noobijup Lake were similar throughout the study, with Bokarup Swamp having consistently lower concentrations. A habitat difference was also evident at Bokarup Swamp, with concentrations in the unvegetated area up to four times higher than those within emergent macrophyte habitat.

Table 3.5. Two-way ANOVA (Wetland by Sampling Event) results for biofilm chlorophyll *a*.

Source	df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	2.50	1.25	798.87	0.0001
Sampling Event	5	36.24	7.24	6715.00	0.0018
Wetland x Sampling Event	10	4.47	0.44	0.41	0.91

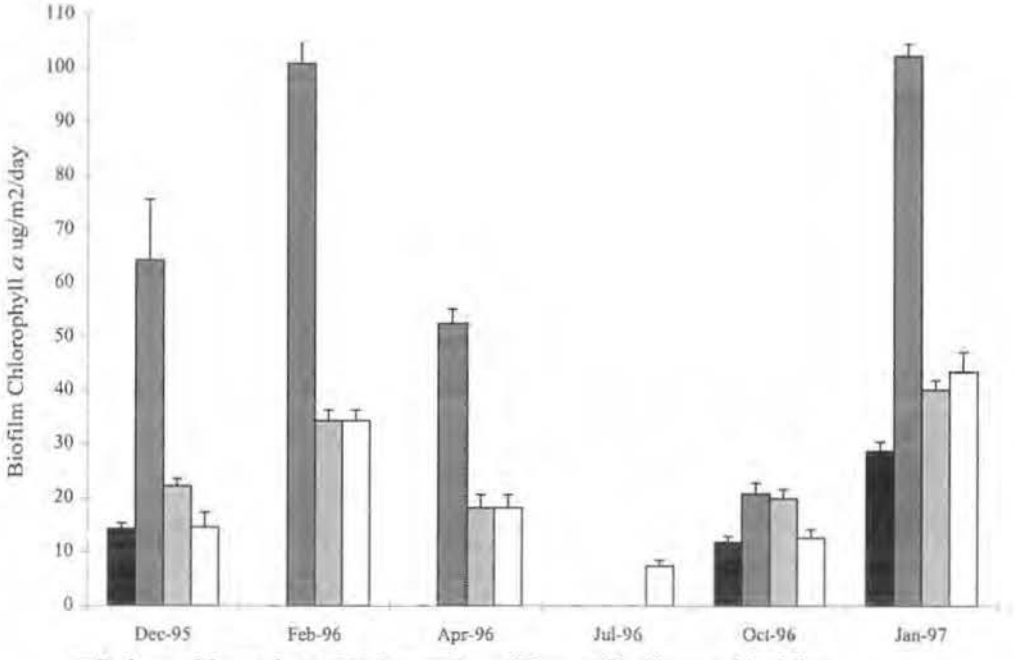


Figure 3.4. Average biofilm chlorophyll *a* (±SE) μg/m^2/day concentrations for each sampling occasion in vegetated habitats in each wetland, and unvegetated and vegetated habitats in Bokarup Swamp from December 1995 to January 1997. An absence of data indicates insufficient water levels for biofilm development.

3.3.4.2 Biomass

Consistent with biofilm chlorophyll *a* trends, significant differences for biomass were evident between wetlands ($P<0.0001$) and seasons ($P<0.0054$) (Table 3.6), with a strong seasonal change in biofilm biomass. Biofilm biomass values were very high, accruing up to 84.1 ± 9 mgAFDW/m^2/day in the open water habitat at Bokarup Swamp over the 14 day period (Figure 3.5). Bokarup Swamp and Noobijup Lake had similar biomass values, with Bokarup Swamp having a slightly higher biomass. Kodjinup Swamp consistently had the lowest biomass and did not exhibit the marked seasonal change in biomass of the other wetlands. A Tukey-Kramer post hoc test revealed no significant difference in biofilm biomass between Bokarup Swamp and Noobijup Lake.

Table 3.6. Two-way nested ANOVA (Wetland by Sampling Event) results for biofilm AFDW.

Source	df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	16.03	8.019	11794.83	0.0001
Sampling Event	5	31.66	6.332	5286.00	0.0054
Wetland x Sampling Event	10	7.91	0.719	0.66	0.74

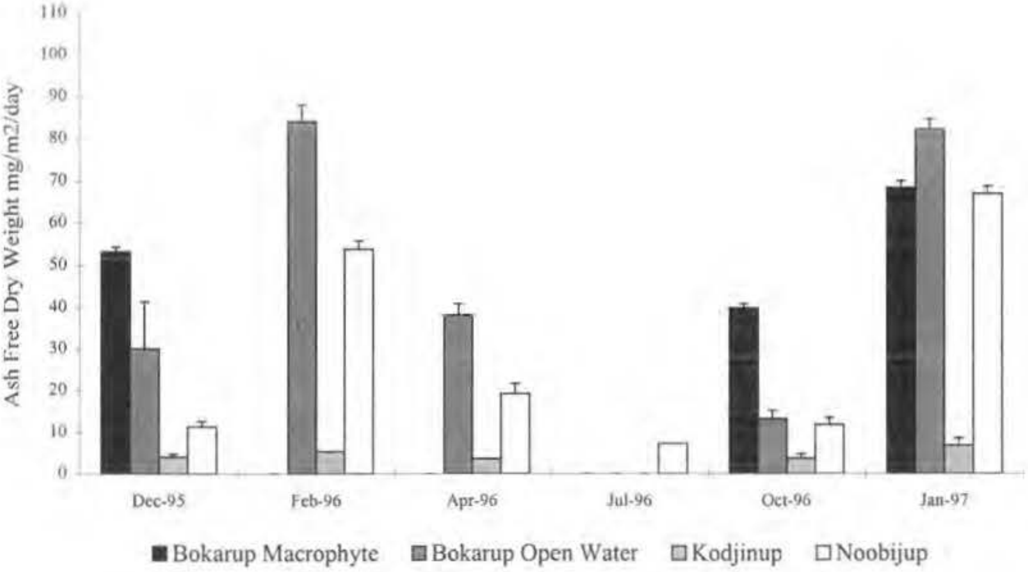


Figure 3.5. Average biofilm AFDW (±SE) mg/m^2/day for each sampling occasion in vegetated habitats in each wetland, and unvegetated and vegetated habitats in Bokarup Swamp from December 1995 to January 1997. An absence of data indicates insufficient water levels for biofilm development.

3.3.4.3. Biofilms : natural vs artificial substrates

Artificial substrates produced significantly higher chlorophyll *a* ($P<0.0001$) and biomass ($P<0.0001$) values than those found on the emergent macrophyte leaves (Tables 3.7 and 3.8). Significant wetland differences ($P<0.0001$) were found for both parameters, with values consistent with those from the field sampling data (Figures 3.6 and 3.7). Chlorophyll *a* levels were relatively low in all wetlands (particularly Kodjinup Swamp), however the biomass was up to 3 times higher on the artificial substrates. Biofilm biomass was highest at Bokarup Swamp for both substrates with Noobijup Lake having the highest chlorophyll a concentrations despite having a lower biomass.

Table 3.7. Two way ANOVA (Wetland by Substrata) results for biofilm chlorophyll *a* from natural and artificial substrates.

Source	df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	0.99	0.49	227.00	0.0001
Substrate	1	0.16	0.16	75.56	0.0001
Wetland x Substrata	2	0.01	0.004	1.66	0.21

Table 3.8. Two-way ANOVA (Wetland by Substrata) results for biofilm AFDW from natural and artificial substrata.

Source	df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	9.90	4.54	1469.00	0.0001
Substrata	7	1.12	1.12	363.00	0.0001
Wetland x Substrata	14	0.08	0.40	12.935	0.0702

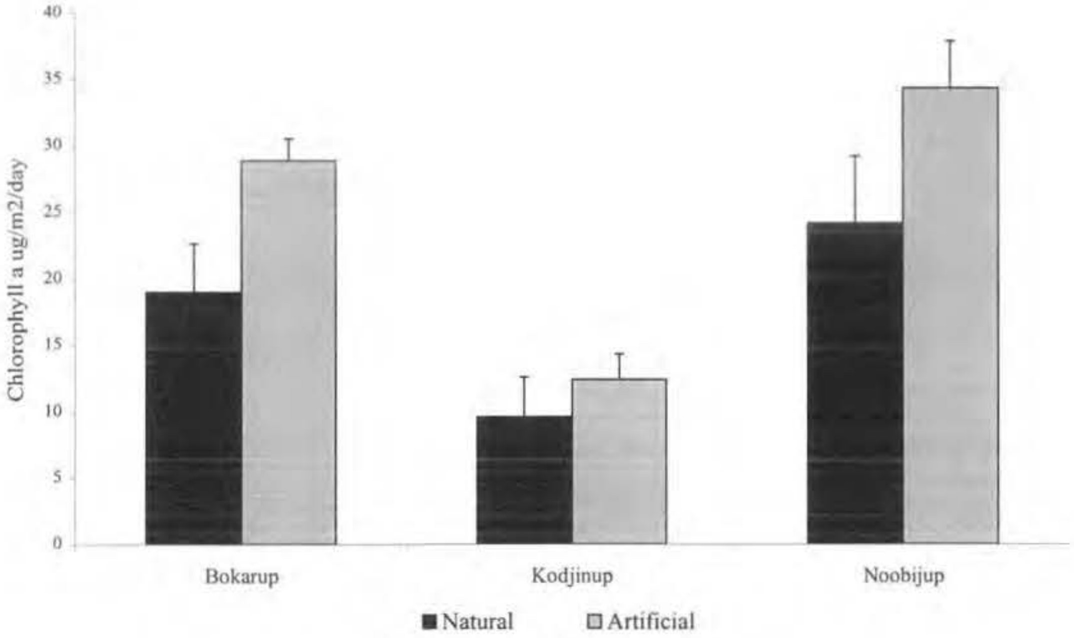


Figure 3.6. Comparison of average (±SE) chlorophyll *a* $\mu g/m^2/day$ from artificial substrata (glass slides) and natural substrata (*B.articulata* leaves) in each wetland in January 1997.

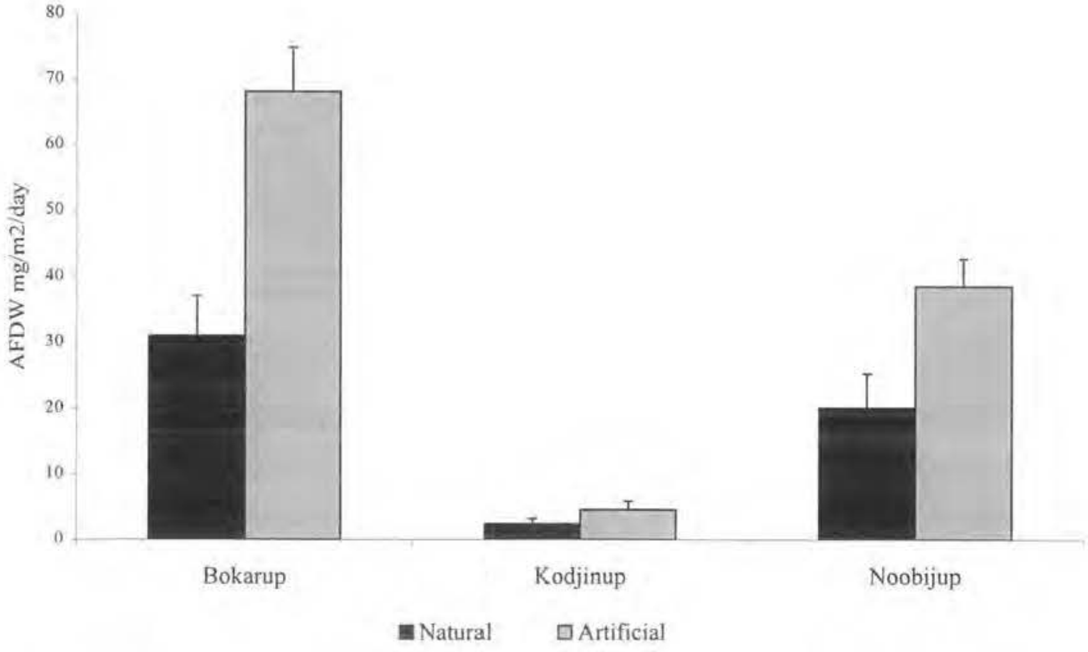


Figure 3.7. Comparison of average (±SE) AFDW mg/m^2/day from artificial substrata (glass slides) and natural substrata (*B.articulata* leaves) in each wetland in January 1997.

3.3.5 Dissolved organic matter

DOM concentrations varied significantly between both wetlands ($P<0.0001$) and seasons ($P<0.0001$) (Table 3.9). Concentrations were consistently highest in Kodjinup Swamp reaching 59.08 ± 5.3 mg/L in February 1996 and lowest in Noobijup Lake, generally below 18 mg/L (Figure 3.8). DOM peaks for Bokarup and Kodjinup Swamps followed a predictable trend of summer maxima and winter troughs. Noobijup Lake displayed little variability, however, maximum values were found in April and July of each year that declined over the summer months.

Table 3.9. Two-way ANOVA (Wetland by Sampling Event) results for DOM.

Source	Df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	8.41	4.20	3252.00	0.0001
Sampling Event	7	0.36	0.05	39.87	0.0001
Wetland x Sampling Event	14	0.29	0.02	16.31	0.51

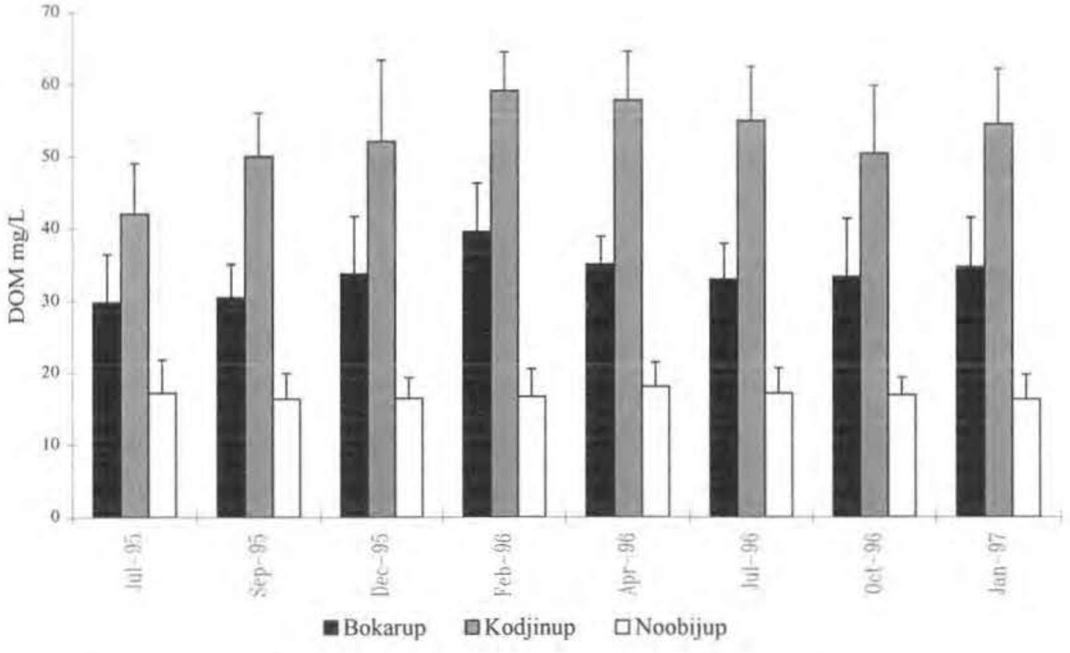


Figure 3.8. Average DOM (±SE) concentration (mg/L) in each sampling occasion for each wetland from July 1995 to January 1997.

3.4 DISCUSSION

This aim of this chapter was to quantify the input of dominant allochthonous and autochthonous sources of organic matter to Bokarup Swamp, Kodjinup Swamp and Noobijup Lake in the Muir-Unicup region. Allochthonous litter fall was measured using litter traps and separated into aquatic and riparian taxa and individual plant components such as leaves, stems, bark and reproductive parts. Emergent macrophyte leaf litter fall was measured using floating litter traps and constituted the dominant source of particulate organic matter in all wetlands. Water column phytoplankton, biofilm from natural and artificial substrata and DOM were also quantified as major autochthonous sources of organic matter contributing to the carbon dynamics in these wetlands.

Allochthonous and autochthonous inputs were dominated by a strong seasonal cycle of higher inputs during the summer periods of each year than inputs during the colder winter months. This seasonal cycle produced significant differences between sampling events for all sources of organic matter. Increased inputs during warmer periods coincided with periods of maximum wetland water levels and temperatures. High water levels during this period may be important for providing the low benthic oxygen conditions at the time of the highest organic inputs and therefore favouring the accumulation of peat. The presence of the physico-chemical conditions most conducive to peat accumulation coinciding with peak organic matter inputs has not been noted in the Australian limnological literature. The co-occurrence of these conditions may be the predominant reason explaining the occurrence and distribution of peat deposits in south-western Australia. Changes to the local and regional hydrology can therefore impact on rates of peat accumulation by altering the timing and duration of wetland water levels, which can influence wetland physico-chemistry and macrophyte distribution (Froend & McComb 1994).

There was also evidence of interannual variability in many of the inputs, which may be driven by climate variations. Rainfall during 1996 was well above average at 1092.4 mm, substantially wetter than 1995 at 930.8 mm and rainfall by July 1997 was also well below average (Section 2.6.1). The variability in rainfall was reflected in significant differences between wetlands for all sources, which may have resulted in differences in hydrology, physico-chemistry and vegetation associations between years within each wetland (see Chapter 2).

Litterfall in all of the wetlands studied displayed seasonal peaks in summer, with the December to April period contributing around 60% of total annual input. Numerous studies in south-eastern Australian riparian forests have identified that maximum litterfall occurs in summer (December to February) (eg. Lake *et al.* 1985; Bunn 1986; Campbell *et al.* 1992; Briggs *et al.* 1993). However, this seasonality in litterfall is less marked than in the Northern Hemisphere where deciduous forests dominate. Litterfall in an Australian cool temperate stream was 18% of total annual load during winter, compared to around 5% in the Northern Hemisphere (Campbell & Fuchshuber 1994). Pozo *et al.* (1997) noted a 32% reduction in annual litterfall from a *Eucalyptus globulus* plantation compared to an adjacent mixed deciduous forest. Peak deciduous litterfall was in autumn, whereas the Eucalypt plantation displayed a less marked seasonal pattern with peak litterfall in summer. Intrinsic site characteristics such as hydrology and species composition, density and distribution therefore play an important role in the extent to which Australian native riparian litterfall vary with season. In wetlands such as those in the Muir-Unicup region which experience highly seasonal water levels, alterations to local and regional hydrology may influence the timing and quantity of litterfall.

Total annual allochthonous litterfall rates differed substantially between wetlands, with Bokarup Swamp at 925 gDW/m^2/year having almost twice the annual litterfall of Kodjinup Swamp and almost five times that of Noobijup Lake. Studies quantifying litterfall are generally from riparian habitats dominated by Eucalypts, *Casuarina* or *Melaleuca*. Annual litterfall rates in Australian temperate streams dominated by Eucalypts range from 310 gDW/m^2/year (Campbell & Fuchshuber 1994) through to 800 ± 99 g DW/m^2/year (Campbell *et al.* 1992). Annual *Melaleuca* litterfall ranged from 430 g DW/m^2/year in a south-west Australian estuary (Congdon 1979) to 809 ± 135 gDW/m^2/year in a south-east Australian wetland (Greenway 1994). Riparian zones in the study wetlands contain mixed stands of Eucalypts, *Melaleuca* and *Banksia* (Appendix 1), with *Melaleuca* components (particularly leaves) dominated litterfall at both Bokarup and Kodjinup Swamps, contributing around 90% of total litterfall. In contrast, Noobijup Lake had a much lower proportion of litterfall from *Melaleuca*, and a much lower total annual litterfall. Variations in the rate and timing of allochthonous litterfall in each wetland, particularly in Noobijup Lake, may be a result of riparian assemblages dominated by a few species, which will directly effect the composition of litter contributing to the sediment.

Early studies by Bärlocher *et al.* (1978) estimated inputs of organic matter from emergent macrophytes by harvesting above ground biomass, and assuming the entire biomass entered the water column annually. Similar assumptions have been made by studies quantifying above ground productivity and rates of macrophyte senescence to estimate organic matter contributions (Brinson *et al.* 1981; Bartsch & Moore 1985; Hocking 1989; Gessner *et al.* 1996; Kuehn & Suberkropp 1998). These studies have the potential to overestimate the input of macrophyte organic matter by assuming total litterfall of the standing biomass each season. This overestimate is evident when litter trap results are compared to inputs generated from productivity data. Productivity values for emergent macrophytes range from 689 to 4510 gDW/m^2/year for *Phragmites australis* (Gessner *et al.* 1996; Reitner *et al.* 1999) to 1300 gDW/m^2/year for *Juncus krausii* (Congdon & McComb 1980). Peak inputs in litter traps were 239.91 gDW/m^2/year in Kodjinup Swamp. Peak productivity for *Baumea articulata* of 2.8 gDW/m^2/day has been found in south-west Australian wetlands (Froend & McComb 1994), however this is still almost three times the maximum litterfall found with litter traps. In wetlands such as those in the Muir-Unicup Region where organic inputs are obviously dominated by emergent macrophytes, and dominant species do not completely senesce, accurate estimates of litterfall are required to determine their contribution to peat accumulation.

Macrophyte litterfall displayed a similar seasonal cycle and significant differences between wetlands to allochthonous inputs. Differences in litterfall did not reflect the density and biomass of macrophytes in each wetland (Section 2.6.6). Highest litterfall

(239.91 gDW/m^2/year) in Kodjinup Swamp did not correspond to highest biomass or density of leaves recorded. However, the largest change in biomass was recorded at Kodjinup Swamp, almost doubling between April and September. This indicates that *B.articulata* productivity in Kodjinup Swamp was higher than the other two wetlands, which may have lead to increased leaf fall.

Together with providing organic matter to wetland sediments, emergent macrophytes provide a substratum for biofilm growth. Biofilms provide a major energy source for aquatic food webs by contributing organic material to the water through leached exudates, sloughed dead and senescent material, and live cells (Rounick & Winterbourn 1986; Lock *et al.* 1984). Biofilms were low in chlorophyll *a* in the macrophyte habitat (less than 45 μg/m^2/day) and coincide with very low water column productivity (less than 10 μg/L). In a review of aquatic biofilms, Goldsborough and Robinson (1996) suggested that chlorophyll concentrations in freshwater systems rarely exceeded 10 mg/m^2. In south-east Australian wetlands, biofilm chlorophyll measurements range from 0.2 - 42 mg/m^2 (see review in Burns & Ryder in press), substantially higher than in the study wetlands. The presence of high concentrations of DOM (see review in Kirk 1986) in these wetlands may be responsible for low algal productivity. DOM has the potential to promote the growth of bacteria, algae and plants by acting as a food source (eg. DeHaan 1976; Geisy 1976; Wilson 1991), however, it generally inhibits biological activity through the fixation of trace metals or phosphate, inhibition of enzymes, absorption of light or lowering the ambient pH (Jackson & Hecky 1980). Nutrient limitation (as proposed in Chapter 2) in aquatic systems may also contribute to low biofilm and water column chlorophyll productivity (Mosisch *et al.* 1999).

Biofilm organic biomass differed greatly between wetlands and displayed little association with trends in chlorophyll concentrations. The organic biomass in Kodjinup Swamp was notably lower than the other wetlands, yet the ratio of chlorophyll to organic biomass was lowest in this wetland. This is in contrast to the other wetlands (particularly Bokarup Swamp), which had a very high chlorophyll to organic biomass ratio. This indicates that the majority of the biofilm biomass in Kodjinup Swamp was algal, whereas in the other wetlands the biomass was dominated by other biotic or abiotic sources of organic matter. Biofilms are a diverse assemblage of autotrophic and heterotrophic organisms (Lock *et al.* 1984) and therefore may contain a substantial heterotrophic component which can contribute to organic biomass (eg. Sinsabaugh *et al.* 1991; Scholz & Boon 1993; Sobczak 1996). As with algal productivity, heterotrophic microorganisms can also be supported or inhibited by high levels of water column DOM, depending on the successional stage of the biofilm (Goldsborough & Robinson 1996). Blenkinsopp & Lock (1994) found biofilms in low light environments are predominantly heterotrophic and dominated by bacteria. High levels of DOM in Kodjinup Swamp may therefore be inhibiting both algal and bacterial biofilm productivity.

A comparison of artificial (glass slides) and natural (*B.articulata* leaves) substrata found artificial substrata significantly overestimated biofilm biomass and chlorophyll *a* concentrations in all wetlands. Artificial substrata are commonly used to sample biofilm colonisation. Critical reviews by Cattaneo & Amireault (1992) and Morin & Cattaneo (1992) argue the ability of artificial substrata to reproduce natural substrata, concluding they often misrepresent both the quantity and composition of natural biofilms. Lui *et al.* (1993), Cronk & Mitsch (1994) and Lowe *et al.* (1996) have all demonstrated an increased biomass from artificial compared to natural substrata. Despite the limitations there are many benefits to using artificial substrata for measuring biofilm parameters. They can reduce the heterogeneity of the naturally occurring substrata, permit standardisation of substrata between sites, and allow colonisation when substrata may be limited (Cattaneo & Amireault 1992).

Some wetland macrophytes produce allelochemicals which can limit biofilm growth (Gross *et al.* 1996; Nakai *et al.* 1999). This may also account for differences noted between the open water and macrophyte habitats. Significantly higher chlorophyll concentrations and organic biomass were found in the open water areas of Bokarup Swamp compared to within the macrophytes communities. Weeks (1988) suggested allopathy to explain differences in algal species diversity and biomass on artificial substrata in macrophyte habitats compared with unvegetated habitats. Macrophytes can also negatively alter the environment for algae through shading. Light availability is one of the most important factors influencing primary productivity in aquatic systems, especially where nutrients are limiting (Winterbourn 1990). The presence of dense assemblages of *B.articulata* has resulted in chlorophyll concentrations up to 7 times lower than in unshaded open water. Shading from riparian vegetation in temperate streams has also produced a four to five time's reduction in chlorophyll and organic biomass (Hill & Knight 1988).

3.4.1 Summary

This chapter quantified the dominant sources of organic matter into Bokarup Swamp, Kodjinup Swamp and Noobijup Lake. The average daily inputs of organic matter from allochthonous and emergent macrophyte litter, phytoplankton, biofilms and DOM form the basis of the carbon budget (Chapter 6) which is used to calculate the biomass of organic matter contributing to peat accumulation in each wetland.

Allochthonous and autochthonous inputs were dominated by a strong seasonal cycle of increased inputs during the summer periods, coinciding with periods of maximum wetland water levels and temperatures. The presence of the physico-chemical conditions most conducive to peat accumulation coinciding with peak organic matter inputs is important in explaining the occurrence and distribution of peat soils in south-western Australia. Inputs from riparian allochthonous sources contributed significant amounts of organic matter to the sediments of each wetland. However, inputs from these sources are restricted to the margins of each wetland, limiting their contribution to peat accumulation in the wetland basin. Above ground components of emergent macrophytes, particularly *B.articulata*, dominated the carbon supply in each wetland. Macrophytes contributed highly refractory particulate organic matter to sediments, provided a source of DOM and a colonisable substratum for biofilms.

It is evident from these results that the maintenance of macrophyte communities is essential to continue the process of organic matter accumulation in these wetlands. Management of these wetlands must therefore include the provision of hydrologic regimes and water quality that maintains emergent macrophyte community structure and productivity. Changes to the local and regional hydrology can therefore impact on rates of peat accumulation by altering the timing and duration of wetland water levels, which can influence wetland physico-chemistry and macrophyte distribution (Froend & McComb 1994).

CHAPTER 4

TRANSFORMATIONS AND LOSSES OF ORGANIC MATTER

Microorganisms and Carbon Gases

4.1 INTRODUCTION

The relationship between organic matter production and organic matter decomposition determines the rate of peat accumulation. Macrophytes provide a major source of organic matter to wetland sediments through root and rhizome turnover, the secretion of organic compounds from roots and the loading of organic particles settling on the sediment surface (Chanton & Dacey 1991; Muller *et al* 1994). The colonisation of this benthic organic matter by aquatic microorganisms such as fungi and bacteria is termed 'conditioning', and results in an increase in the quality of the detritus as a food source for detritivores (Anderson & Seddell 1979). In addition to turning the detritus into a more palatable food source, microorganisms transform detrital organic matter into their own biomass, a form in which the material is more accessible to detritivores.

Chemoorganotrophic organisms (primarily bacteria) do not require oxygen to combust organic matter, but can use a variety of alternate terminal electron acceptors (Kortmann & Rich 1994). These microorganisms are an important link between primary and secondary production in aquatic detrital food webs, controlling the flux of carbon and energy within aquatic systems (Boon & Shiel 1990). The organic matter produced from this process can be in the form of the microorganisms themselves or by-products of their respiration (such as carbon dioxide - CO_2 and methane - CH_4) which can be utilised by successive trophic levels. These reduced products contain residual energy which supports further oxidation by bacteria, which can be preyed upon by bactivorous organisms, and hence enter the food web. However, in areas exposed to prolonged inundation, their respiration may lead to a substantial depletion of oxygen (Segers & Kengen 1998) which in turn may effect the distribution and abundance of other aquatic flora and fauna (Choudrey 1988).

In wetlands with no surface drainage, a large proportion of the organic matter production remains within the system and passes to the sediment for microbial decomposition. The conversion of this organic matter to microbial biomass and the atmospheric flux of carbon gases represent the major loss of organic matter from these systems. Quantifying these losses is an integral component in the determination of the rates of peat accumulation.

4.1.1 Bacterial production of methane and carbon dioxide

Organic matter is decomposed to carbon dioxide by bacteria preferentially under aerobic conditions using oxygen, nitrate and sulfate electron acceptors (Sorrell & Boon 1992; Muller *et al.* 1994). As benthic consumers use oxygen, biogenic methane production becomes the dominant pathway for organic matter decay (Boon & Mitchell 1995). Methane is produced by methanogenic bacteria using a limited range of substrates, primarily hydrogen, carbon dioxide or acetate which are produced by other anaerobic bacteria mineralising more complex organic substrates (Holzapeel-Pschorn *et al.* 1986). A food chain involving fermentative and methanogenic bacteria guarantees that organic matter will be mineralised to gaseous products (carbon dioxide and methane) even under oxygen deficient conditions. Measurements of biogenic methane production from wetland environments are important in estimating rates of breakdown of carbon molecules.

The locality and productivity of freshwater systems result in varying concentrations of dissolved carbon dioxide. Photosynthesis and respiration are the two major factors that influence the abundance and distribution of carbon dioxide, with atmospheric diffusion contributing to dissolved levels. Carbon dioxide is very soluble in water, some 200 times greater than oxygen (Wetzel 1975). As carbon dioxide dissolves in water, the solution contains unhydrated carbon dioxide at around the same concentrations. The carbon dioxide of the water hydrates to yield carbonic acid using the following equation .

$$CO_2 + H_2O \leftrightarrow H_2CO_3$$

As water enters the sediment it becomes enriched with carbon dioxide from plant and microbial respiration (Wetzel 1975). The aerobic zone of waterlogged sediments is generally limited to the water column and the upper most millimetres of the sediment surface (King *et al.* 1990). As a result of oxygen secretion from the underground portions of macrophytes an aerobic zone is created proximate to these parts in the sediment (Holzapfel-Pschorn *et al.* 1986). These zones increase the production of carbon dioxide as well as providing carbon dioxide for use in anaerobic metabolism and creating a site for the oxidation of methane from surrounding anoxic sediments.

In wetland sediments, oxygen consumption usually exceeds the rate of oxygen diffusion below surface sediments (Westermann 1993). Microbes can mineralize organic molecules completely to carbon dioxide under aerobic conditions. Under anaerobic conditions, bacteria are responsible mainly for biological mineralization, requiring a complex microbial food web where the product of one microbial group serves as a substrate for subsequent microbial assemblages (Westermann 1993). Organic matter can therefore be mineralized completely to carbon dioxide under aerobic conditions or to methane and carbon dioxide by oxidation-reduction reactions (Westermann 1993). The former reaction is dependent on the presence of appropriate electron acceptors and oxidation-reduction potential. Therefore, the respiratory processes in aquatic sediments are dependent on concentrations of specific electron acceptors and the availability of organic matter.

Methane production is the terminal anaerobic mineralisation process in wetland systems where, other than carbon dioxide, inorganic electron acceptor concentrations are low. The production of methane and carbon dioxide from organic matter occurs in two stages. Firstly, an assemblage of facultative and obligate anaerobic bacteria convert proteins, carbohydrates and fats into simple sugars and fatty acids by hydrolysis and fermentation (Wetzel 1975). Methanogenic bacteria utilise these products in the production of methane and carbon dioxide through energy yielding oxidation-reduction reactions resulting in reduced fatty acid products and oxidised carbon as carbon dioxide (Wetzel 1975). This primarily occurs through two reactions.

$$CO_2 + 8H \rightarrow CH_4 + 2H_2O$$

$$CH_3COOH \rightarrow CH_4 + CO_2$$

Methane produced in the sediments can be oxidised by methane oxidising bacteria (methanotrophs) in the overlying water column and in aerobic zones of sediments. The empirical equation for methane oxidation is :

$$5CH_4 + 8O_2 \rightarrow 2(CH_2O) + 3CO_2 + 8H_2O$$

Methanotrophs are an important sink for methane in aerobic zones (McDonald *et al.* 1996) and as such play an important role in carbon cycling. Little dissolved oxygen is required as methanotrophs can persist in concentrations as low as 0.1 mg/L, highlighting their ability to scavenge any oxygen present in waterlogged soils (Rudd *et al.* 1976).

4.1.2 Methane and carbon dioxide dynamics

Natural wetlands are thought to be major sources of atmospheric greenhouse gases, primarily carbon dioxide and methane, with numerous studies attempting to quantify global emissions from these habitats (eg. Cicerone & Oremland 1988; Schultz *et al.* 1991; Neue 1993). These are estimated to be responsible for 20 to 40% of global emissions. Wetlands with peat soils, being waterlogged organic deposits, are natural environments for the bacterial production of methane, which comprises 60 to 70% and carbon dioxide at 30 to 40% of the gaseous products (Dinel *et al.* 1988). Methane produced in unvegetated soils can be released to the atmosphere via molecular diffusion, the ebullition of gas bubbles from the sediment and its oxidation by methanotrophic bacteria in the aerobic zone of the water column (Chanton *et al.* 1989; Conrad & Rothfuss 1991; Krumholz *et al.* 1995). Emergent vegetation can influence methane and carbon dioxide emissions through the aeration of underground organs and the oxidation of the rhizosphere, as well as providing a pathway for methane transport through emergent leaves (Brix *et al.* 1992; Yavitt 1997; Vandernat & Middleberg 1998).

Atmospheric concentrations of carbon dioxide and methane are increasing rapidly, with profound effects for the future global climate (Bridgham & Richardson 1992). Atmospheric methane is an important greenhouse gas that is 21 times as radiatively effective as carbon dioxide and has been increasing globally at around 1% per year during this century (Bubier *et al.* 1993). Natural wetlands therefore, play an important role in the atmospheric chemistry of carbon (Bridgham & Richardson 1992).

There is a wealth of global literature dealing with emissions of carbon gases (particularly methane) from freshwater aquatic systems, with countless examples from Northern Hemisphere peatlands (eg. Bartlett *et al.* 1989; Moore & Knowles 1989; Yavitt & Lang 1990; Bridgham & Richardson 1992; Bubier *et al.* 1993; Pulliam 1993; Grunfeld & Brix 1999; Kettunen *et al.* 1999). However, our understanding of methane emissions and their controlling factors come from environments far removed from the warm temperate climate experienced in southern Australia. These temperate wetlands are often small, shallow and ephemeral, containing highly productive macrophyte communities and do not experience regular winter stratification common in the Northern Hemisphere (Boon & Mitchell 1995). Australian literature is dominated by studies of floodplain habitats in south-eastern Australia. These studies examine the influence of macrophytes on methane atmospheric flux (Boon & Sorrell 1991; Brix *et al.* 1992; Sorrell & Boon 1994; Muller *et al.* 1994; Boon & Sorrell 1995) and aspects of sediment biogeochemistry affecting methane production (Sorrell & Boon 1992; Boon & Mitchell 1995). The paucity of long-term studies on the dynamics of carbon gases in temperate aquatic systems highlights the current lack of knowledge concerning carbon dynamics and greenhouse gas contributions from these systems.

This chapter reports on a modified phospholipid procedure (after White *et al.* 1979) to examine transformations of organic matter by sediment microbial biomass between wetlands, seasonal changes in biomass and the influence of sediment depth to changes in biomass. The sediment microbial biomass in two discrete habitats, an area of open water and one of a dense, uniform stand of *B.articulata* is also examined in Bokarup Swamp. The biogenic production and atmospheric flux of methane and carbon dioxide are also examined to quantify losses of organic matter from each wetland. Seasonal, wetland and diurnal variations in the flux of methane and carbon dioxide from wetland sediments and emergent vegetation (*B.articulata*), the *in situ* concentrations of each gas in wetland sediments and emergent macrophyte leaves are used to quantify atmospheric gas flux as the major loss of carbon in these systems.

4.2 METHODS

4.2.1 Phospholipids: measures of sediment microbial biomass

Determining the viable biomass of a microbial community provides an estimate of the amount of active microorganisms in a particular environment and, therefore, the capability for metabolic transformations in that environment (Vestal & White 1989). The accurate determination of sediment microbial biomass poses many problems, as changes to the structure and function of microbial communities have proven difficult to measure without distorting the *in situ* population (Bobbie & White 1980). Previous studies have shown that lipid phosphate is an accurate measure of the microbial biomass under a variety of conditions (White *et al.* 1979; Vestal & White 1989; Mancuso *et al.* 1990).

Phospholipids have a relatively rapid turnover in sediments, so the analysis of phospholipids provides a more accurate measure of the viable cellular biomass than other measures of biomass such as enzyme activities, muramic acid levels and total ATP (Rajendran *et al.* 1992). Extractable lipid phosphate has been highly correlated with other measures of microbial biomass such as extractable ATP in microflora (White *et al.* 1979). An increased recovery of microbial biomass from phospholipids than for epifluorescence microscopy (EFM) in estuarine sediments has been demonstrated (Findlay *et al.* 1989). The determination of microbial biomass by phospholipid analysis was used in this study as it provides an accurate determination of microbial biomass, is not technically cumbersome and time consuming and is not reliant on expensive instrumentation.

4.2.1.1 Preliminary experiment

A preliminary experiment in July 1995 examined the spatial variability and vertical distribution of microbial biomass using phospholipid concentrations. Fifteen sediment cores of 50 cm depth were collected from random locations within Kodjinup Swamp using the D-section corer as outlined in Section 2.5.2. Each core was removed from the corer and divided into 3 equal 15 cm sections, from consecutive depths, and placed in sealed plastic bags. These were immediately placed on ice in the dark and frozen within 1 hour of collection.

In the laboratory, phospholipids were extracted from sediment samples using a modified procedure of White *et al.* (1979). Each section was homogenised using a blender and a 30 gm wet weight subsample added to a 100 ml sealed separatory funnel. The sediment was suspended in 15 ml of 50 mM phosphate buffer (prepared with 8.7 g of dipotassium hydrogen phosphate (K_2HPO_4)) neutralised with 1N hydrochloric acid (HCl) to pH 7.4, and 18.75 ml of chloroform ($CHCl_3$) and 37.5 ml of methanol (CH_3OH) added. The solution was thoroughly mixed using a vortex stirrer for 3 minutes and allowed to extract for 2 hours. A single-phase solution resulted. If two phases were present, methanol was added in 1ml increments, mixing thoroughly after each addition until a single-phase solution was attained. An additional 18.75 ml of chloroform and 18.75 ml of deionised water were added to the solution, mixed as above and allowed to separate for 24 hours.

The upper phase of methanol and water were removed by aspiration through the top of the separatory funnel. The chloroform above the sediment was decanted through a Whatman 2E filter paper using a Büchner funnel and glass vacuum flask. The filtrate was transferred to a graduated cylinder and the volume recorded. Samples were transferred to 50ml boiling tubes and the chloroform evaporated under nitrogen. Immediately following evaporation samples were transferred to a preheated Thermocline dry block heater and a total phosphorus digestion performed followed by analysis for orthophosphate using the procedures described in section 2.5.3. This procedure is a modification of the Bligh & Dwyer (1959) extraction procedure and allows for around 80% recovery of phospholipid containing chloroform. The volumes can be altered using this procedure as long as the proportions of K_2HPO_4 : methanol : chloroform are 0.8:2:1 in the single phase solution and 0.9:1:1 after separation into the biphasal solution (White *et al.* 1979).

Sediment samples from each extraction were placed in individual crucibles and dried in a Contherm series 5 drying oven at 105°C for 48 hours, removed and weighed to 2 decimal places. The dry weight for each sediment sample was used to obtain results in $\mu gPO^4/gDW$.

A significant difference ($P<0.001$) was found between the three sediment sections. These three section dimensions were used throughout the field sampling. Running standard errors were obtained for each sediment section using the 15 samples from the preliminary experiment. All sediment sections had a maximum standard error with two samples, and a minimum standard error at seven, four and seven samples for surface, middle and lower sediments respectively (Appendix 2). Five replicates of each section were chosen for the field collections as it represented a manageable and achievable number of replicates and was less than one standard error from the lowest found with fifteen samples.

4.2.1.2 Field collections

Five sediment cores were collected from random locations within the macrophyte habitat within each wetland, corresponding to the locations of the five replicate *in situ* gas collections. Samples were collected and analysed as described above. The habitat classification (Section 2.6.4) found two discrete habitats within Bokarup Swamp, vegetated and unvegetated. To assess the effect of emergent vegetation on microbial biomass, 5 additional cores from the open water habitat were collected in January 1997, and analysed for phospholipid concentration using the methods described.

4.2.2 Methane and carbon dioxide dynamics

The release of methane and carbon dioxide to the atmosphere from unvegetated wetland sediments and emergent leaves of *B.articulata* was measured using the Static Chamber Method. This method was chosen as it allows the measurement of gas ebullition from both sediments and emergent vegetation and from dry and inundated habitats, all of which were encountered during this study. Two chambers were constructed from clear 3 mm acrylic to cover a surface area of 0.25 m^2 to a height of 0.7 m. A rubber septum located at the top of each chamber was used to remove gas samples and was replaced at the end of each time period. A 3 volt fan was attached to the inside of each chamber to ensure mixing of the air and was run throughout each time period (90 min). To check for chamber leakage, the open base of each chamber was sealed using laboratory grade parafilm and the chamber filled with pure CO_2 for 30 seconds through the septa. Samples were removed via the septa at five minute intervals for 20 minutes, placed in Vaccutainers™ and immediately analysed for CO_2 concentration using 10 µl samples. There was no change in gas concentration over the 20 minute trial period.

In the field, for each wetland, gas ebullition was measured at five random locations at three fixed times within emergent vegetation and open water habitats. This represented a manageable number of replicates for both gas collection and analysis. Chambers were deployed at 0900, 1300 and 1700 hours each day. At each location when water levels were sufficient, one chamber was placed over open water (between emergent plants) and the other over 10 - 12 leaves of *B.articulata*. The chambers were placed at each location using a punt to minimise disturbance to the sediment and gas release. As each chamber was deployed, the septum was removed, the fans turned on and the chambers left to stabilise for 5 minutes before sampling (as per Muller *et al.* 1994). Both chambers were run concurrently at each location for 90 minutes and sampled at 30 minute intervals beginning at time zero. Samples were removed via the septa using a 10 ml syringe and immediately transferred to a 7 ml Vaccutainer™. Samples were wrapped in aluminium foil, placed on ice in the dark and stored at 4°C until analysis. Samples were analysed within 7 days of collection.

In the laboratory samples were analysed on a Varian 6500 Gas Chromatograph housed at Edith Cowan University. Samples were manually injected and concurrently analysed for methane using a flame ionisation detector (FID) and carbon dioxide using a thermal conductivity detector (TCD) using Helium as the carrier gas at 24 ml/minute. The TCD used a Poropaq 80 to 100 µm column at 150°C, and an ambient oven temperature of 32 °C. The FID used a filament temperature of 210°C. Analytical grade methane and carbon dioxide were used as standards. The gas from an unused Vaccutainer™ was injected at the beginning and end of each sample run to check for residual gas or contaminants. Residual gas concentrations were always below detection. Results were produced using the Varian STAR computer package and individual sample peak areas calibrated against a standard curve for each gas.

4.2.2.1 Diurnal methane and carbon dioxide gas ebullition

The collection of field data on the ebullition of methane and carbon dioxide from wetland sediments and emergent vegetation could not be standardised by time. As a result the temporal variability of gas flux was unknown, especially at night. In January 1997 gas flux was measured in each wetland over a 24 plus 4 hour period at 4 hour intervals. This time of year was chosen to represent a period of maximum gas flux and potential variation. At each time period, the gas chambers were deployed, samples collected, stored and analysed as previously described.

4.2.2.2 Sediment gas concentrations

Methane and carbon dioxide concentrations were taken from the surface 10 cm of sediment underlying the *in situ* chambers (0.25 m^2). A glass funnel with a 20 cm diameter and a septum at the tip was filled with lake water, voided of all bubbles and submerged with the funnel opening facing the sediment. The top 10 cm of sediment was disturbed using a length of dowel with a plastic disk located 10cm from the base to prevent deeper penetration into the sediment. The funnel trapped the gas released from the sediment by displacing the water. The top of the funnel was brought to the water surface and a gas sample removed via the septum. Where water levels were insufficient for this method to be used no samples were taken. Samples were stored and analysed as above. Sampling could not be conducted at times of year when water levels were insufficient.

4.2.2.3 Emergent macrophyte leaf gas

Methane and carbon dioxide concentrations in leaves of differing age were sampled in January 1997. Leaves were classified into three categories, dead (completely dry, brown), senescent (yellowed) and live (green). Gas concentrations were measured from emergent leaves of *B.articulata* using the displacement method as described in Section 4.2.2.2. Five replicate samples were taken from each wetland by cutting five individual leaves below the water line and squeezing them along the length of the cut leaf section and collecting the evolved gas in a submerged inverted funnel. Gas samples were removed via the septa and stored and processed as above. Gas concentrations for each replicate were analysed as described above.

4.2.3 Data analysis

Differences in mean numbers of values for each data set were compared by analysis of variance (ANOVA). Prior to analysis, the variances of sets of replicate samples were tested for homogeneity with Cochran's test. If variances of raw data were unequal, values were $\log_{10}$ transformed or $\log_{10} + 1$ transformed where zero values were present and then retested. Significance levels for ANOVA's were set at $\alpha = 0.05$. Missing data were included in the ANOVA model design. Anova models were constructed for each hypothesis using Underwood (1995). For simple one-way and two-way Anova's with orthogonal designs and fixed factors, the mean squares (MS) error value is the residual and common to all effects and interactions. For models that incorporate a random factor, such as Sampling Event, the MS error for each effect and interaction has been calculated using the 'table of multipliers' procedure outlined in Underwood (1995 pages 364-374). The following models were analysed using Statistica (Statistica 1995). Relationships between variables were analysed using the regression analysis function of Statistica.

Microbial biomass (phospholipid concentrations)

Null Hypothesis: there is no difference in microbial biomass (measured as phospholipid concentration) between continuous depths of a sediment profile, wetlands and sampling occasions.

ANOVA Model Design: (3 factor ANOVA)

Wetland - fixed factor with 3 levels

Sampling occasion - random factor with 8 levels

Depth - fixed factor with 3 levels

Microbial biomass (habitat differences)

Null Hypothesis: there is no difference in microbial biomass (measured as phospholipid concentration) between depths and emergent macrophyte and open water habitats in Bokarup Swamp in January 1997.

ANOVA Model Design: (2 factor ANOVA)

Habitat - fixed factor with 2 levels

Depth - fixed factor with 3 levels

Methane and carbon dioxide flux

Methane and carbon dioxide *in situ* flux, *in situ* concentrations, leaf concentrations and *in vitro* flux were analysed using separate 3 factor ANOVA's as the concentrations of these gases are not independent. Habitat was treated as a fixed factor (not nested) to allow a direct comparison.

***In situ* methane and carbon dioxide flux**

Null Hypothesis: there is no difference in methane/carbon dioxide flux between emergent macrophyte and open water habitats, sampling occasions or wetlands.

ANOVA Model Design: (3 factor ANOVA)

Wetland - fixed factor with 3 levels

Season - random factor with 7 levels

Habitat - fixed factor with 2 levels

***In situ* methane and carbon dioxide sediment concentrations**

Null Hypothesis: there is no difference in methane/carbon dioxide concentrations in sediments between sampling occasions or wetlands.

ANOVA Model Design: (2 factor ANOVA)

Wetland - fixed factor with 3 levels

Sampling occasion - random factor with 7 levels

Phospholipid/gas flux correlation

Null Hypothesis: there is no significant correlation between methane and carbon dioxide flux (all seasons and habitats) and microbial biomass (measured as phospholipid concentrations)(surface depths) in each wetland.

Tukey-Kramer post hoc tests were used to further examine the data set where significant differences were found within single factor analyses. Where significant differences were found in multiple interactions, the percent of total sum of squares of each factor was used to explore sources of variation (after Zar 1984).

4.3 RESULTS

4.3.1 Sediment Microbial Biomass

There was a marked seasonal cycle of summer maxima and winter troughs, and a decrease in phospholipid concentrations with depth in all wetlands (Figures 4.1a, b & c). These trends are supported by significant differences between depths ($P<0.0001$) and between sampling occasions ($P<0.0001$) (Table 4.1). Tukey-Kramer post hoc tests reveal all three depths are significantly different ($P<0.05$) from each other in all wetlands. Generally, depths were most similar in phospholipid concentration when values were lowest. All two-way interactions of depth, wetland and season were not significant, indicating a consistent response of microbial flora with depth to seasonal changes in each wetland.

Phospholipid concentrations peaked in February 1996 or January 1997 in all wetlands and were lowest in July of each year of the study. This indicates that the microbial biomass may be temperature driven, increasing the decomposition of organic matter during summer. However, these dates also correspond to periods of highest and lowest water levels. A significant interaction between wetland and sampling occasion ($P<0.0001$) suggest that intrinsic wetland features, such as hydroperiod, may be influencing wetland microbial biomass. Interannual variability was also evident in the response of microbial communities as the highest concentrations for all depths were found in January 1997. In Kodjinup Swamp, concentrations in January 1997 were almost double those of previous summer samples in December 1995 and February 1996.

Highly significant differences in phospholipid concentration between wetlands ($P<0.0001$) were also noted, with Kodjinup Swamp consistently having the highest sediment microbial biomass in all seasons. Tukey-Kramer post hoc tests reveal Kodjinup Swamp was significantly different ($P<0.05$) from the other two wetlands. Bokarup Swamp and Noobijup Lake concentrations generally peaked around 80 μg/L/gDW, with Kodjinup Swamp peaking at 198 ± 19.6 μg/L/gDW (Figure 4.1).

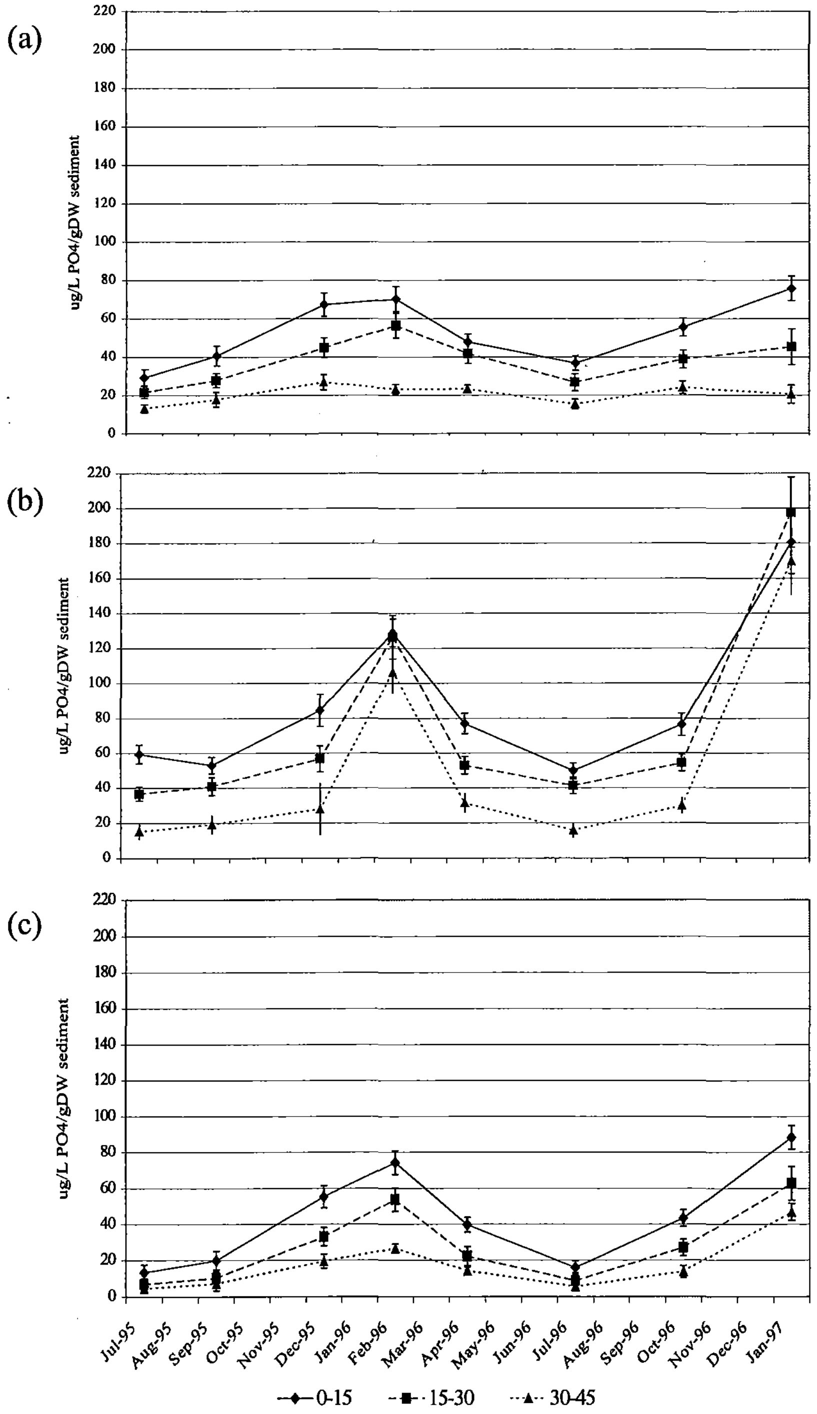


Figure 4.1. Average (±SE) sediment microbial biomass µg/L/gDW from three consecutive soil layers, 0-15cm, 15-30cm and 30-45cm in (a) Bokarup Swamp, (b) Kodjinup Swamp and (c) Noobijup Lake from July 1995 to January 1997.

Table 4.1 Three-way ANOVA results (Wetland by Sampling Period by Depth) for sediment phospholipid concentrations.

Source	df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	10.97	5.48	1986.00	0.0001
Sampling Period	7	18.40	2.62	628.74	0.0001
Depth	2	9.74	4.87	2036.20	0.0001
Wetland x Sampling Period	14	3.86	0.27	66.02	0.08
Wetland x Depth	4	0.17	0.04	10.46	0.07
Sampling Period x Depth	14	0.22	1.6×10^{-3}	0.53	0.89
Wetland x Sampling Period x Depth	28	0.84	0.03	7.20	0.001

4.3.1.2. Sediment microbial biomass: habitat differences

Phospholipids concentrations were significantly different between the open water and emergent macrophyte habitats ($P<0.0001$) in Bokarup Swamp in January 1997 (Table 4.2). Concentrations were consistently higher in the macrophyte habitat over all three depths, although the difference between habitats decreased with depth (Figure 4.2). Significant differences in phospholipid concentrations were found between depths ($P<0.0001$). However, the two-way interaction between habitat and depth was not significant, indicating differences between habitats were consistent over the sediment profile.

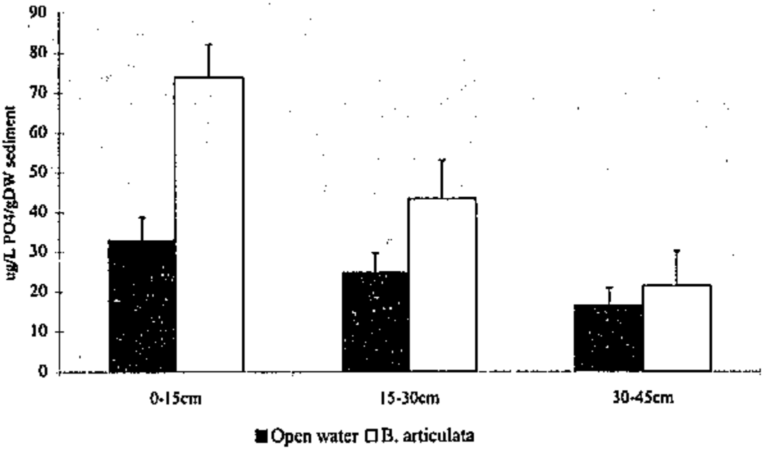


Figure 4.2 Average (±SE) sediment microbial biomass µg/L/gDW (expressed as phospholipid concentration) from each sediment layer in unvegetated and emergent macrophyte habitats in Bokarup Swamp from in January 1997.

Table 4.2 Two way ANOVA results (Habitat by Depth) for sediment phospholipid concentrations.

Source	df	Sum of Squares	Mean Squares	F-value	*P*-value
Habitat	1	0.080	0.08	12.20	0.0001
Depth	2	2.80	1.40	214.00	0.0001
Habitat x Depth	2	0.15	0.06	9.15	0.91

4.3.2 Methane and carbon dioxide dynamics

4.3.2.1 Atmospheric gas flux

Trends in atmospheric fluxes of methane and carbon dioxide from wetland sediments and through emergent macrophytes were inconsistent, although some generalisations can be made. Overall the flux of carbon dioxide to the atmosphere was higher than methane in all wetlands, with fluxes from unvegetated areas consistently higher than through emergent vegetation (Figure 4.3 a, b & c). Conversely, atmospheric fluxes of methane were higher through the emergent vegetation than from unvegetated areas.

Carbon dioxide ($P<0.0001$) and methane ($P<0.0298$) flux was significantly different between wetlands (Tables 4.3 & 4.4 respectively). Tukey-Kramer post hoc test showed no difference in methane flux between Bokarup and Kodjinup Swamps, however Noobijup Lake was significantly different ($P<0.05$) to the other two wetlands for both gases. Bokarup Swamp had higher rates of carbon dioxide flux from unvegetated areas during summer/autumn reaching 2.17 +- 0.2 mM/m^2/day in January 1997. The remaining carbon dioxide and methane flux rates displayed little variability over time and were all generally below 1.0 mM/m^2/day. There was a large range of flux rates in Kodjinup Swamp in all sampling periods, ranging from unvegetated carbon dioxide fluxes of 1.81 +- 0.2 mM/m^2/day to 0.32 +- 0.2 mM/m^2/day in April 1996. Noobijup Lake had the lowest flux rates for both gases and displayed a lesser seasonal response compared with the other two wetlands. Flux rates peaked in February 1996 at 1.62+- 0.2 mM/m^2/day from carbon dioxide from unvegetated areas, two months before the peak flux in the other wetlands.

Seasonal trends were inconsistent between vegetated and unvegetated habitats and between the two carbon gases (Figure 4.3 a, b & c). Flux rates from all sources were higher in the February-April period and in January 1997 and lowest in July of each year. Significant differences were found between sampling occasions for both carbon dioxide ($P<0.001$) and methane ($P<0.001$) (Tables 4.3 & 4.4).

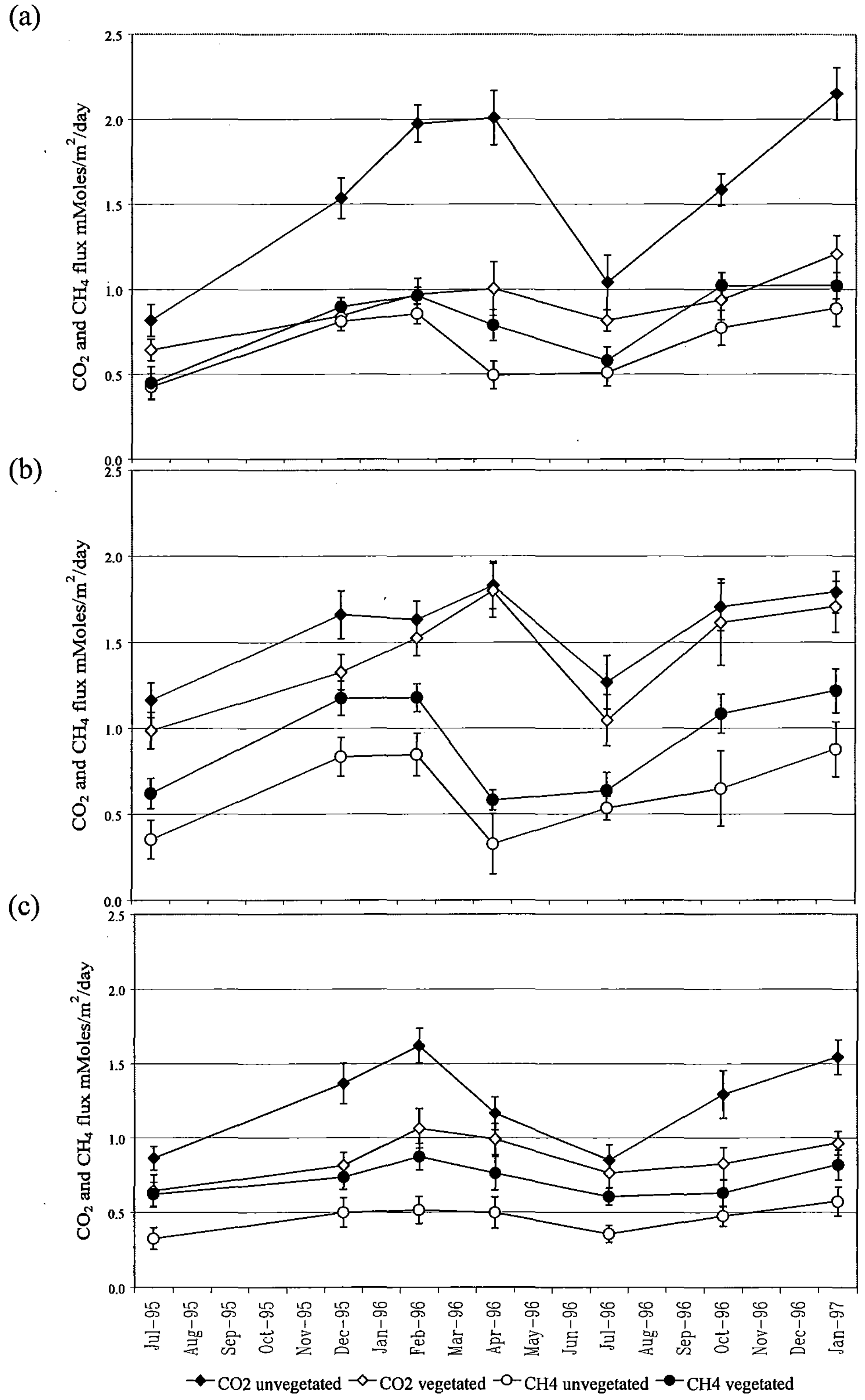


Figure 4.3 Mean methane and carbon dioxide flux (mM/m^2/day) (±SE) from unvegetated and emergent macrophyte habitats in (a) Bokarup Swamp, (b) Kodjinup Swamp and (c) Noobijup Lake from July 1995 to January 1997.

Table 4.3. Three-way ANOVA results (Wetland by Habitat by Sampling Period) for carbon dioxide flux.

Source	df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	0.94	0.47	42.71	0.0001
Sampling Period	6	1.69	0.28	148.57	0.0001
Habitat	1	1.04	1.04	83.63	0.0001
Wetland x Sampling Period	12	0.13	0.01	5.78	0.0001
Wetland x Habitat	2	0.26	0.13	12.65	0.0011
Sampling Period x Habitat	6	0.07	0.01	6.56	0.0001
Wetland x Sampling Period x Habitat	12	0.12	0.01	5.60	0.0001

Table 4.4. Three-way ANOVA results (Wetland by Habitat by Sampling Period) for methane flux.

Source	df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	0.43	0.21	4.77	0.02
Sampling Period	6	2.34	0.39	98.34	0.0001
Habitat	1	1.14	1.13	25.91	0.04
Wetland x Sampling Period	12	0.54	0.4	11.44	0.0001
Wetland x Habitat	2	0.16	0.8	10.77	0.0021
Sampling Period x Habitat	6	0.06	0.01	2.70	0.01
Wetland x Sampling Period x Habitat	12	0.09	0.08	1.95	0.03

A significant two-way interaction for both gases ($P<0.001$) of wetland by season shows the inconsistency in flux rate over different seasons. This indicates flux rates in each wetland do not respond consistently over time, being more similar in the cooler, winter months. The carbon dioxide fluxes in the vegetated and unvegetated areas in Bokarup and Kodjinup Swamps increased from the February to April 1996 sample dates, while methane flux rates decreased in both habitats. These decreases corresponded to the periods of minimal surface waters in these two wetlands.

Significant differences were evident in the flux of both carbon dioxide and methane between the vegetated and unvegetated areas of each wetland. These trends were not consistent between gases. The flux of carbon dioxide was significantly higher in the unvegetated area ($P<0.0001$), whereas methane flux was significantly higher in the areas vegetated by emergent macrophytes ($P<0.0454$). Significant differences were also found in the interaction of wetland by habitat for carbon dioxide ($P<0.0011$) and methane ($P<0.0021$) indicating that flux rates are responding differently within the two habitats of each wetland. This was most evident at Bokarup Swamp where there were larger differences in carbon dioxide flux between the two habitats. Significant interactions were also found for habitat by sampling period for carbon dioxide ($P<0.0001$) and methane ($P<0.0158$), seen in increased flux rates between habitats in the summer months.

There was a significant three way interaction for both the carbon dioxide analysis and ($P<0.0001$) and the methane analysis ($P<0.0316$), highlighting the complexity of mechanisms affecting gas flux in these systems. Wetlands not only vary in their flux rates depending on hydroperiod and other intrinsic factors, but each one is further influenced by the presence of emergent vegetation and a seasonal cycle.

Oxygen availability within sediments has the potential to impact upon the structure and biomass of gas producing microbial populations. To determine if such relationship existed, average phospholipid concentrations from all depths for all and sampling periods wetlands (except September 1995 when no gas samples were taken) were plotted against the flux of each gas from the corresponding wetland and period. There was significant positive relationship ($P<0.05$, n=125) between sediment phospholipid concentration and carbon dioxide (R^2 0.739) and methane flux (R^2 0.848), indicating that increased microbial biomass in the sediment leads to increased atmospheric gas release.

4.3.2.2 Diurnal methane and carbon dioxide gas ebullition

Low level diurnal patterns of methane and carbon dioxide flux were evident in both habitats and all wetlands. Maximum carbon dioxide and methane production were generally found at 1600 hours and lowest values at 0800 hours (Figures 4.4 a, b & c).

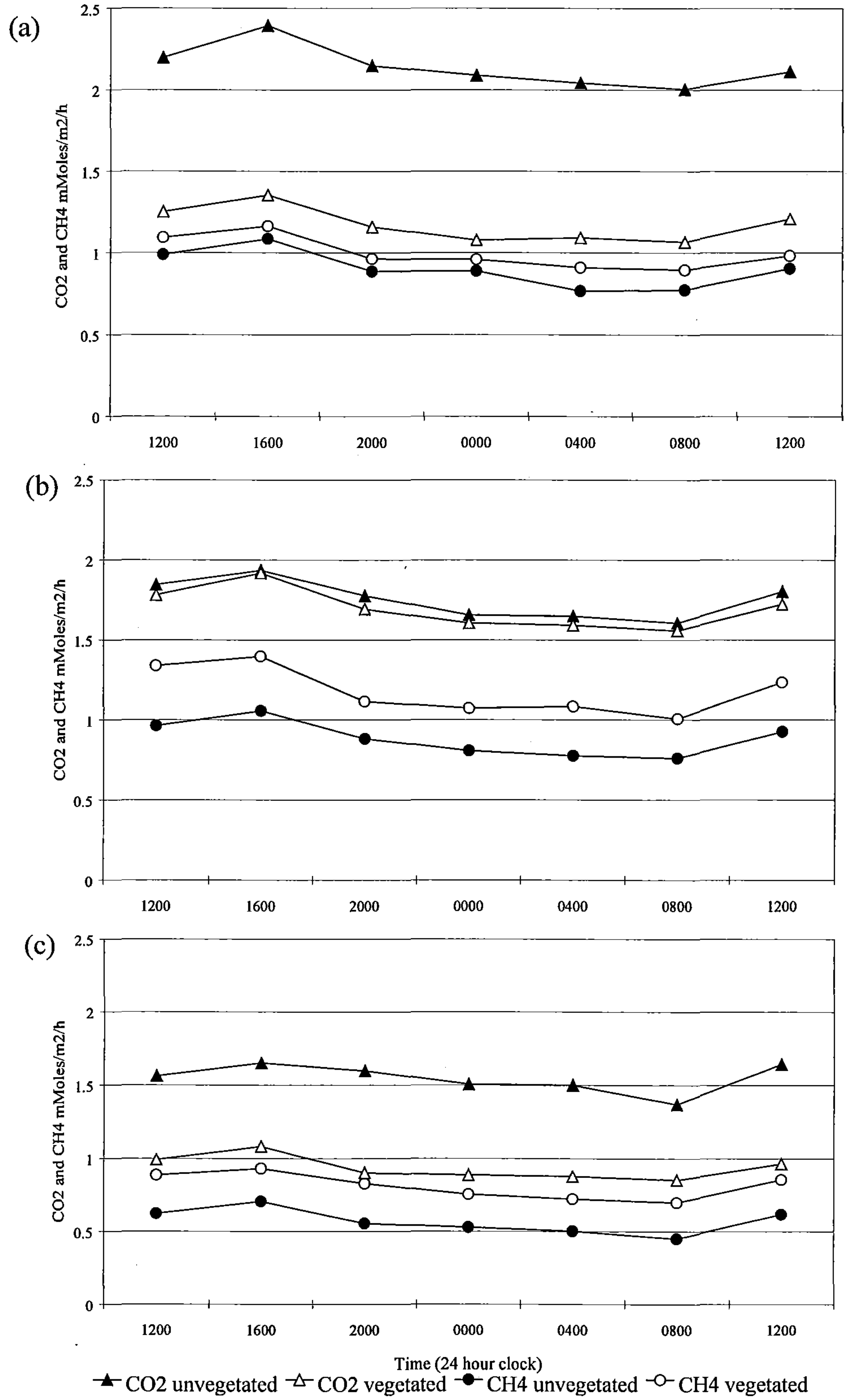


Figure 4.4 Diurnal variation in methane and carbon dioxide flux (mM/m^2/day) from unvegetated and emergent macrophytes at (a) Bokarup Swamp, (b) Kodjinup Swamp and (c) Noobijup Lake in January 1997.

Habitat differences did not alter the timing of the maximum and minimum flux rates. Similar to the field data collected over 18 months, Kodjinup Swamp had the highest overall flux rates and Noobijup had the lowest. Differences between habitats and gases were also similar to the field monitoring, data with the highest flux rates from carbon dioxide in unvegetated areas and the lowest from methane in the same habitat. In all wetlands the flux of carbon dioxide is almost twice that of methane in unvegetated areas.

4.3.2.3 Sediment gas concentrations

The most striking result was the high concentrations of methane in wetland sediments. Methane concentrations were consistently three to four times higher than carbon dioxide on all sampling occasions (Figure 4.5 a, b & c). Concentrations of carbon dioxide were similar between wetlands in all sampling periods, however there was a significant difference ($P<0.0001$) between wetlands for methane (Table 4.5 & 4.6).

Highly significant differences between sampling periods were found for both carbon dioxide ($P<0.0001$) and methane ($P<0.0176$) (Table 4.5 & 4.6). Peak concentrations of sediment gases did not occur at the same time of year for both gases or for each wetland, leading to significant interactions between wetlands and sampling occasion ($P<0.0001$). Peak concentrations of between 400 and 500 ml/L occurred in all wetlands in the warmer summer months of each year. Sediment gas concentrations were unable to be sampled from the macrophyte habitat in Bokarup and Kodjinup Swamps during April to July 1996 due to insufficient water levels for sampling equipment. In Noobijup Lake where permanent surface water was present, the lowest concentrations of methane and carbon dioxide were found in July 1996. Minimum concentrations of each gas occurred during October 1996 in the other two wetlands. These data generally correspond to the peaks and troughs of atmospheric gas flux in each wetland.

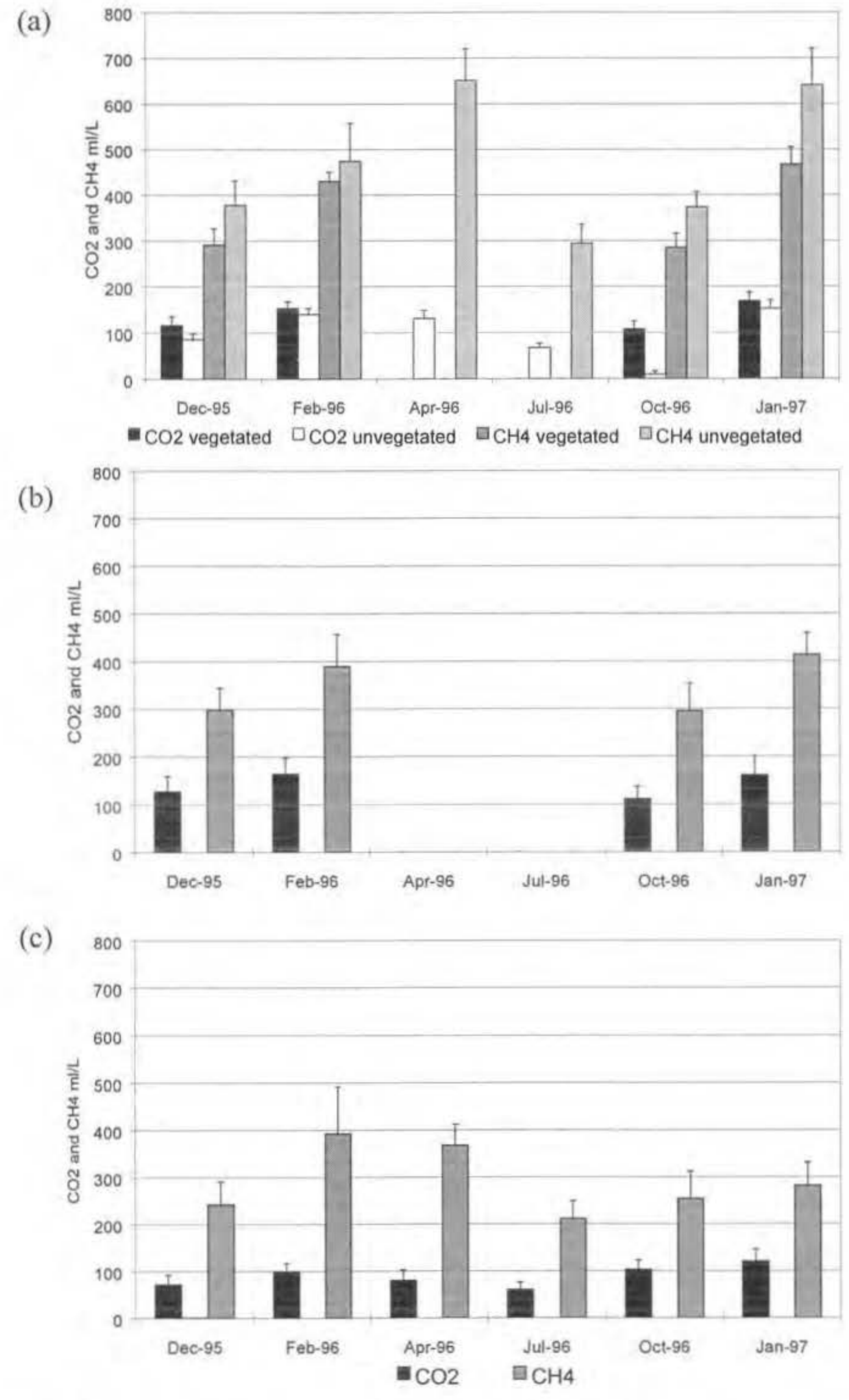


Figure 4.5 Mean *in situ* concentrations of methane and carbon dioxide (ml/L) (±SE) from sediments in unvegetated and vegetated habitats in (a) Bokarup Swamp, and vegetated habitats only in (b) Kodjinup Swamp and (c) Noobijup Lake from December 1995 to January 1997 in Noobijup Lake. Missing values indicate no samples taken.

The sampling of the vegetated and unvegetated habitats in Bokarup Swamp revealed a reverse of the trend found in the atmospheric gas flux data. Higher concentrations of carbon dioxide were found in vegetated sediments and higher concentrations of methane occurred in the unvegetated habitat (Figure 4.5a). Carbon dioxide concentrations were marginally higher in the vegetated habitat in all periods, except where sediment concentrations in the vegetated area were over ten times higher than the vegetated areas in October 1996. Habitat differences for methane concentrations were most pronounced in January 1997.

Table 4.5 Two-way ANOVA results (Wetland by Sampling Period) for *in situ* carbon dioxide concentrations.

Source	df	Sum of Squares	Mean Squares	F-value	*P*-value
Wetland	2	0.07	0.03	3.94	0.05
Sampling Period	5	1.67	0.33	516.31	0.01
Wetland x Sampling Period	10	0.09	0.01	14.79	0.0001

Table 4.6 Two-way ANOVA results (wetland by Sampling period) for *in situ* methane concentrations.

Source	df	Sum of Squares.	Mean Squares	F-value	*P*-value
Wetland	2	1.25	0.68	23.57	0.0001
Sampling Period	5	1.64	0.38	346.77	0.0001
Wetland x Sampling period	10	0.26	0.06	27.74	0.0001

4.3.2.4 Emergent macrophyte leaf gas

Carbon dioxide concentrations displayed little variation between wetland or life stage of the emergent leaf, with concentrations consistently around 75 to 80 ml/L (Figure 4.6). Methane concentrations within emergent *B.articulata* leaves did show variation between wetlands and life stages (Figure 4.7). In both live and senescent leaves, methane concentrations were consistently lower in Kodjinup Swamp. Surprisingly, methane concentrations in all wetlands were highest in senescent leaves, followed closely by live emergent leaves. In contrast to carbon dioxide, methane concentrations were substantially lower in all wetlands in dead *B.articulata* leaves.

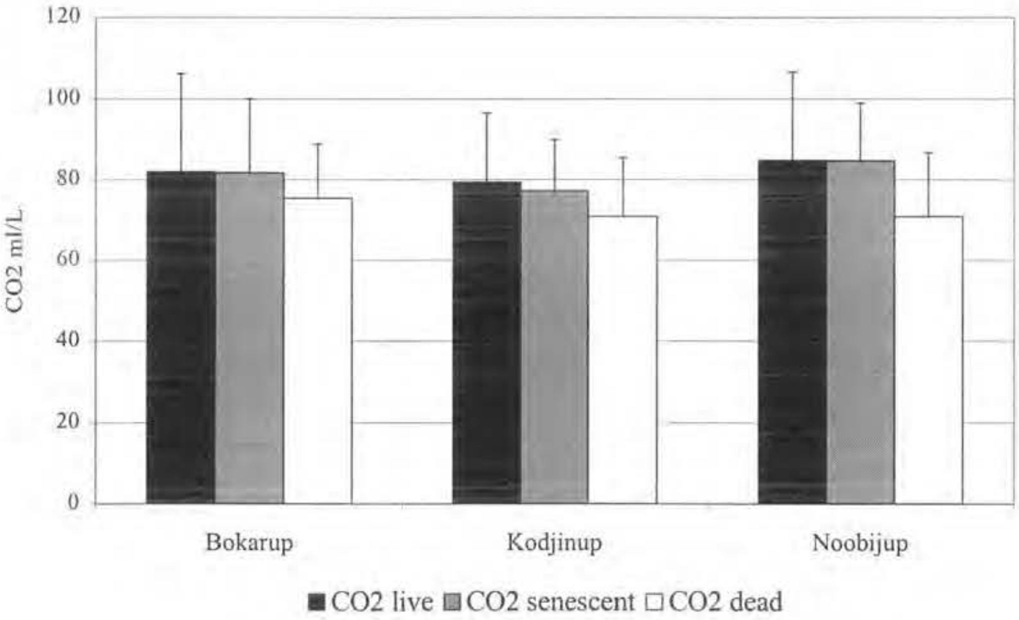


Figure 4.6 Mean carbon dioxide concentrations (ml/L) (±SE) in live, senescent and dead emergent *Baumea articulata* leaves in January 1997 from each wetland.

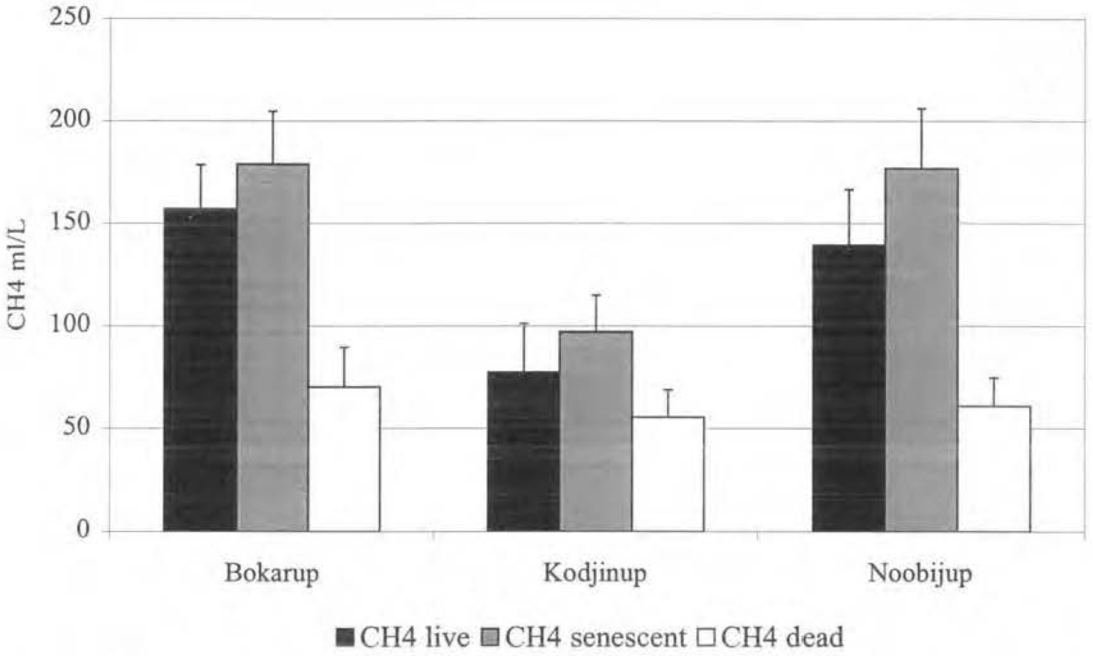


Figure 4.7 Mean methane concentrations (ml/L) (±SE) in live, senescent and dead emergent *Baumea articulata* leaves in January 1997 from each wetland.

4.4 DISCUSSION

4.4.1 Sediment microbial biomass

The high rates of productivity of sediment dwelling bacteria results in them being a major sink of dissolved and particulate organic carbon in aquatic systems. Such microorganisms are responsible for the degradation of organic matter and the cycling of key nutrients and therefore are critical regulators of wetland productivity (Wetzel 1992). Variations in microbial processes within and between wetlands are caused by a variety of factors including the organic matter quality and quantity, hydrology, plant type and dynamics and disturbance (Groffman *et al.* 1996). Recent studies in Australian floodplain wetlands have shown that the hydrological cycle, presence of emergent or submerged vegetation and season all influence the biomass and diversity of sediment microbial communities (Boon *et al.* 1996). These influences are apparent in the study sites, with strong seasonal trends of increased microbial biomass in the summer periods and reduced biomass in the colder months. This also mirrors the trends found in the rates of organic matter supply (Chapter 3). Increased concentrations of sediment microorganisms corresponded to periods of maximum wetland water levels, and temperatures in the wetlands. Significant differences were also found between habitats vegetated by macrophytes and unvegetated habitats, with increased microbial biomass in vegetated areas.

Only few data are available on the biomass of microorganisms in peat soils (eg. Williams & Sparling 1984; Sparling & Williams 1986; Hart *et al.* 1986; Borga *et al.* 1994; Groffman *et al.* 1996; Brake *et al.* 1999). Comparisons between systems are often difficult because the composition and concentration of organic matter in peat soils and the local conditions for microbial decomposition influence microbial biomass (Charman *et al.* 1994). Furthermore, there are a variety of methods which can be used to quantify microbial biomass in sediments. The primary methods for measuring microbial biomass in sediments have involved epifluorescence microscopy (EFM) and cultures or a number of techniques based on biochemical components of cells (eg. Adenosine triphosphate (ATP), muramic acid and phospholipid phosphates, Findlay *et al.* 1989). The analysis of lipids, especially phospholipids, have been extensively used to quantify both viable microbial biomass and community structure from aquatic sediments (eg. White *et al.* 1979; Dowling *et al.* 1986; Rajendran *et al.* 1992; Rajendran *et al.* 1994; Sundh *et al.* 1997). Extensive use of this technique in Australian wetlands by Boon (1991; 1992; 1993; 1994), Boon & Mitchell (1995) and Boon *et al.* (1996) provide examples of the community structure and biomass of microbial assemblages and their interactions with the biota in south eastern Australian floodplain wetlands. Sediment microbial biomass measured using phospholipids was strongly correlated to atmospheric methane flux and carbon dioxide in these wetlands (Section 4.3.2.1). The measurement of phospholipid concentrations from sediments therefore provides a good estimation of viable microbial biomass but also potential rates of microbial decomposition. However, this study only examined total biomass, and so shifts from anaerobic to aerobic microbial communities under exposed conditions were not detected. This shift may have profound effects on the rates of organic matter loss from peat soils.

Consistent significant differences in microbial biomass between the three sediment horizons (0-15, 15-30 and 30-45 cm) were found in all wetlands. These results are consistent with studies in raised bogs which have shown that microbial biomass decreases with depth, influenced by the composition and chemistry of wetland sediments (Borga *et al.* 1994). Aerobic conditions have been shown to be the primary controller of microbial biomass in a range of wetlands with peat soils (Sundh *et al.* 1997). Maximum microbial biomass in the three study wetlands did occur in the surface zones, however, peak biomass did not occur during periods of no surface water when sediments would be most aerobic, suggesting other factors are influencing microbial biomass in these wetlands.

The presence or absence of vegetation can influence both the biomass and depth distribution of microbial communities. Variability in microbial biomass associated with major habitat types have been described for various wetland types and support the significant differences between vegetated and unvegetated habitats in this study. Differences between vegetated and unvegetated habitats decreased with depth, resulting in similar concentrations in the 30 to 45cm horizon. This suggests that the influence of macrophyte roots (or their absence) on sediment biogeochemistry is restricted to the surface 30cm of sediment. Aeration of the rhizosphere by the roots and rhizomes of emergent macrophytes resulted in an increase in microbial biomass in floodplain wetlands (Boon 1991; Boon *et al.* 1996), constructed wetlands (Duncan & Groffman 1994) and rice fields (Bai *et al.* 2000). Changes in community composition were also noted, with a 44% increase in aerobic bacteria in vegetated habitats (Bai *et al.* 2000). Highly labile leachates and decay products from macrophyte litter might be responsible for increased biomass in these habitats (Kirschner & Velimirov 1999).

Significant differences in microbial biomass between wetlands indicate that local conditions, such a hydrologic regime, may influence microbial populations. Alternate wetting and drying cycles has been shown to stimulate the decomposition of organic matter in aquatic systems (eg. Reddy & Patrick 1975; Taylor & Parkinson 1988; Ryder & Horwitz 1995a). A corresponding increase in microbial biomass following rewettting of wetland soils has also been observed (Ryder & Horwitz 1995a; Boon *et al.* 1996; Groffman *et al.* 1996). Both Kodjinup and Bokarup Swamps had significant periods of exposed surface sediments during autumn and winter, yet they responded differently to periods of no surface water. Differences in the response of microbial communities between wetlands to hydrologic regime may be due to intrinsic peat characteristics such as particle size and organic content. Sediment particle size and organic matter content was found to influence microbial biomass in wetland sediments (Sinsabaugh & Findlay 1995; Groffman *et al.* 1996; Brake *et al.* 1999) with decreased biomass associated with decreased particle size. Differing patterns of sediment particle size and organic matter content (Section 2.6.2), may partly explain differences in microbial biomass found between the study wetlands. This indicates that total microbial biomass in some wetlands may be less influenced by exposure of surface sediments and more influenced by peat characteristics.

The importance of high water levels and peak organic matter inputs occurring at the same time to provide conditions conducive to peat accumulation was noted in Chapter 3.

Maximum microbial biomass in all wetlands also occurred during the period of maximum water depths and maximum water temperature. The influence of temperature on microbial processes has been well documented (eg. Dunfield *et al.* 1993; Chapman *et al.* 1996, van Hulzen *et al.* 1999). The strong seasonal trends of increased microbial biomass in the summer periods and reduced biomass in the colder months confirm the influence of temperature in these systems. The response to changes in water column depth can be seen in the final sampling period (Oct 1996 to Jan 1997), where all wetlands recorded their highest biomass at all depths. Temperatures were similar to the previous summer period, however water depth was between 10 and 20cm deeper. Prolonged flooding has been found to increase microbial biomass as a result of severe deoxygenation of the sediments in wetland habitats (Sundh *et al.* 1997). Physico-chemical profiles during the summer period revealed that the water column in all wetlands was strongly stratified, with epibenthic dissolved oxygen levels approaching 0.1mg/L. Similar to the impact on organic matter inputs, changes to the timing and duration of water levels may result in altered rates of sediment microbial decomposition, with subsequent impacts on rates of peat accumulation.

4.4.2 Sediment gas flux

Compared with other methanogenic systems, wetlands with peat soils are unique environments as they have plants growing in anoxic, methane producing, saturated soil. Methane is produced in environments where organic matter accumulates and oxygen is absent. The atmospheric flux of methane is therefore typically high in these wetland environments. A significant positive correlation between sediment microbial biomass and rates of atmospheric fluxes of methane and carbon dioxide indicates the gas production is biogenically derived from the sediment. The net flux of gas is a result of a complex set of interacting controls on production, transport and consumption. The complexity of these mechanisms is highlighted by the significant three way interaction for both carbon dioxide and methane in all wetlands. Wetlands not only varied in their flux rates depending on intrinsic wetland features such as sediment type and hydrological cycles, but each is further influenced by emergent vegetation and a seasonal cycle.

The emissions of both methane and carbon dioxide are extremely variable in both space and time. Underlying variables controlling gas production and release include temperature, pH and redox status (Bridgham & Richardson 1992; Crozier *et al.* 1994), nutrients and salinity (Dise 1993; Prieme 1994), availability of labile soil carbon (Whiting & Chanton 1993), hydroperiod (Crozier *et al.* 1995) and presence of emergent vegetation (Boon & Sorrell 1995). The range of methane flux rates (incorporating all habitats, wetlands and seasons) from 0.327 ± 0.072 to 1.128 ± 0.16 mM/m^2/day are lower when compared to the fluxes from a range of wetland types reviewed by Kiene (1991) for northern peatlands (0.1 to 120 mM/m^2/day), rice paddies 1 to 40 (mM/m^2/day) and northern wetlands (<0.1 mM/m^2/day). Rates of methane flux were also lower than those recorded in south-east Australian floodplain wetlands (eg Sorrell & Boon 1992; Muller *et al.* 1994; Sorrell & Boon 1994; Boon & Sorrell 1995). The lower rates of gas fluxes from the study wetlands suggest their deep peat deposits and overlying water columns result in extremely anoxic peat profiles that severely hinder the biogenic production of methane.

There was an increase in both carbon dioxide and methane flux rates from July to October in all wetlands regardless of their water depth, indicating other environmental factors such as temperature may be providing more control over flux rates than wetting cycles. The temperature dependence of methane production in peat soils has been well documented (eg. Bridgham & Richardson 1992; Schultz *et al.* 1997; Segers 1998; van Bodegom & Stams 1999). Van Hulzen *et al.* (1999) examined the effect of temperatures up to 30°C on methane emissions from peat soils. They found that at low temperatures, the availability of electron acceptors and methanogenic biomass limited methane release. Alternatively, at high temperatures methanogenesis was limited by anaerobic carbon metabolism. Dunfield *et al.* (1993) showed a marked dependence of methane production on temperature with optima in the region of 25 to 30°C, followed by a dramatic fall in production beyond these temperatures. This is supported by Webster & Benfield (1986) who demonstrated a decrease in bacterial biomass when optimal temperatures were exceeded. In this study, the rapid attenuation of temperatures resulting from the thermally stratified water column in all wetlands during the warmer months may have prevented the sediment microbial communities from exceeding their optima. The influence of temperature on methane production is supported by the presence of a seasonal cycle of summer maxima and minimum flux rates in the cooler winter period, however significant interactions indicate multiple controls of gas release.

Fluctuations in the water table have been found to be a controlling factor in production and consumption of carbon gases from wetland sediments (Moore & Knowles 1989). Bokarup and Kodjinup Swamps displayed trends in flux rates of carbon gases that were linked to water table fluctuations. Each wetland displayed a decrease in methane flux and a corresponding increase in carbon dioxide flux during periods of no surface water. It was suggested that changes to hydrostatic pressure from lowering the water table can lead to the degassing and dissolution of substantial volumes of methane in peat sediments (Moore *et al.* 1990; Fechner-Levy & Hemond 1996). Silvola (1986) noted a ten-fold increase in carbon dioxide flux from a Finnish peatland following drainage of surface waters, while drainage of northern peatlands led to a significant decrease in methane production (Freeman *et al.* 1993). The shift from methane to carbon dioxide flux has also been attributed to increased consumption of methane by methanotrophic bacteria in aerobic zones created by reduced water levels or exposed sediments (Kettunen *et al.* 1999). Prolonged exposure of sediments to the atmosphere can also influence methane flux by reducing methanogenic bacterial biomass, as they are unable to recover to pre-drying methane flux rates following rewetting (Crozier *et al.* 1995; Mitchell & Baldwin 1999). The duration and frequency of wetting and drying cycles therefore has a profound influence on the structure of wetland microbial communities, which can directly affect rates of organic matter decomposition from wetland sediments.

Significant differences were evident in the flux rates of methane and carbon dioxide between vegetated and unvegetated habitats. The flux of methane from vegetated habitats was consistently higher than from unvegetated areas in all wetlands. Conversely, the flux of carbon dioxide was consistently higher from the unvegetated sediments in all of the study wetlands. These data are supported by numerous studies that found emergent vegetation can account for up to 90% of the total methane flux to the atmosphere (Crill 1988; Brix *et al.* 1992; Muller *et al.* 1994; Sorrell & Boon 1994; Boon & Sorrell 1995) by providing a direct conduit to the atmosphere. This transport through emergent plants may occur as either simple diffusion or as convective flow, generated by temperature and/or humidity gradients in the aerial shoots of the plants (Brix *et al.* 1992). Numerous studies have demonstrated an increase in atmospheric methane flux provided by emergent vegetation either through static chamber comparisons (Muller *et al.* 1994; Shannon *et al.* 1996) or direct measurements of methane concentrations in the lacunar systems of macrophytes (Sorrell & Boon 1994; Boon & Sorrell 1995; Yavitt 1997; Yavitt & Knapp 1998). *Baumea articulata*, the dominant rush in the study wetlands, generally had higher concentrations of methane than carbon dioxide within live and senescent leaves and lower concentrations in dead leaves, suggesting active transportation of gases by this species. The maintenance of healthy communities of *B.articulata* (live leaves) in these wetlands therefore becomes important in maintaining the processes controlling the transport and release of methane to the atmosphere.

In unvegetated sediments, atmospheric fluxes of methane can occur as either molecular diffusion or bubble ebullition and must pass through the water column before release to the atmosphere. This provides an opportunity for oxidation by methanotrophic bacteria and conversion to carbon dioxide (Kettunen *et al.* 1999). Methane oxidation requires methane as a substrate and oxic conditions, and therefore methanotrophs are most active close to the oxic-anoxic interface where the gradients of methane and carbon dioxide overlap but also in the aerated rhizosphere created by emergent vegetation. (Denier van der Gon & Neue 1996). Oxygen concentrations as low as 0.1mg/L have been shown to support substantial methane oxidation (Rudd *et al.* 1976). Macrophytes rely on the transport of oxygen to below ground structures for aerobic respiration (Armstrong 1978). The oxidation of the rhizosphere is caused partly by enzymatic oxidation but mostly through radial oxygen loss through the root wall. This forms a thin oxidised layer around the roots in an otherwise anoxic environment, creating a habitat for aerobic microorganisms such as methanotrophs (Ando *et al.* 1983). The examination of sediment gases in vegetated and unvegetated habitats in Bokarup Swamp revealed lower methane and higher carbon dioxide concentrations in vegetated areas, providing supporting evidence for increased methane oxidation in these habitats. Elevated fluxes of carbon dioxide from unvegetated sediments, despite very high concentrations of methane in the sediment, suggest that a large proportion of methane in the sediments is oxidised and released to the atmosphere as carbon dioxide.

Diurnal variability may be an important factor when reliably quantifying the loss of carbon from wetlands. Static chambers were used to quantify methane and carbon dioxide flux rates only during daylight hours. Very low variations in the release of methane and carbon dioxide were detected during the summer period in both vegetated and unvegetated habitats and from all wetlands. Diurnal patterns of methane release from aquatic macrophytes have generally followed changes in soil and air temperature (Whiting & Chanton 1992; Mikkelä *et al.* 1995; Thomas *et al.* 1998). Maximum flux rates occurred at around 1600 hours and minimum rates at 0800 hours. However, different patterns of diurnal emissions have been shown between plants that have pressurised flow (driven by solar heating) and plants that rely on molecular diffusion of gases (Chanton *et al.* 1993; Whiting & Chanton 1996; Satpathy *et al.* 1997). Plants with pressurised flow have highly variable flux rates up to four times greater during the daylight (Dacey & Klug 1979). These trends were not apparent in this study, with exceptionally low levels of diurnal variability that were consistent between carbon dioxide and methane and between vegetated and unvegetated habitats. Jedrysek (1999) found the magnitude of the diurnal variation decreased with increased water depth. All wetlands were close to maximum water depth at the time of sampling and displayed prolonged periods of thermal and oxygen stratification. This may have produced relatively consistent conditions within the sediment leading to low levels of diel variability in both vegetated and unvegetated habitats. This low-level variability supports the use of the field data from fixed times as a measure of long-term organic matter losses.

Estimates of the flux of gases from wetland sediments and plants using static chambers have been criticised as altering natural rates of gas flux. Despite this they have been used successfully to examine methane and carbon dioxide fluxes from wetland environments (eg. Chanton *et al.* 1988; Sorrell & Boon 1995; Shannon *et al.* 1996; Vandernat & Middleberg 1998). The use of chambers was necessary in this study as some wetlands had periods of no surface water, making other techniques impossible. Chambers allowed for consistency in method regardless of habitat or water depth. Static chambers are thought to affect air temperature, humidity, wind speed and stomatal pressure (Mosier 1989; Knapp & Yavitt 1992; Healy & Streigl 1993). Increases in humidity and temperature within chambers can affect gradients that control gas diffusion rates across the culm wall of emergent vegetation (Boon & Sorrell 1995). Changes in humidity and temperature within chambers accounted for methane emissions to be underestimated when small chambers (250 ml) were placed around leaves of *Typha* (Knapp & Yavitt 1992). Chambers may also decrease wind-driven mixing and surface turbulence and could result in an underestimate of gas flux. Boon & Sorrell (1995) conducted numerous experiments examining types of disturbances associated with static chambers. Disturbances such as rocking the chamber and the presence of a recirculation fan produce little variation in methane flux rates. Disturbance to the sediment resulted in immediate increases in methane concentrations within the chamber as methane rich bubbles were released from the sediment. These data were important in designing and deploying the chambers in this study to remove sources of variability between samples. Consistent methods were used throughout the field study and resulted in a linear rate of methane and carbon dioxide flux ($R^2 > 0.9$) which supports the accuracy of these measurements.

4.4.3 Summary

This chapter quantified the transformations (microbial biomass) and losses (carbon dioxide and methane gas flux) of organic matter from Bokarup Swamp, Kodjinup Swamp and Noobijup Lake. The sediment microbial biomass, when combined with the data on organic matter inputs from Chapter 3, form the total input of organic matter into each wetland. The flux of methane and carbon dioxide from wetland sediments and emergent vegetation provides the total organic matter losses from each wetland. These data form the basis of the carbon budget (Chapter 6) which is then used in the descriptive model to examine peat accumulation rates in each wetland (Chapter 7).

Transformations (sediment microbial biomass) of organic were strongly influenced by a seasonal cycle of summer maxima and winter minima that corresponded to periods of maximum wetland water levels and temperatures. Significant differences in microbial biomass between the three sediment horizons (0-15, 15-30 and 30-45 cm) found in all wetlands were consistent with other studies in similar peat deposits. Temperature appears to be the controlling factor of sediment microbial biomass in all of the study wetlands, although significant differences between wetlands may result from intrinsic wetland features such as local hydrology, the distribution of emergent vegetation and peat characteristics such as organic matter content.

Organic matter losses (carbon dioxide and methane) were also strongly influenced by a seasonal cycle, following the same trends as the sediment microbial biomass. The presence or absence of emergent vegetation exerted a strong influence on the flux rates of methane and carbon dioxide from all of the study wetlands. Methane flux rates were significantly higher through emergent vegetation indicating *B.articulata* acts as a conduit for gas transport from the sediments to the atmosphere. Conversely, rates of carbon dioxide flux were higher from unvegetated sediments, which may have resulted from the aerobic consumption of methane by methanotrophic bacteria in surface sediments or in the water column. Methane flux rates from the study wetlands were lower than those recorded for other peat forming systems and may be due to the extremely anoxic, deep peat deposits limiting the biogenic production of methane. Low level diurnal patterns of carbon dioxide and methane flux from vegetated and unvegetated areas were evident in all wetlands. These patterns were similar to other studies that found flux rates follow changes in soil and air temperature, with maximum flux at peak temperatures.

These results show that maximum organic matter inputs (Chapter 3) and losses occur at the same time of year, the period of maximum water levels and temperatures. The coincidence of these processes is important as the difference between inputs and losses of organic matter control the rate of peat accumulation. The significant difference between wetlands for inputs and losses of organic matter indicates that peat accumulation may be occurring at different rates in different wetlands and is influenced by localised factors such as hydrology, vegetation, peat characteristics or disturbance history.

CHAPTER 5

ORGANIC MATTER TRANSFORMATIONS IN WETLAND FOOD WEBS - A STABLE ISOTOPE ANALYSIS

5.1 INTRODUCTION

Microbial transformations of organic matter and the atmospheric flux of carbon dioxide and methane are major pathways for the breakdown of organic material (Chapter 4). Aquatic macroinvertebrates are also involved in organic matter transformations, converting carbon into their own biomass and acting as a potential loss of organic matter through flying adult stages. Emergent macrophyte leaf litter (predominantly *B.articulata*) was identified as the dominant source of organic matter contributing to peat accumulation in all wetlands (Chapter 3). The carbon produced by macrophytes has traditionally been thought to enter aquatic food webs as detritus, rather than direct herbivory (Webster & Benfield 1986; Mann 1988). The importance of macrophyte litter as a carbon source for aquatic macroinvertebrates in the study wetlands is unknown, and therefore their impact on the breakdown of this material is also unknown. The ability of the stable isotope technique to discriminate between sources of organic matter will help identify those sources important to wetland foodwebs and examine the role of aquatic macroinvertebrates in the breakdown of different sources of organic matter. Furthermore, the identification of organic matter sources important to aquatic foodwebs in these wetlands will determine the impact of wetland management on the supply of different organic matter sources.

Wetland ecosystems in forested landscapes can link autochthonous and allochthonous carbon sources and are characterised by complex food webs that span both terrestrial and aquatic environments (Haines & Montague 1979). Traditionally, carbon resources used by consumers have been identified by gut contents analysis, laboratory or field feeding observations or radioisotopic tracing (Rounick & Winterbourn 1986). However, because of the complex intermeshing of carbon pathways and invisible routes of carbon flow in aquatic systems, these methods prove inadequate. Stable isotopes of $\delta^{13}C$ and $\delta^{15}N$ provide an alternative approach to elucidate carbon pathways and processes (Peterson & Fry 1987). The technique utilises differences in the natural abundance of the stable carbon (^{12}C and ^{13}C) and nitrogen (^{14}N and ^{15}N) isotopes as tracers which move with little or predictable alteration through food chains (Peterson & Fry 1987). Differences in $\delta^{13}C$ among plants using the Calvin cycle (C_3), Hatch-Slack cycle (C_4), and Crassulacean acid metabolism (CAM) photosynthetic pathways are due to differences in their fractionation processes (Lajtha & Marshall 1994). Fractionation of carbon isotopes can therefore only occur during photosynthesis, with the isotopic composition of plant material remaining unchanged throughout decomposition (Haines & Montague 1979). Numerous food web studies have demonstrated that the isotopic composition of animal tissue reflects that of the diet with only slight modification (eg. Zohary *et al.* 1994; Gu *et al.* 1997; Kwak & Zelder 1997). Consumers are expected to be within 2‰ enriched and 1‰ depleted of the mean $\delta^{13}C$ (Bunn & Boon 1993) and 2 to 5‰ enriched relative to their diet in $\delta^{15}N$ (Minagawa & Wada 1984). Stable isotopes possess the advantage over more traditional techniques of reflecting only the material actually assimilated and incorporated into tissue, reflecting the long term diet of consumers (Peterson & Fry 1987).

Stable isotope analysis has been used widely in food web studies of terrestrial (Boutton 1994), marine (Fourqurean *et al.* 1997), estuarine (Schlacher and Wooldridge 1996) and freshwater systems (Keough *et al.* 1996). Most studies have used carbon isotopes to examine energy flow between primary producers and consumers and links among consumers and nitrogen to determine the position of organisms in foodweb structure. This technique has been used successfully to elucidate trophic interactions in a variety of Australian habitats from intertidal marine systems (Boon *et al.* 1997; Loneragan 1997), sub-tropical streams (Bunn *et al.* 1997), lowland rivers (Burns 1997; Sheldon & Walker 1997) and floodplain billabongs (Bunn & Boon 1993). Additionally, Bunn & Boon (1993) were able to reliably discriminate between allochthonous and autochthonous sources and between autochthonous sources such as algae, biofilms and emergent and submergent macrophytes. Despite the ability of stable isotopes to elucidate trophic pathways this technique has rarely been employed in peatland systems, where studies are restricted to northern hemisphere freshwater marshes (Neill & Cornwell 1992; Jacobo & Veron 1995). Isotope studies in these habitats focus on wetland palaeoecology, using the technique to identify plant sources in peat profiles (Ayliffe *et al.* 1996; Grocke 1998) and processes of isotope depletion through bacterial consumption (Rask & Schoenau 1993; Hornibrook *et al.* 1997). Peatlands provide an ideal opportunity to use stable isotopic analysis to elucidate food web interactions in a habitat where detrital energy cannot be determined visually and the dominance of the detrital pathway can obscure the origins of organic matter to food webs.

France (1996) demonstrated that when organisms utilise a mixture of autochthonous and allochthonous energy sources the true enrichment of ^{13}C might be masked. Thus, stable isotope analyses should not be used alone in determination of invertebrate diets. A simpler, more widely used technique has been to infer food quality of different carbon sources from the carbon to nitrogen ratio (C:N), with a lower ratio indicating a more easily digestible food source (White *et al.* 1979). This technique has been used for a variety of habitats including fresh water wetlands (Royer & Minshall 1997), lowland rivers (Sheldon & Walker 1997), mangroves (Lee 1997) and marine systems (Fourqurean *et al.* 1997) to demonstrate a preference by invertebrate grazers and detritivores for food with lower C:N. Steinmann (1996) recognised algae as a dominant source of carbon in freshwaters and summarised the chemical composition of different algal groups and establishing C:N ranges for major algal orders.

This chapter examines the trophic interactions of aquatic foodwebs in Bokarup Swamp, Kodjinup Swamp and Noobijup Lake using δ^{13}C and δ^{15}N isotopic signatures of dominant sources and consumers of organic matter, and C:N ratios to examine the palatability of the different sources to aquatic macroinvertebrates.

5.2 METHODS

5.2.1 Sample collection

At each wetland replicate samples of dominant autochthonous and allochthonous sources of organic material were collected. Samples were collected during the sampling periods in April 1996 (Autumn), July 1996 (Winter), October 1996 (Spring) and January 1997 (Summer) (see Section 2.4). Bokarup and Kodjinup Swamps were not sampled in April 1996 as they had insufficient surface water for sampling. Planktonic algae were not collected from any of the wetlands due to their very low abundance (concentrations peaked at 8.87 ± 0.17 μg/L, see Section 3.3.3) making isolating phytoplankton difficult.

Four replicate samples of the following sources were collected on each sampling occasion:

- Attached, senescent leaves from upland plants (*M.raphiophylla* and *E.rudis*) were collected from plants at the edge of the wetland basin. Replicate samples were collected randomly from individual trees adjacent to four of the five allochthonous litter traps (locations in Plates 3.1a, b & c).

- Attached, senescent leaves from the dominant emergent macrophytes of *B.articulata, B.preisii* & *B.arthrophylla* were collected from within the water column in each wetland. All samples were thoroughly scrubbed and rinsed to remove epiphytic growth. Replicate samples were collected randomly from individual macrophytes adjacent to four of the five autochthonous litter traps (locations in Plates 3.1a, b & c).

- Rhizomes and roots from *B. articulata* were removed from the surface 15cm of sediment using a corer. All samples were thoroughly scrubbed and rinsed to remove sediment from the plant material. Replicate samples were collected randomly from individual macrophytes adjacent to four of the five autochthonous litter traps (locations in Plates 3.1a, b & c).

- Leaves from dominant submerged macrophytes (*Nymphoides, Triglochin*, and *Myriophyllum*) were collected from within the water column in each wetland. All samples were thoroughly scrubbed and rinsed to remove epiphytic growth. Replicate samples were collected from random locations within each wetland.

- Biofilms were collected from artificial substrates (glass slides) in vegetated habitats of each wetland using the methods outlined in Section 3.2.4. Biofilms were collected from vegetated and unvegetated habitats in Bokarup Swamp only. Replicate samples were collected from individual artificial substrata deployed in each wetland (locations in Plates 3.1a, b & c).

- Organic detritus from the surface layer of sediment was collected from each wetland. All samples were washed through a 1mm sieve to remove large particles of plant material. Samples were collected from random locations within each wetland.

All samples were placed on ice in the field and frozen within 6 hours of collection. In the laboratory replicate samples were oven dried at 90°C until constant weight and ground into a fine powder using a mortar and pestle. The methods of Dzurec *et al.* (1985) were used in the preparation of soil organic matter samples. Once prepared, the four replicate samples were divided into two pooled samples, each containing two original replicates. Samples were pooled to increase the representativeness of each replicate source given the constraints of limited replication due to costs of samples. Pooled, replicate samples were wrapped in foil and stored in a desiccator pending analysis.

Four replicate samples of the following heterotrophic organisms were collected on each sampling occasion:

- Macroinvertebrates

- Small vertebrates (tadpoles, fish)

- Zooplankton

Macroinvertebrates and small aquatic vertebrates were sampled using integrated sweeps covering a 20 m transect from the edge towards the centre in random locations in each wetland using a standard square framed 500 µm mesh net. A minimum of 10 sweeps was taken in each wetland on each sampling occasion to a maximum of 16. The number of sweeps was determined by the relative abundance of dominant taxa on each sampling occasion and ability to gain sufficient biomass for analysis (7 to 10mgDW per sample for duplicates of 2 replicate samples) for each of these taxa. The contents of the net were passed through 4 mm, 2 mm, 1 mm and 500 µm and sorted live on site. Individuals from all sweeps were separated by Order level classification in the field to determine their abundance and the number of sweeps necessary to gain sufficient biomass for analysis. A 125 µm mesh plankton sampler was used to sample zooplankton using the same methods as the square framed net. Zooplankton samples were repeatedly passed through 125µm mesh to remove detrital material.

All consumer organisms were kept alive in aerated, distilled water for 12 hours to void their gut contents. Zooplankton and microinvertebrate samples were concentrated by passing through 125 µm mesh before being placed into vials and frozen. In the laboratory macroinvertebrate samples were defrosted, re-identified and pooled at Family level classification. Pooled samples were divided into 4 replicate samples. Replicate samples were acid washed (according to Bunn *et al.* 1995) in 1M HCl and rinsed in 4 washes of distilled water to avoid contamination of organic carbon from the carbonate fraction of the exoskeleton (Haines & Montague 1979). Samples of muscle tissue were removed from the small vertebrates for determination of their isotopic signature. In the laboratory pooled samples were oven dried at 90°C until constant weight and ground into a fine powder using a mortar and pestle. Once prepared, the four replicate samples were divided into two pooled samples, each containing two original replicates. Pooled, replicate samples were wrapped in foil and stored in a desiccator pending analysis.

5.2.2 Analysis

Seven to 10 mg of each pooled replicate was weighed into each of two capsules. This creates duplicates of two replicates of each organic matter source and consumer. Each duplicate sample was analysed for their δC and δN composition and percentage elemental C and N using an isotope ratio mass spectrophotometer (Europa Tracermass). The analysis was carried out in the School of Natural Sciences, Edith Cowan University, Perth, Western Australia. Carbon and nitrogen delta values were calculated against a conventional standard (PDB Carbonate and air N_2 respectively) according to the following equation:

$$\delta X = \{(R_{sample} / R_{standard}) - 1] \times 1000 \text{ (‰)}$$

where $X = \delta^{13}C$ or $\delta^{15}N$ and $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$.

Incomplete combustion due to insufficient sample weight, and excess carbon leading to saturation of the detector led to no result obtained for some sources (particularly the sediment samples) and consumers (such as Ostracods, Cladocerans and Copepods with small sample weights).

5.3 RESULTS

5.3.1 Bokarup Swamp ($\delta^{13}C$, $\delta^{15}N$ and C:N)

Surface sediments were consistently the most depleted source of carbon within the wetland (Figure 5.1). Sediment $\delta^{13}C$ values were most depleted in summer at –38.69‰ with values in winter and spring around -35‰. Biofilm $\delta^{13}C$ values were depleted in spring and enriched in winter, ranging from –33.96‰ ± 0.2 to –32.78‰ ± 0.5 in the open water habitat and –32.78‰ ± 0.5 to –30.71‰ ± 0.1 in the emergent macrophyte habitat. Values were most depleted in spring/summer and in open water. Most emergent macrophyte species had $\delta^{13}C$ values similar to each other, generally between –25‰ and –28‰, except *B.arthrophylla* that was a slightly enriched source in summer and winter. There were distinct seasonal variations in $\delta^{13}C$ values for emergent macrophytes, but no clear seasonal trends were evident between species despite similar growth habits. The submerged macrophyte *Nymphoides* showed little temporal variation with values in the range of emergent macrophytes. *Triglochin*, another submerged macrophyte exhibited a large seasonal variation of around 4‰, with values more depleted than other macrophyte sources in winter (-28.5‰ ± 0.5) and spring (-29.03‰ ± 0.08). Fringing species of *M.raphiophylla* and *E.rudis* displayed very little seasonal variation. *E.rudis* had $\delta^{13}C$ values in a similar range to the emergent macrophytes, however, *M.raphiophylla* had values around –30‰, and consistently more depleted than the other plant sources.

The C:N values for Bokarup Swamp indicate that very few of the carbon sources are available for direct use by primary consumers (Table 5.1). Biofilms and submerged macrophytes had the lowest ratios, generally below 15, therefore most digestible of the available food sources measured. However, *Triglochin* had a marked increase in its C:N value in winter and spring to 32.1. The leaves of the emergent macrophytes consistently had the highest ratio, with values of up to 78.94 found in *B.arthrophylla* leaves. As with the δC^{13} values there were large seasonal variations within the emergent macrophytes, but no trends apparent for all species.

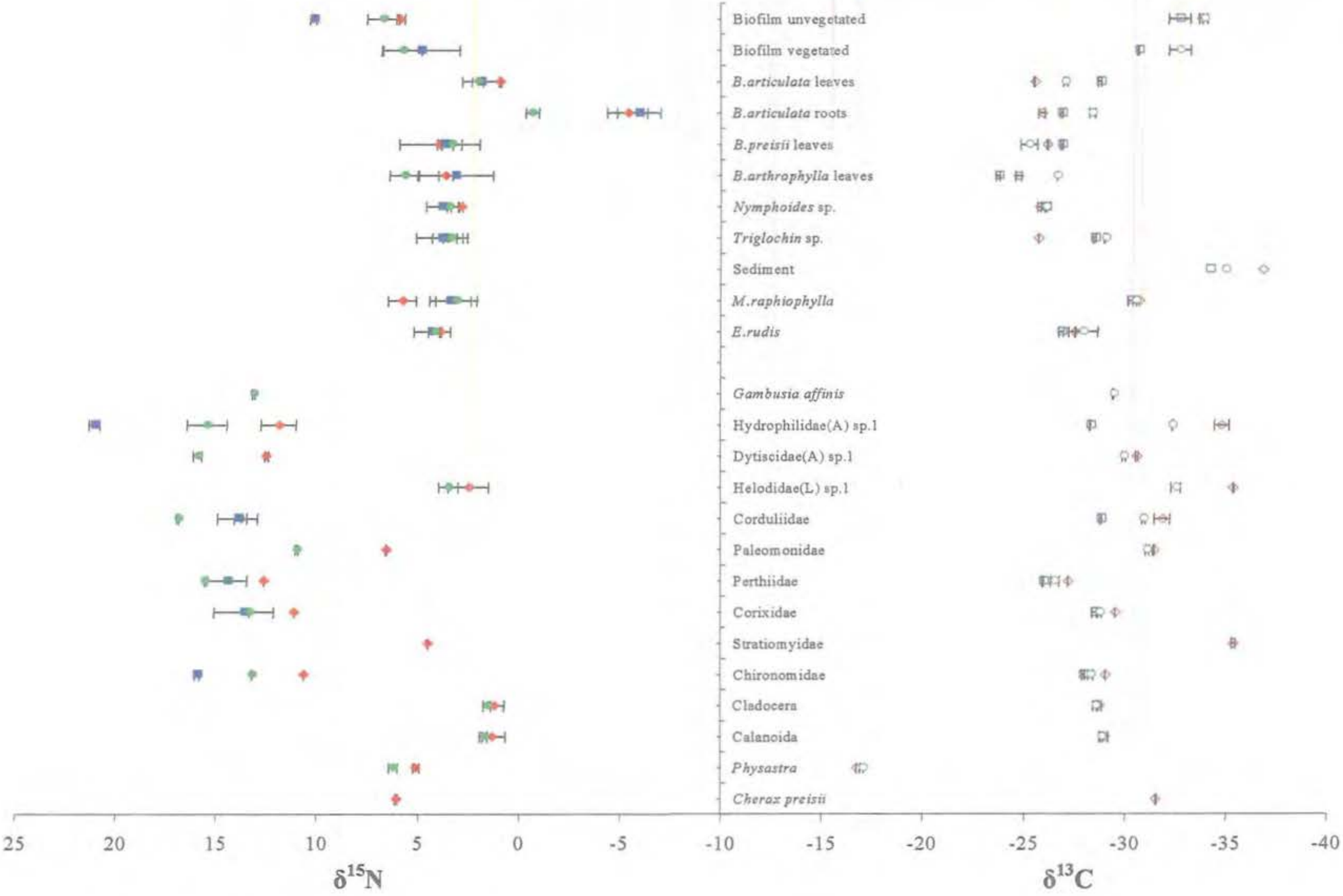


Figure 5.1. $\delta^{13}C$ and $\delta^{15}N$ isotopic signatures (mean ± SE) for dominant carbon sources and sinks in Bokarup Swamp in Summer, Winter and Spring. (A) Adult, (L) Larvae. n = 1 where no standard errors are shown. Winter δN ■, Spring δN ●, Summer δN ◆: Winter δC □, Spring δC ○, Summer δC ◊.

Table 5.1. C:N values (±SE) for sources of organic matter from Bokarup and Kodjinup Swamps and Noobijup Lake in Summer, Autumn, Winter and Spring.

	Summer	*S.E*	**Autumn**	*S.E*	**Winter**	*S.E*	**Spring**	*S.E*
Bokarup Swamp								
Biofilm unvegetated	13.61	*0.02*			10.34	*0.23*	11.73	*1.06*
Biofilm vegetated					10.45	*1.09*	13.33	*0.29*
B.articulata leaves	64.73	*0.08*			38.03	*0.70*	58.08	*1.08*
B.articulata roots	28.08	*1.15*			23.69	*1.02*	31.30	*0.22*
B.preisii leaves	39.76	*1.00*			66.80	*0.96*	45.34	*1.18*
B.arthrophylla leaves	53.36	*0.50*			78.94	*0.92*	65.33	*2.07*
Nymphoides sp.	11.72	*0.16*			9.98	*0.16*	16.76	*1.42*
Triglochin sp.	9.99	*0.62*			19.87	*1.34*	32.21	*2.13*
M.raphiophylla	29.00	*0.26*			37.30	*0.59*	32.47	*1.51*
E.rudis	25.44	*0.20*			33.62	*0.75*	35.96	*0.11*
Kodjinup Swamp								
Biofilm vegetated	13.32	*0.33*			10.93	*0.35*	10.08	*0.55*
B.articulata leaves	79.58	*1.03*			48.37	*1.00*	54.59	*0.29*
B.articulata roots	47.14	*3.25*			29.07	*3.20*	26.83	*0.52*
Nymphoides sp.	13.25	*3.68*			16.76	*3.33*	16.73	*0.88*
Triglochin sp.	9.97	*0.25*			10.92	*0.55*	9.78	*2.03*
M.raphiophylla	27.82	*0.31*			27.07	*0.33*	31.43	*1.08*
E.rudis	20.88	*0.21*			35.75	*0.23*	34.75	*1.08*
Noobijup Lake								
Biofilm vegetated	15.15	*0.73*	13.37	*0.06*	10.97	*0.49*	13.41	*1.19*
B.articulata leaves	64.81	*0.22*	65.58	*0.80*	47.61	*0.28*	55.59	*0.15*
B.articulata roots	28.50	*0.30*	30.65	*0.26*	29.11	*0.93*	27.06	*0.39*
B.arthrophylla leaves	45.65	*0.19*	42.55	*0.66*	68.96	*0.25*	69.30	*0.27*
Nymphoides sp.	11.10	*0.41*	18.66	*1.35*	16.43	*1.73*	16.91	*1.92*
Triglochin sp.	11.48	*0.28*	8.35	*1.46*	11.93	*1.20*	10.22	*0.70*
Myriophyllum sp	19.80	*0.65*	21.31	*0.84*	20.66	*2.08*	24.25	*0.16*
M.raphiophylla	27.67	*0.62*	25.71	*0.18*	35.13	*2.99*	33.64	*0.42*
E.rudis	19.47	*3.59*	17.59	*2.64*	29.13	*1.12*	35.15	*0.12*

The two fringing species, *M.raphiophylla* and *E.rudis* both had C:N values around 25 to 35, mid way between submergent and emergent macrophytes.

Primary consumers such as Chironomidae, Perthiidae, Calanoida and Daphnia, all of which can consume a variety of plant parts, algal cells and bacteria, were identified as first order consumers in Bokarup Swamp. Isotopic signatures of these taxa varied little seasonally and were generally too depleted in $\delta^{13}C$ for macrophytes to be the sole source of carbon. During spring and summer when biofilm biomass was high, a combination of emergent macrophytes and biofilm would produce values in the range seen in these taxa. In winter when biofilm biomass was lower, $\delta^{13}C$ values of first order consumers are closer to macrophyte values, particularly *Triglochin*. Stratiomyidae had a carbon isotopic signature too depleted at –35.4‰ ± 0.1 to have consumed any carbon source measured. *Physastra* are known biofilm scrapers, but had values far more enriched than any potential source. The largest primary consumer sampled, *Cherax preisii*, had a carbon isotopic composition depleted compared to that of all macrophytes at –31.53‰ ± 0.3.

Higher level consumers such as Coleoptera (Hydrophilidae, Dytiscidae and Helodidae) and Odonata (Corduliidae) had large seasonal variations, with consistent trends of winter enrichment and summer depletion. In winter the $\delta^{13}C$ of these taxa are similar to many of the primary consumers indicating they may be a large food source at this time. However, the isotopic composition of these organisms in the other seasons is too depleted for these primary consumers to constitute their sole diet. *Gambusia holbrookii*, an introduced fish had a signature of –29.45‰ ±0.4 in spring, indicating a diet of primary consumers such as the Chironomidae and Zooplankton.

The $\delta^{15}N$ values of most sources are around 3 to 5‰, with the biofilm in both habitats slightly enriched. *B.articulata* was slightly enriched to all other macrophytes. The $\delta^{15}N$ values for Cladocerans and Calanoid Copepods are too depleted at around 1‰ to have come from any source measured. Helodidae larvae also have a $\delta^{15}N$ signature more depleted than all measured sources. The $\delta^{15}N$ values for *Cherax preisii* are slightly enriched from that of the emergent macrophytes indicating it may be deriving its carbon from the detritus. Higher order consumers had enormous variability in their nitrogen isotopic composition, such as the predator Hydrophilidae, varying from 11.86‰ ± 0.8 in summer to 21.00‰ ± 0.2 in winter. This indicates that many of the higher order consumers are changing their diet seasonally depending on available food sources. This seasonal trend is not apparent in the primary consumers. A major anomaly in the dataset is the lack of $\delta^{15}N$ values between the primary and higher consumers. There is a gap of around 12‰ between the zooplankton and predatory organisms indicating missing trophic levels in the food web of this wetland.

5.3.2 Kodjinup Swamp ($\delta^{13}C$, $\delta^{15}N$ and C:N)

Kodjinup Swamp had the least variety of macrophyte carbon sources with the wetland basin dominated by monospecific stands of the emergent macrophyte *B.articulata*, with *Nymphoides* and *Triglochin* in the shallow edge margins. *B.articulata* leaves had similar $\delta^{13}C$ values in summer and spring around –27‰, however, in winter the isotopic signature was depleted to –29.49‰ ± 0.1 (Figure 5.2). Roots from the emergent macrophyte showed little seasonal variation with values around –28‰ throughout the year. The submergent macrophyte *Nymphoides* showed little temporal variation with values in the range of *B.articulata*. *Triglochin*, the other submergent macrophyte exhibited a large seasonal variation of around 2.5‰, with values consistently enriched to other source in all seasons. Sediments and biofilms were again the most depleted carbon source in the wetland. Sediment $\delta^{13}C$ values were most depleted in summer at –38.67‰ and most enriched in spring at -33.76‰. Biofilms carbon isotope ratios showed little seasonal variation with values ranging from –37.00‰ ± 0.5 in summer to –36.00‰ ± 0.8 in spring. The fringing species of eucalypt, *E.rudis*, had $\delta^{13}C$ values in a similar range to the emergent macrophytes with a seasonal trend of winter enrichment (-26.5‰ ± 0.1) and spring depletion (-28.96‰ ± 2.2). *M.raphiophylla*, the other littoral tree species had values around –30‰, consistently more depleted than the other plant sources.

As with Bokarup Swamp, the C:N values for Kodjinup Swamp indicate few sources of carbon are available for direct use by primary consumers (Table 5.1). Biofilms and the two species of submerged macrophytes had C:N ratios generally below 17, making them the most digestible carbon sources measured. *Triglochin* had the lowest C:N ratios in all

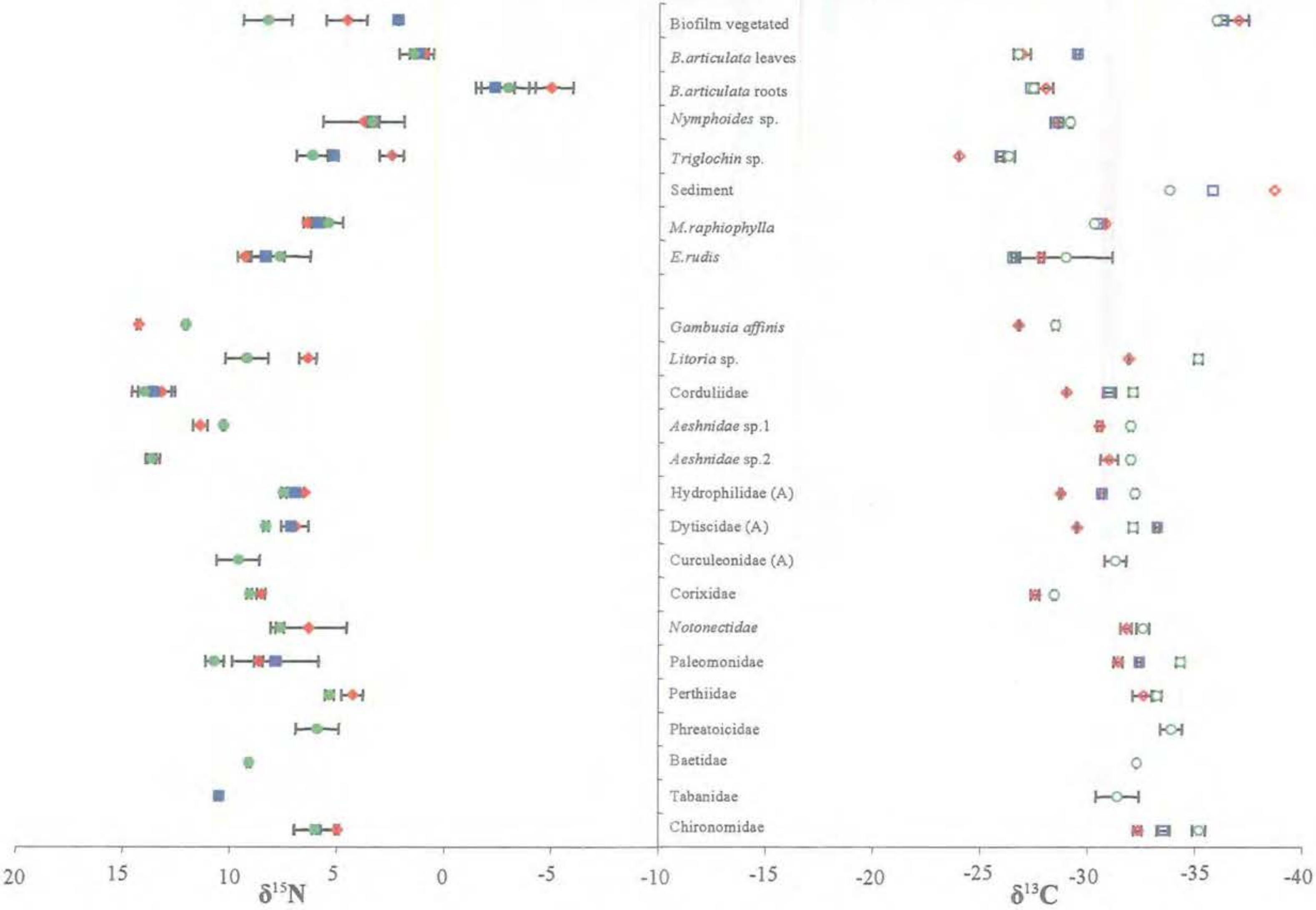


Figure 5.2. δ^{13}C and δ^{15}N isotopic signatures (mean ± SE) for dominant carbon sources and sinks in Kodjinup Swamp in Summer, Winter and Spring. (A) Adult, (L) Larvae. n = 1 where no standard errors are shown. Winter δN ■, Spring δN ●, Summer δN ◆: Winter δC □, Spring δC ○, Summer δC ◊.

seasons, with values ranging from 9.97 ± 0.2 in summer to 10.92 ± 0.5 in winter. The leaves of *B.articulata* had the highest C:N ratios in all seasons. Large seasonal variations were evident from this source, lowest in winter (48.37 ± 1.0) and peaking in summer (79.58 ± 1.1). The roots of this macrophyte showed a similar trend of maximal values in summer, but ratios up to half those found in the leaves. The two fringing tree species had ratios between the more digestible submergent sources and the emergent macrophyte leaves. *E.rudis* showed a large seasonal variation with a low C:N ratio of 20.88 ± 0.2 in summer, which increased to around 35 in winter and spring.

In general, the $\delta^{13}C$ values of primary consumers fell between the macrophyte signatures (~ -27‰) and those of the biofilm (~ - 36‰), indicating a combination of carbon sources would most likely constitute their diet. All primary consumers had depleted $\delta^{13}C$ values in spring, and enriched values in summer, indicating their reliance on biofilms as a food source during spring. The collector-grazers, particularly the Chironomidae and Palaeomonidae displayed a large seasonal variation in their carbon signatures of around 3 to 4‰ that did not display the same pattern of seasonality as potential sources. The tadpoles also displayed a large seasonal variation, with a carbon isotopic signature of –35.15‰ ± 0.2 in spring suggesting a diet of biofilms or becoming a secondary consumer and using lower organisms such as Chironomidae as a food source. However, in summer the carbon signature of tadpoles becomes more enriched indicating a change from a biofilm dominated diet to one that includes more macrophyte tissue, or the increased consumption of primary consumers. Zooplankton were not sampled from this wetland in any season due to very low abundances.

As with Bokarup Swamp, secondary consumers showed a large seasonal variation in their carbon isotopic signatures, with the majority of taxa being most depleted in spring and most enriched in summer. This matches the seasonal trend displayed by the primary consumers. The Coleopterans and Odonates that make up the majority of the secondary consumers all have carbon isotopic signatures that are more enriched than those of the range of primary consumers measured. This is particularly evident in summer when secondary consumers were up to 4‰ enriched from their potential sources and so could not be eating many of the primary consumers measured. In spring there is surprising uniformity in the $\delta^{13}C$ signatures of most secondary consumers, all falling within the range of potential carbon sources from lower consumers. In winter there is a distinct lack of primary consumers present in the wetland, with only Palaeomonidae shrimp and Chironomidae in sufficient numbers to be sampled. Carbon isotopic signatures of secondary consumers during winter are within the range to be consuming these organisms. As predatory organisms, the Corixidae and the *Gambusia* both have signatures too enriched during spring and summer to come from any measured source.

The $\delta^{15}N$ values of sources showed great variability both seasonally and between taxa. Biofilm nitrogen signatures varied greatly being most depleted in winter (2.16‰ ± 0.1) and most enriched in spring (8.26‰ ± 1.1). The submergent macrophyte *Triglochin* also displayed marked seasonality, with the summer value of 2.5 ‰ ± 0.6 markedly enriched to the winter and spring samples. *B.articulata* was again the macrophyte with the most depleted $\delta^{15}N$ signatures, with its roots consistently being the most depleted source.

The $\delta^{15}N$ data for Kodjinup swamp indicate distinct trophic levels within the wetland. Little seasonal variability is apparent in the $\delta^{15}N$ data indicating the majority of consumers maintain their trophic position but change food sources seasonally. The Perthiidae, Phreatiocidae, Chironomidae and Notonectidae all have nitrogen signatures that are depleted to all other consumers. Potential sources for these taxa are biofilm in spring and summer or macrophyte tissue. However, these taxa are potentially omnivorous feeders, with the Notonectidae and Corixidae more predatory organisms. These data suggest that lower order consumers such as the Daphnia and Copepoda that were found in Bokarup Swamp are present in this wetland but not in sufficient numbers to sample. The tadpoles, Palaeomonidae and Baetidae have signatures that support the $\delta^{13}C$ data for their reliance on biofilm as a food source. The $\delta^{15}N$ data show a slight enrichment of the Coleoptera from many of the primary consumers. The Odonata, together with *Gambusia holbrookii* are the most enriched taxa sampled in the wetland highlighting their position as high order consumers.

5.3.3 Noobijup Lake (δ^{13}C, δ^{15}N and C:N)

As with the two previous wetlands, sediments were the most depleted source of carbon within Noobijup Lake (Figure 5.3). Sediment δ^{13}C values were most depleted in summer and spring around –35‰ with autumn values the most enriched at 31.67‰. Little season variation was apparent in the δ^{13}C of biofilms, ranging from –31.82‰ ± 0.2 in spring to –33.79‰ ± 0.04 in summer. Macrophytes were in the range of values found in the other wetlands, generally between –25‰ and –28‰. Seasonal differences were apparent in all macrophytes except *Myriophyllum*, but no consistent seasonal trends were apparent between taxa. *B.articulata* leaves had similar values during autumn, summer and spring around –25.5‰, but were depleted in winter to –29.43‰ ± 0.1. Fringing tree species of *M.raphiophylla* and *E.rudis* displayed carbon isotope ratios similar to those found in the other two wetlands. Values were slightly depleted to macrophytes, with signatures around –30.5‰ for *M.raphiophylla* and –28 for *E.rudis*.

The C:N ratios for Noobijup Lake, as with the other wetlands indicate few of the sources are available for direct use by primary consumers (Table 5.1). Biofilms and submerged macrophytes had the lowest ratios, generally less than 16. Biofilm showed little seasonal variation, ranging from 10.97 ± 0.5 in winter to 15.15 ± 0.7 in summer. *Triglochin* consistently had the lowest ratios of all sources. Emergent macrophyte tissue has the highest ratios of all sources measured, with values in the range of 42 to 69. The two fringing species, *M.raphiophylla* and *E.rudis* both had C:N values ranging from 19 to 35, between submergent and emergent macrophytes.

Very few primary consumers were sampled from Noobijup Lake. *Physastra* (a known scraper), and Chironomidae both have δ^{13}C signatures that are between the signatures of macrophytes and biofilm. These signatures varied seasonally by up to 4‰, indicating these taxa change their dominant source of carbon. The tadpoles also had carbon signatures that varied greatly throughout the year. Signatures were close to that of the biofilm, except in spring when the isotopic signature of the tadpole was too depleted at –35.67‰ ± 0.2 to have derived its carbon from any of the measured sources.

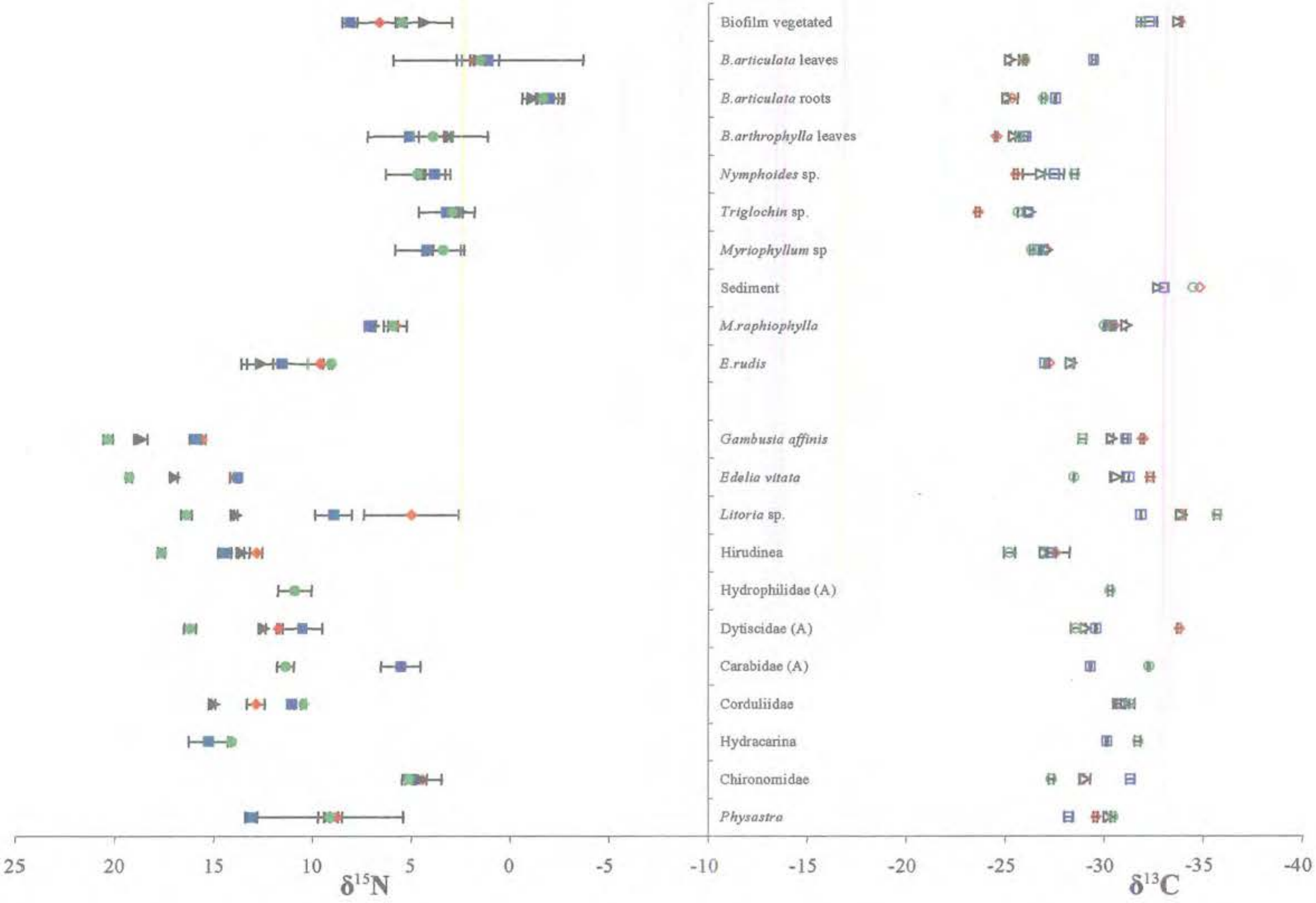


Figure 5.3. δ^{13}C and δ^{15}N isotopic signatures (mean ± SE) for dominant carbon sources and sinks in Noobijup Lake in Summer, Winter and Spring. (A) Adult, (L) Larvae. n = 1 where no standard errors are shown. Winter δN ■, Spring δN ●, Summer δN ◆, Autumn δN ▶: Winter δC □, Spring δC ○, Summer δC ◊, Autumn δC ▷

Secondary consumers in Noobijup showed enormous variation both seasonally and between taxa. The Coleoptera generally had carbon isotopic signatures in winter and autumn within the range for primary consumers such as the Chironomidae to be a carbon source. However in summer and spring, $\delta^{13}C$ values are too depleted for this taxon to have been consumed. This again suggests that some lower order consumers were missing from those organisms sampled during these times. The Hydracarina and Odonata showed little seasonal variation and similar δC^{13} signatures (~ -31‰), with no clear, single carbon source. Hirudinea, a known predator consistently had δC^{13} signatures too enriched for any of the taxa sampled within the wetland to be a source of carbon. The two species of fish within the wetland, *Gambusia holbrookii* (exotic taxa) and *Edelia vitata* (native taxa), had almost identical carbon signatures in each season. The signatures and seasonal trends mimic those of the Chironomidae, suggesting these may be an important carbon source for these organisms.

The $\delta^{15}N$ values of sources showed little variability seasonally or between taxa. Biofilm nitrogen signatures varied seasonally, being most depleted in autumn (4.34‰ ± 1.4) and enriched in winter (8.08‰ ± 0.3). The submergent macrophytes and *B.arthrophylla* displayed little seasonality and δN15 signatures consistently between 3 and 5‰. *B.articulata* was again the macrophyte with the most depleted δN^{15} signatures, with its roots consistently being the most depleted source. *E.rudis* was the most enriched nitrogen source with values ranging between 9.03‰ ± 0.1 in spring to 12.62‰ ± 0.6 in autumn.

The $\delta^{15}N$ data for Noobijup Lake indicate there is enormous seasonal variability in the majority of consumers indicating they, or their source of carbon, change trophic position seasonally. The $\delta^{15}N$ signature of *Physastra* is within the range of submergent and emergent macrophytes, except in winter when its signature is enriched by around 4‰, indicating a shift to a more biofilm or terrestrially derived carbon source. The tadpoles have an enormous range in their nitrogen signatures, from 5.00‰ ± 2.4 in summer to 16.39‰ ± 0.3 in spring, indicating a marked shift in trophic position. The Coleoptera, Odonata and Hydracarina all show large seasonal variation in nitrogen signatures with no obvious sources, as their signatures are generally too enriched for the Chironomidae to have been a source. This suggests that as with the other two wetlands, there may be organisms being consumed that were not in sufficient biomass to be sampled. This is supported by data such as the Carabidae in winter, with a $\delta^{15}N$ signature of 5.52‰ ± 1.0. This value is too depleted to be derived from any measured source. The $\delta^{15}N$ identifies the two fish species as the highest trophic level, and as with the carbon isotopic data they have similar values throughout the year.

5.4 DISCUSSION

5.4.1 Variation in sources

Considerable variability was detected in the $\delta^{13}C$ and $\delta^{15}N$ values of both primary sources and consumers. Large seasonal variations and inconsistent trends made it difficult to discriminate between sources of organic matter both within and between wetlands. Biofilms and organic sediments formed a distinct group consistently being the most depleted carbon sources in each wetland. This is in contrast to most Australian studies that generally have riparian or upland vegetation as the most depleted carbon source. All three wetlands studied had exceptionally unproductive water columns with high DOC concentrations, and as such would be classified as ultra-oligotrophic (Section 3.3.3). In wetlands where the photic depth is limited by dissolved organic matter, algal productivity is restricted and heterotrophic bacteria have tended to dominate biofilms (Findlay *et al.* 1986; Edwards & Meyer 1987; Couch & Meyer 1992). The depleted carbon signature of biofilms in the study wetlands may therefore be due to a high heterotrophic component.

Artificial substrata were used for biofilm colonisation in this study and are commonly used to sample biofilm colonisation. Critical reviews (Cattaneo & Amireault 1992; Morin & Cattaneo 1992) however, argue the ability of artificial substrata to reproduce natural substrata, concluding artificial substrata often misrepresent both the quantity and composition of natural biofilms. The length of sampling time and the nature of the substrata used in this study may have caused the biofilm composition, and therefore the isotopic signatures to be different to those consumed by invertebrates. Boon & Bunn (1994) demonstrated carbon and nitrogen isotopic signatures varied between the same source collected from one site at different times of year, and collected from different sites at the same time of year. However, the use of artificial substrata in this study with consistent deployment times, surface area and depth should have reduced the variability encountered by Boon & Bunn (1994) and aid the interpretation isotopic signatures.

Emergent and submerged macrophytes, and *E.rudis* (fringing upland tree species) values ranged between –24 and –28‰ $\delta^{13}C$. Results also varied seasonally by up to 4.5‰, making discrimination between these sources difficult. Nitrogen isotopic signatures also showed little variation between species, with signatures masked by large standard errors and seasonal variation, although *B.articulata* leaves and roots were consistently the most depleted of these sources. There were small variations in the carbon signature between *B.articulata* leaves and roots from the same plant, however, the roots were substantially enriched in $\delta^{15}N$ by 5 to 10‰.

Macrophyte carbon and nitrogen isotopic signatures are congruous with other Australian studies in billabongs (Bunn & Boon 1993; Boon & Bunn 1994) and lowland rivers (Sheldon & Walker 1997) and fall within the range for macrophytes outlined in the review of Keeley & Sandquist (1992). These are however, in contrast to values for aquatic plants with similar growth habits in many Northern Hemisphere wetlands, with LaZerte & Szalados (1982) reporting submergent macrophyte carbon signatures in the range of –15 to –20 ‰ and Hecky & Hesslein (1995) finding macrophytes with signatures ranging from –12 to – 22 ‰. As with biofilms, Boon & Bunn (1994) demonstrated considerable variation in emergent and submerged macrophyte signatures between sites and seasons. Unlike other studies however, the seasonal trends of enrichment and depletion for each source were not consistent between wetlands. Carbon isotopic signatures of *B.articulata*, the dominant macrophyte in each wetland, was consistently most depleted in winter, but most enriched in summer, spring and autumn in Bokarup Swamp, Kodjinup Swamp and Noobijup Lake respectively. *B.arthrophylla* and *B.preisii* also displayed seasonal and spatial variations in their carbon signatures that did not match the patterns displayed by other emergent macrophytes. Jennings *et al.* (1997) demonstrated $\delta^{13}C$ and $\delta^{15}N$ spatial variability within species for marine seagrasses that was largely attributable to collection site differences. Root and growing conditions for macrophytes were different in each of the wetlands. Depth and duration of inundation would have been different for each wetland, leading to variations in sediment and water column anoxia and exposure of leaves out of the water column. Leuschner & Rees (1993) showed that intertidal populations of *Zostera* were able to maintain considerable rates of net photosynthesis during low tide exposure by utilising 'lighter' carbon (-7.8‰) instead of bicarbonates from the water column. Significant differences were found in the methane and carbon dioxide concentrations of gases found in both sediment and within emergent *B.articulata* leaves (Chapter 4). This indicates that seasonal differences in isotopic signatures of emergent macrophytes may be due to changes in their carbon dioxide sources, such as sediment microbially, produced or atmospheric carbon dioxide or water column bicarbonates.

The organic surface sediments of each wetland were consistently the most depleted source of carbon ranging from around -32 to -38‰. Emergent macrophytes were the dominant source of organic matter contributing to the detritus (Chapter 3), however, the surface sediments have δC^{13} signatures depleted from the macrophyte source. This supports the findings of Rask & Schoenau (1993) and Hornibrook *et al.* (1997) who demonstrated the processes of isotope fractionation and depletion through bacterial consumption. During early decomposition, a portion of the biogenic elements of the detrital organic matter is revolatilised to the atmosphere as carbon dioxide and methane (Appleby & Oldfield 1992). Methanogenic bacteria are known for their extremely low $\delta^{13}C$ ratios with values exceeding -70‰ (eg. Bartlett & Harris 1993; Chanton & Whiting 1996). Novak *et al.* (1999) also demonstrated an increase in $\delta^{13}C$ depletion in peat soils as a result of an isotope-selective process. During decomposition, microbial communities preferentially consumed the labile component of the detrital matter, leaving the residual organic matter depleted in $\delta^{13}C$. The incorporation of microbial biomass into the sediment or the selective microbial consumption of the detritus may be responsible for the sediment $\delta^{13}C$ signature in these wetlands being more depleted than its source.

The two species of upland vegetation sampled, *M.raphiophylla* and *E.rudis*, had quite distinctly different carbon signatures despite both being terrestrial C_3 plants. As mentioned, *E.rudis* could not be discriminated from emergent and submergent macrophytes using carbon isotopic signatures, however, in both Kodjinup Swamp and Noobijup Lake which both receive agricultural runoff, it had distinctly enriched nitrogen signatures. Carbon isotopic signatures for *E.rudis* in these habitats (~ -27‰) are similar to those recorded for a range of riparian vegetation in the Northern Jarrah Forest of Western Australia (-26.9 ± 0.1‰) (Bunn *et al.* 1999). *M.raphiophylla* formed a third distinguishable group with carbon isotopic signatures around -30‰ occurring between the macrophytes and biofilm. The lack of seasonal variation and depleted carbon signatures found in *M.raphiophylla* may in part be a result of the roots of the trees being permanently waterlogged and presumably in low oxygen conditions, providing constant conditions both temporally and between wetlands.

An index of food quality is given by the ratio of carbon to nitrogen, indicating the protein content of the food (McMahon *et al.* 1974). A low ratio arises from either a high nitrogen content (high quality) or a low carbon content combined with residual refractory nitrogen (low quality) (Naiman 1983). The emergent macrophytes had C:N ratios <38 in all wetlands in all seasons. Biofilms and submerged macrophytes had the lowest C:N ratios in all wetlands, varying from 10.08 in Kodjinup Swamp to 15.15 in Noobijup Lake, peaking in each wetland during summer. Diatoms have been recorded with C:N ratio from 4.4 to 6, non filamentous green algae with C:N ratio from 4.3 to 13.8 and Cyanobacteria from 4.3 to 8.3 (Steinman 1996). Values from these wetlands fall within ranges of values from other Australian studies, with C:N ratios of 10.34 to 14.44 (Burns 1997) and 7.5 to 10.5 (Sheldon & Walker 1997) found in lowland rivers. The higher C:N ratios of biofilms and macrophyte tissue compared to other studies indicates much of the carbon entering the system is too refractory for direct invertebrate consumption and would require microbial conditioning prior to invertebrate consumption (see Webster & Benfield 1986).

5.4.2 Wetland food webs

The carbon produced by macrophytes has traditionally been thought to enter aquatic food webs as detritus, rather than direct herbivory (Webster & Benfield 1986; Mann 1988). Macrophytes are also important substrata for periphytic algae, thought to be an important food supply and of better quality than macrophytes (Eunn & Boon 1993, Hecky & Hesslein 1995). Despite the clear discrimination of biofilms, macrophytes and upland vegetation using carbon isotopes, none of these sources appear as an obvious carbon source for most consumers in these wetlands, as invertebrate signatures were generally more depleted than any single source. Primary consumers exhibited carbon signatures between macrophyte values and those of biofilms, indicating a diet containing both sources. Common grazers, including atyid shrimps and gastropods in south-east Australian wetlands were also thought to have a diet containing both epiphytic and macrophytic material (Bunn & Boon 1993). However, the $\delta^{15}N$ values in this study are often too depleted for consumers to have derived their carbon from a mixture of biofilm and macrophyte. Furthermore, seasonal variations in most primary consumers were lower than those of carbon sources and followed a different pattern of seasonal change. These data suggest that some consumers would have to change their proportion of carbon from different sources seasonally, or utilise an unmeasured source that did not seasonally vary in order to maintain fairly static signatures.

It can therefore be hypothesised that alternative sources of carbon are available for primary consumers that were not measured in this study. In a review of carbon signatures for phytoplankton, Zohary *et al.* (1994) found signatures varied by season and site from −15 to −35‰ for the same planktonic taxa in the 58 to 100um size range. Depleted nitrogen signatures have also been reported for phytoplankton (Hecky & Hesslein 1995; Keogh *et al.* 1996). These reported values indicate that planktonic algae possess isotopic signatures that can account for the signatures of primary consumers found in these wetlands. The distinct lack of phytoplankton productivity in these wetlands (Chlorophyll *a* < 9 µg/l; Chapter 3), and a low abundance of primary consumers to heavily graze plankton, indicates that phytoplankton are not present in sufficient biomass to represent a viable food source for primary consumers. Alternatively, grazing of phytoplankton by primary consumers, who in turn are grazed by higher order consumers could explain the low phytoplankton biomass.

Microorganisms form an important link between primary and secondary production in the detrital food webs of aquatic systems. They are responsible for the degradation of plant litter and the alteration of its chemical composition and the provision of a palatable food source for consumers (Boulton & Boon 1991). Colonisation of detrital leaf litter by aquatic microorganisms such as fungi and bacteria (termed 'conditioning') results in the increase in the quality of the detritus as a food source for primary consumers (Webster & Benfield 1986). It was hypothesised by Sheldon and Walker (1997) that macroinvertebrate grazers consume the heterotrophic microorganisms that use detritus as their primary carbon source. Numerous authors have studied the modification of isotopic signatures through trophic levels with carbon ratios of consumers being up to 1‰ depleted and 2‰ enriched from the source (Jackson & Harkness 1987; Bunn & Boon 1993; France & Peters 1996). Sheldon and Walkers' hypothesis is therefore also appropriate for these habitats. The consumption of detrital bacteria or heterotrophic organisms utilising DOM would result in many primary consumers possessing a depleted signature from those of the dominant macrophytes. The carbon isotopic signature of the sediment is consistently depleted from the *B. articulata* leaf material, which dominates the detritus. This indicates the microbial conditioning of the detritus in these systems has resulted in a marked depletion of the original source macrophyte tissue.

A final explanation could be the consumption of sediment derived chemoautotrophic bacteria, either directly by primary consumers or in successive trophic levels. Peterson *et al.* (1980) observed a large amount of the energy fixed in salt marsh macrophytes is lost in the form of reduced sulfur compounds, which can be used as alternate electron acceptors for chemoautotrophic bacteria. The result was bacterial assemblages with carbon isotopic signatures that did not reflect the original macrophyte tissue. Bunn and Boon (1993) proposed that methanogenic bacteria could use this mechanism, resulting in primary consumers with signatures distinct from obvious detrital sources. Biogenic methane is noted to have highly depleted carbon signatures, ranging from –52 to –80‰ (Chanton *et al.* 1988; Chanton & Martens 1988; Hornibrook *et al.* 1997). Diets consisting of $\delta^{13}C$ depleted bacteria or organic sediments in conjunction with other carbon sources available within these wetlands could therefore reflect many of the primary consumer signatures. Corpe and Jensen (1992) suggested the picoplankton of small dystrophic lakes may comprise up to 20% methanotrophs and other chemoautotrophic bacteria. Methane concentrations in the wetlands studied were very high, comprising up to 80% v/v of sediment gases (Chapter 4). Given the high concentrations of methane present, and the extreme efficiency of bacteriovores (Boon & Shiel 1990), this pathway may dominate the carbon cycle in these wetlands.

In many cases (particularly summer) carbon signatures of secondary consumers were also too depleted to have derived their carbon from any measured source. In Bokarup Swamp, adult Hydrophilidae beetles had a carbon signature of ~ -35, up to 6‰ depleted from any measured primary consumer and 10‰ depleted from macrophyte tissue. Added to this is the dominance of second order consumers in the collection, with few primary consumers with sufficient biomass to enable sample collection and analysis. These data are supported by the $\delta^{15}N$ values that suggest there are 'missing' trophic levels in each wetland, with signatures of higher order consumers up to 12‰ enriched from the few potential food sources quantified. As $\delta^{15}N$ is enriched between 2 to 5‰ relative to the source (Minagawa & Wada 1984), there would have to be at least one other trophic level with $\delta^{15}N$ signatures between the low and high order consumers identified in this study. This pattern is most evident in Bokarup Swamp and Noobijup

Lake. Reinforcing this hypothesis are the signatures of many secondary consumers, which display seasonal differences that are often larger than differences between species, with variations of up to 6‰ for $\delta^{13}C$ and 12‰ $\delta^{15}N$ found within the one taxon.

Competition has been suggested as the primary structuring force in natural communities (Bronmark *et al.* 1992). However, Hairston *et al.* (1960) hypothesised that the factor regulating a specific population depends on its position in the food chain, and the number of trophic levels in the chain. For example, in a food chain with three trophic levels, predators will be resource limited, herbivores regulated by predators, and primary producers limited by the availability of resources. More recent hypotheses have developed from Hairston's model, two of which focus on predator control. These are the 'biomanipulation concept' (Shapiro *et al.* 1975) and the 'cascading trophic interaction' theory (Carpenter *et al.* 1987), which suggest predator abundance will cascade down through trophic levels. The third theory is proposed by McQueen *et al.* (1986), the 'bottom up:top down' model. This explicitly combines the predicted influences of both predators (top down) and primary production (bottom up). This model appears to be most applicable to these wetlands. The high biomass and species richness of predators, low biomass and richness of primary consumers, 'missing' trophic levels as revealed by stable nitrogen isotopes and an ultra-oligotrophic water column lead to the hypothesis that low primary productivity is limiting the biomass of successive trophic levels within these wetlands.

5.4.3 Conclusion

To fully elucidate the trophic links within these wetland types a more thorough and detailed sampling protocol is required. Although present, taxa with low abundance (hence biomass) were not collected. Increased sample replication until a sufficient biomass for analysis is gained from all taxa collected may elucidate the trophic links that are absent in the current study. The identification of taxa beyond family level may also aid in the interpretation of data as the large seasonal variations seen in predator groups such as Coleopterans and Hemipterans may be due to taxonomic as much as dietary shifts. A more complete collection of source material is also required, especially in systems where detrital pathways are thought to dominate. The complexity of sample collection and preparation for the bacterial component of sediment, detritus and water column has deterred many authors from quantifying these isotopic signatures. This study highlights the need for their determination, where visually dominant sources may not be directly consumed. A compilation of carbon isotope data from the literature for coastal seagrass meadows, estuarine salt marshes and freshwater lakes and rivers by France (1996), indicates that animal $\delta^{13}C$ values more closely approximate those of biofilm than those of vascular plants. This study suggests that macrophytes play a more central role in the aquatic foodwebs of these shallow, macrophyte dominated wetlands. Primary consumers are consistently depleted in $\delta^{13}C$, with values most similar to the biofilms and organic detritus, suggesting that aquatic macroinvertebrates play a role in the breakdown of detrital organic matter in these wetlands. These data also highlights the importance of macrophytes in the foodwebs of these wetlands as substrate for biofilms, a source of organic matter for detrital microflora or a source of energy for anaerobic sediment bacteria. The preservation of these macrophyte communities is therefore paramount in maintaining the ecological processes within these wetland types.

CHAPTER 6

WETLAND CARBON BUDGETS

Sources or Sinks of Organic Matter?

6.1 INTRODUCTION

In recent years, there has been considerable interest in evaluating carbon cycling in freshwater ecosystems due to their important role as global carbon sources and sinks (Dixon *et al.* 1994). The potential importance of peatlands to the global carbon cycle has been discussed by numerous authors (most notably Gorham 1991) and estimates of the global carbon pool range from 329 to 528 Gt (Lappalainen 1996). It has also been noted that boreal wetlands have the potential to change from a carbon sink to a source in years when the summer water table is below the long term average (Carrol & Crill 1997; Waddington & Roulet 2000). Consequently, understanding the rates of carbon supply and utilisation in freshwater systems has become more important in terms of their relevance to climate change and global warming. Limnological studies yielding data on sources and sinks have been used to develop carbon budgets. The formulation of a carbon balance which will calculate the difference between the annual income of plant litter and losses due to decomposition provides an understanding of the processes involved in organic matter accumulation.

A variety of methods have been used to quantify carbon balances in aquatic systems. Long-term carbon budgets have been developed using widely available dating techniques and volumetric samples. Carbon budgets are simply calculated by dividing the height of the deposit by the radiocarbon date, correcting for bulk density and determining a long-term annual carbon budget. This technique has been used in peatlands where deposits can be many thousands of years old (eg. Charman *et al.* 1994; Makila 1997; Aucour *et al.* 1999). The majority of studies have used the concept of Net Ecosystem Exchange (NEE), which is derived from the exchange of measures of ecosystem production (carbon dioxide from photosynthesis) and ecosystem respiration (carbon dioxide and methane) across wetland surfaces (Waddington & Roulet 2000). This technique has been successfully applied in pelagic systems where phytoplankton dominates wetland productivity (eg. Ramlal *et al.* 1994; Anderson *et al.* 1996; Kankaala 1996) and in ombrotrophic mires and poor fens (Carroll & Crill 1997; Alm *et al.* 1999; Waddington & Roulet 2000). Duartè & Agusti (1998) provide an extensive review of the carbon dioxide balance in unproductive freshwater systems that allows for wide comparisons of results using this method. However, the use of NEE as a measure of carbon gain or loss is less applicable to systems that have substantial allochthonous inputs.

Detailed carbon budgets in wetland systems dominated by macrophytic production are rare. Early researchers such as Olsen (1963) and Walker (1970) used measurements of organic inputs minus losses from decomposition to quantify simple carbon budgets in these habitats. Reader & Stewart (1972) used measures of plant biomass, net primary productivity and allochthonous litter income and losses derived from decomposition coefficients to quantify the annual accumulation of organic matter. Similarly, plant biomass and carbon gas flux measurements were measured by Kelly *et al.* (1997) to determine the carbon status (source or sink) of a flooded boreal forest wetland.

Carbon budgets such as these for wetland systems do not appear in the Australian literature. Organic matter dynamics have been studied in Australian estuarine habitats (eg. Robertson & Diniel 1989; Robertson *et al.* 1992; Wolanski *et al.* 1998) where mangroves provide significant proportions of organic matter to the sediment. As mentioned previously (Chapters 3 and 4), studies have quantified the inputs of organic matter into wetlands or decomposition rates through loss of biomass or gas flux, but rarely both. Briggs & Maher's (1983) examination of leaf litter fall and decomposition of *Eucalyptus camaldulensis* in south-east Australian floodplain wetlands provides an insight into carbon dynamics in these systems. Bunn & Boon (1993) have used stable isotopes of carbon and nitrogen to determine the importance of various carbon sources in wetland food webs, yet no studies have quantified the proportion each of these sources provide to the wetland carbon budget. A recent review on biogeochemical cycling of carbon and nutrients in lakes and estuaries by Harris (1999) provided no examples of carbon budgets in Australian freshwater lakes, let alone macrophyte dominated wetlands.

As highlighted in previous chapters, organic matter dynamics in wetland ecosystems are affected by many external influences such as altered hydrology, water quality and other direct management practices such as prescription burning. A thorough understanding of the dominant sources of organic matter and their rates of supply and losses will allow the identification of management practices that may alter these wetlands from carbon sinks to carbon sources. This chapter contains a detailed seasonal and annual carbon budget for each of the study wetlands. Organic matter inputs (allochthonous and macrophyte litter, DOM, biofilm, phytoplankton - Chapter 3 and microorganisms - Chapter 4) and losses (carbon dioxide and methane atmospheric flux - Chapter 4) are used to construct a carbon budget for each wetland. This budget is used to examine current wetland carbon dynamics relative to contemporary environmental conditions and management regimes.

6.2 METHODS

6.2.1 Carbon budget

All major inputs and losses of organic matter were used to construct an annual and seasonal carbon budget for each wetland. Data quantifying the organic matter supply from major allochthonous and autochthonous sources (Chapter 3) and rates of decomposition (Chapter 4) were collected from July 1995 to January 1997. A carbon budget is constructed for each sample date, and then sample dates are pooled into seasonal categories (Section 2.4) to allow a seasonal carbon budget to be developed. Total combined carbon inputs and losses from each wetland (derived from the sum of the means for each categorised season) are used to construct an annual carbon budget. The delineation of discrete habitat boundaries and the calculated surface area of each of these habitats in Section 2.5.1 allows seasonal and annual carbon budget to be constructed for each habitat type within each wetland as well as an overall budget for the whole wetland.

Each carbon budget quantifies the net gain or loss of organic carbon in each habitat/wetland and each is standardised to $gC/m^2/day$. A Standardised Wetland Unit (SWU) was created to standardise organic carbon inputs for each wetland and each habitat. A SWU consisted of one square meter of wetland surface area to a peat depth of 0.3 m to allow for the below ground contribution of carbon from macrophytes. It also includes the depth of the overlying water column for inclusion of water column and biofilm productivity and dissolved organic matter. It assumes that carbon can occur at any point in the water column represented by the SWU. Absolute values for these measurements are calculated based on the average water column height on respective sampling occasions. The contribution of sediment microbial biomass to the carbon budget is calculated for the surface 30 cm of sediment and quantifies biotic transformations of organic carbon to the abiotic sediment carbon pool. Carbon losses from the SWU are calculated from measured of CO_2 and CH_4 fluxes across the air-water interface and are also standardised to $gC/m^2/day$.

6.2.2 Sources of organic carbon

Sources of organic carbon were quantified using methods outlined in previous chapters as follows:

- allochthonous litterfall – Section 3.2.1;
- emergent macrophyte litterfall – Section 3.2.2;
- emergent macrophyte below ground structures - Section 2.5.6;
- water column productivity – Section 3.2.3;
- biofilm – Section 3.2.4;
- DOM – Section 3.2.5; and
- sediment microbial biomass – Section 4.2.1.

The following equations describe the methods for calculating each of the sources of carbon.

6.2.2.1 Allochthonous and Autochthonous litterfall.

Average litterfall data for allochthonous and emergent macrophyte inputs from each wetland and sampling period were standardised to gC/m^2/day using the average percent elemental carbon of major litterfall species determined by the Isotope Ratio Mass Spectrometer (IRMS) for each sampling period (Appendix 4). Equation 1 is used to calculate the independent input rates from the emergent macrophyte and the fringing vegetation and is applied to each sampling date for each wetland.

$$\textit{Equation}\ 1:\ \overline{\mathrm{X}}\mathrm{sd}l_{(fv\ \mathrm{or}\ em)}\ \mathrm{gC/m^2} = \left(\bar{x}_{l(fv/em)} \bullet \frac{\%\ \mathrm{Organic\ C}}{100}\right) \bullet \mathrm{n}$$

Where $\overline{\mathrm{X}}\mathrm{sd}l$ is the mean sample date input of organic carbon from litterfall in gC/m^2/season, *fv* indicates fringing vegetation inputs and *em* indicates emergent macrophyte inputs, $\bar{x}_l$ is the average dry weight input of leaf litter in gDW/m^2/day, $\frac{\%\ \mathrm{Organic\ C}}{100}$ is the fraction of the average percent organic carbon for litterfall species determined by IRMS and n is the number of days in each season category.

6.2.2.2 Macrophyte below ground structures

The below ground structures of emergent macrophytes have the potential to contribute substantial amounts of organic carbon to a wetland, especially where macrophytes are the dominant source of primary production. In Section 2.6.6 the below ground biomass of emergent macrophytes at the points of maximum (September) and minimum (April) productivity have been quantified. The budget assumes that the difference between these totals is the annual amount contributed as dead particulate matter to the sediment from macrophytes. This total annual input is converted into a daily input (in the form of elemental carbon) in order to calculate its contribution to both seasonal and annual budgets. Equation 2 describes the calculation of below ground contribution of organic carbon for each sample date.

$$\textit{Equation}\ 2:\ \overline{\mathrm{X}}\mathrm{sd}bg\ \mathrm{gC/m^2} = \left\{(\bar{x}_{bt} \bullet \frac{\%\ \mathrm{Organic\ C}}{100})\right\} \bullet n$$

Where $\overline{\mathrm{X}}\mathrm{sd}bg$ is the mean sample date input of organic carbon from below ground macrophyte structures in gC/m^2/day, $\bar{x}_{bt}$ is the annual input of below ground macrophyte structures, $\frac{\%\ \mathrm{Organic\ C}}{100}$ is the average of the average percent of organic carbon for below ground macrophyte structures determined by IRMS, and n is number of days in the sampling period as a proportion of the total year (365 days).

6.2.2.3 Water column productivity

Water column productivity data were standardised to gC/m^2 using conversions from chlorophyll *a* to biomass outlined in APHA (1989) and then converted to gC/m^2 using the average organic carbon percent (Appendix 4). Dissolved organic matter (DOM) values do not require conversion. The wetland basins (as described in Chapter 2) are thought to be seasonal expressions of an unconfined groundwater aquifer. This connection allows the exchange of DOM between wetland and groundwater. This budget assumes the DOM pool in the water column originated within, and is confined to the wetland basin. An absolute value for the quantity of organic carbon from both chlorophyll (Equation 3) and DOM (Equation 4) within the SWU are calculated using average water depth from respective seasons and wetlands. The regeneration time for algae is species specific and influenced by environmental conditions. The budget assumes the turnover rate for phytoplankton in these systems is three days (Baker *et al.*

2000). The production of DOM from leaf litter involved a rapid leaching phase followed by a prolonged release from microbial decomposition (Webster & Benfield 1986). The budget assumes that DOM concentrations remain constant within each categorised season. These equations are applied to each sampling date for each wetland.

$$\textit{Equation}\,3:\ \overline{\mathrm{X}}\mathrm{sd}\mathit{chl}\,\mathrm{gC/m^2} = \left\{(\bar{x}\,sd_{chl} \bullet 150)\cdot\frac{\%\,\mathrm{Organic\ C}}{100}\right\}\bullet v \bullet \frac{n}{R}$$

Where $\overline{\mathrm{X}}\mathrm{sd}\mathit{chl}$ is the mean sample date input of organic carbon from water column chlorophyll in $\mathrm{gC/m^2}$, $\bar{x}_{chl}$ is the average chlorophyll concentration, 150 is the conversion factor from chlorophyll to biomass (APHA 1996), $\frac{\%\,\mathrm{Organic\ C}}{100}$ is the fraction of the average percent organic carbon for biofilm chlorophyll determined by IRMS, v is the volume of water in the SWU based on average water depth, and $\frac{n}{R}$ is number of days in the sampling period divided by the turnover rate of phytoplankton.

$$\textit{Equation}\,4:\ \overline{\mathrm{X}}\mathrm{sd}\mathit{dom}\quad \mathrm{gC/m^2} = \bar{x}sd_{dom} \bullet v$$

Where $\overline{\mathrm{X}}\mathrm{sd}\mathit{dom}$ is the mean sample date input of dissolved organic carbon from the water column in $\mathrm{gC/m^2}$, $\bar{x}sd_{dom}$ is the average input of dissolved organic matter and v is the volume of water in the SWU based on average water depth.

6.2.2.4 Biofilm

Biofilm organic carbon per SWU was calculated by determining the average surface area of a *Baumea articulata* stem per centimetre of stem length and multiplying by the average water depth from respective seasons and wetlands. This value represents the average colonisable surface area for each stem (assuming light penetrates equally to all depths) in each sampling period and is multiplied by the average total number of stems per metre square in September (from Table 2.7) to calculate the total colonisable surface area per SWU. Absolute values for biofilm biomass were calculated by multiplying the average biomass (Section 3.3.4.2) by the total colonisable surface area in the SWU and the number of days in each sampling category. Data are standardised to $\mathrm{gC/m^2}$ using the average percent elemental carbon for biofilm for each season and wetland determined by the IRMS (Appendix 4). The budget assumes that biofilm biomass remains relatively constant within each categorised season. Equation 5 is applied to each sampling date for each wetland

$$\textit{Equation}\,5\text{: } \overline{\mathrm{X}}\mathrm{sd}b\ \mathrm{gC/m^2} = \left[\left\{(\bar{x}_{sa}\cdot\bar{x}_{\mathrm{d}})\cdot\bar{x}_b\right\}\bullet\frac{\%\ \text{Organic C}}{100}\right]\bullet \mathrm{n}$$

Where $\overline{\mathrm{X}}s\mathrm{d}b$ is the mean sample date input of organic carbon from biofilms in gC/m^2, $\bar{x}_{sa}$ is the average colonisable surface area of emergent macrophyte leaf (m^2), $\bar{x}_{\mathrm{d}}$ is the average density of macrophyte leaves (m^2), $\bar{x}_b$ is the average biofilm biomass in gDW/m^2/day, $\frac{\%\ \text{Organic C}}{100}$ is the fraction of the average percent organic carbon for biofilm determined by IRMS and n is the number of days in each season category.

6.2.2.5 Sediment microbial biomass

The contribution of sediment microbial biomass to the SWU was calculated by converting phospholipid concentrations (PL) in µmole PO_4^{3-}/gDW sediment to µgC/gDW sediment. Conversion factors have been calculated for estuarine mudflat sediments (19.17µgC per µmole PL PO_4^{3-} Findlay *et al.* 1989), forest humus soils (41.9µgC per µmole PL PO_4^{3-} Hill *et al.* 1993; 26.43µgC per µmole PL PO_4^{3-} Zelles *et al.* 1995) and arable farming soils (22µgC per µmole PL PO_4^{3-} Hill *et al.* 1993). A direct conversion for wetland or peatland soils is not available. An average of 27.37µgC per µmole PL PO_4^{3-} derived from conversion factors in the literature will be used in the budget. Absolute values for the microbial biomass contributing to the SWU was calculated by multiplying the conversion factor by the average microbial biomass in the surface 0.3 m^3 for each wetland. The budget assumes that microbial biomass remains constant within each categorised season. Equation 6 is applied to each sampling date for each wetland.

$$Equation\ 6:\ \overline{\mathrm{X}}\mathrm{sd}mb\ \mathrm{gC/m^2} = \left\{\frac{\bar{x}_{mb}\ 27.37}{10^{-6}}\right\} \bullet v$$

Where $\overline{\mathrm{X}}\mathrm{sd}mb$ is the mean sample date input of organic carbon from microbial biomass in $\mathrm{gC/m^2}$, $\bar{x}_{mb}$ is the average microbial biomass in μmol PL $\mathrm{PO_4^-}$/L, 27.37 is the conversion factor, and v is the volume of sediment in the SWU ($0.3\mathrm{m^3}$).

Equation 7 can be applied to each wetland to determine the average inputs for any one season and Equation 8 calculates the average annual input from each of the major organic matter sources.

$$Equation\ 7:\ \overline{\mathrm{X}}\mathrm{s}\ \mathrm{gC/m^2} = \left(\frac{\sum \overline{\mathrm{X}}_{sd}}{N}\right)$$

Where $\overline{\mathrm{X}}\mathrm{s}$ is the mean seasonal input of organic carbon from each source in $\mathrm{gC/m^2}$, $\sum \overline{\mathrm{X}}_{sd}$ is the sum of the average sample date inputs for each season category and N is the number of sample dates in that season category.

$$Equation\ 8:\ \overline{\mathrm{X}}\mathrm{a}\ \mathrm{gC/m^2} = \sum \overline{\mathrm{X}}\mathrm{s}$$

Where $\overline{\mathrm{X}}\mathrm{a}$ is the mean annual input of organic carbon from each source in $\mathrm{gC/m^2}$ and $\sum \overline{\mathrm{X}}\mathrm{s}$ is the sum of the average seasonal inputs of organic carbon.

6.2.3 Losses of organic carbon

Organic matter is decomposed to carbon dioxide by bacteria preferentially under aerobic conditions using oxygen as an electron acceptor. As benthic consumers use up oxygen, biogenic methane production becomes the dominant pathway for organic matter decay (Sorrell & Boon 1992, Muller *et al.* 1994). A food web involving fermentative and methanogenic bacteria guarantees that organic matter will be mineralised to gaseous products (CO_2 and CH_4) even under anoxic conditions. As end products in the decomposition of organic carbon, CO_2 and CH_4 fluxes provide quantitative data measuring losses of organic carbon from wetland basins.

The flux of CO_2 and CH_4 was measured using the methods outlined in Section 4.2.2. Equation 9 calculates the average loss of organic matter from each wetland on each sample date in gC/m^2. The equation averages the flux of CO_2 and CH_4 from both emergent macrophytes and open water. These data can then be used in Equations 10 and 11 to calculate seasonal and annual losses or organic carbon.

$$\textit{Equation}\ 9:\ \overline{\mathrm{X}}\mathrm{sd}CO_2 + CH_4\ \mathrm{gC/m^2} = \left\{ \frac{\left[12.01 \cdot \left(\frac{\left(\bar{x}v_{CO2+CH4} + \bar{x}uv_{CO2+CH4}\right)}{2} \right) \right]}{10^{-3}} \right\} \bullet \mathrm{n}$$

Where $\overline{\mathrm{X}}\mathrm{sd}CO_2 + CH_4$ is the mean sample date loss of organic carbon from gas flux in gC/m^2, $\bar{x}v_{CO2+CH4}$ is the average gas flux from vegetated habitats in mmol/L/m^2/hour, $\bar{x}uv_{CO2+CH4}$ is the average gas flux from unvegetated habitats in mmol/L/m^2/hour, divided by 2 to average the flux from both habitats, divided by 10^{-3} to convert to grams, multiplied by 12.01 is the molecular weight of elemental carbon, and n is the number of days in each season category.

$$Equation\,10:\ \overline{\text{X}}\text{s gC/m}^2 = \left(\frac{\sum \overline{\text{X}}_{sd}}{N}\right)$$

Where $\overline{\text{X}}\text{s}$ is the mean seasonal loss of organic carbon in gC/m^2,
$\sum \overline{\text{X}}_{sd}$ is the sum of the average sample date losses for each season category and
N is the number of sample dates in that season category.

$$Equation\,11:\ \overline{\text{X}}\text{a gC/m}^2 = \sum \overline{\text{X}}\text{s}$$

Where $\overline{\text{X}}\text{a}$ is the mean annual loss of organic carbon in gC/m^2 and $\sum \overline{\text{X}}\text{s}$ is the sum of the average seasonal losses of organic carbon.

6.2.4 Seasonal and annual carbon budget

A seasonal carbon budget for the standardised wetland unit can be constructed for each habitat in each wetland using the data calculated in Equations 6 and 9. The budget for the areas of fringing vegetation is calculated using Equation 12 and includes all inputs and losses of organic matter.

Bokarup Swamp contains large open unvegetated areas within the wetland basin. The budget for this area is calculated using Equation 13 and does not include allochthonous and macrophyte litterfall or below ground structures or biofilm inputs of carbon, and losses are calculated only from the unvegetated fluxes of CO_2 and CH_4.

The uniform emergent macrophyte habitat is dominant in each wetland basin. The budget for this area is calculated using Equation 14 and excludes allochthonous inputs and includes all other inputs and losses of organic carbon. Whole habitat seasonal budgets are calculated by multiplying the seasonal results from the standardised wetland surface area for each habitat by the area of that habitat in each wetland basin from Table 2.5.

$$\textit{Equation}\,12:\ \mathrm{OCs}_{\mathrm{fv}}\ \mathrm{gC/m^2} = \sum(\overline{\mathrm{X}}\mathrm{s}_{\mathrm{fv}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{em}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{bg}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{chl}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{doc}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{b}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{mb}}) - \sum(\overline{\mathrm{X}}\mathrm{s}_{\mathrm{CO2+CH4}})$$

$$\textit{Equation}\,13:\ \mathrm{OCs}_{\mathrm{ow}}\ \mathrm{gC/m^2} = \sum(\overline{\mathrm{X}}\mathrm{s}_{\mathrm{chl}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{doc}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{mb}}) - \sum(\overline{\mathrm{X}}\mathrm{s}_{\mathrm{CO2+CH4}})$$

$$\textit{Equation}\,14:\ \mathrm{OCs}_{\mathrm{em}}\ \mathrm{gC/m^2} = \sum(\overline{\mathrm{X}}\mathrm{s}_{\mathrm{em}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{bg}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{chl}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{doc}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{b}} + \overline{\mathrm{X}}\mathrm{s}_{\mathrm{mb}}) - \sum(\overline{\mathrm{X}}\mathrm{s}_{\mathrm{CO2+CH4}})$$

Where $\mathrm{OCs}_{\mathrm{fv}}$ is the seasonal organic carbon balance in fringing vegetation habitat in $\mathrm{gC/m^2}$, $\mathrm{OCs}_{\mathrm{ow}}$ is the seasonal organic carbon balance in the open water habitat in $\mathrm{gC/m^2}$, $\mathrm{OCs}_{\mathrm{em}}$ is the seasonal organic carbon balance in the emergent macrophyte habitat in $\mathrm{gC/m^2}$ $\mathrm{Xs}_{\mathrm{fv}}$ is the average seasonal input from fringing vegetation, $\overline{\mathrm{X}}\mathrm{s}_{\mathrm{em}}$ is the average seasonal input from macrophytes, $\overline{\mathrm{X}}\mathrm{s}_{\mathrm{bg}}$ is the average input of below ground macrophyte structures, $\overline{\mathrm{X}}\mathrm{s}_{\mathrm{chl}}$ is the average seasonal input of water column production, $\overline{\mathrm{X}}\mathrm{s}_{\mathrm{doc}}$ is the average seasonal input from DOC, $\overline{\mathrm{X}}\mathrm{s}_{\mathrm{b}}$ is the average seasonal input from biofilm, $\overline{\mathrm{X}}\mathrm{s}_{\mathrm{mb}}$ is the average seasonal input from microbial biomass and $\overline{\mathrm{X}}\mathrm{s}_{\mathrm{CO2}}$ and $\overline{\mathrm{X}}\mathrm{s}_{\mathrm{CH4}}$ are the average seasonal losses of organic matter from carbon dioxide and methane respectively.

An annual carbon budget for the standardised wetland unit and for whole habitats can be constructed for each habitat in each wetland using the data calculated in Equations 7 and 10. All inputs and assumptions are the same as those described for seasonal carbon budgets. Equations 15, 16 and 17 calculate the annual input of organic carbon per standardised wetland unit for fringing vegetation, open water and macrophyte habitats respectively.

$$\textit{Equation}\,15:\ OCa_{fv}\ gC = \sum(\overline{X}a_{fv} + \overline{X}a_{em} + \overline{X}s_{bg} + \overline{X}a_{chl} + \overline{X}a_{doc} + \overline{X}a_{b} + \overline{X}a_{mb}) - \sum(\overline{X}a_{CO2} + \overline{X}a_{CH4})$$

$$\textit{Equation}\,16:\ OCa_{ow}\ gC = \sum(\overline{X}a_{chl} + \overline{X}a_{doc} + \overline{X}a_{mb}) - \sum(\overline{X}a_{CO2} + \overline{X}a_{CH4})$$

$$\textit{Equation}\,17:\ OCa_{em}\ gC = \sum(\overline{X}a_{em} + \overline{X}s_{bg} + \overline{X}a_{chl} + \overline{X}a_{doc} + \overline{X}a_{b} + \overline{X}a_{mb}) - \sum(\overline{X}a_{CO2} + \overline{X}a_{CH4})$$

Where OCa_{fv} is the organic carbon balance in fringing vegetation habitat in gC/wetland/year, OCa_{ow} is the organic carbon balance in the open water habitat in gC/wetland/year, OCa_{em} is the organic carbon balance in the emergent macrophyte habitat in gC/wetland/year, Xa_{fv} is the average annual input from fringing vegetation, $\overline{X}a_{em}$ is the average annual input from macrophytes, $\overline{X}s_{bg}$ is the annual input from below ground macrophyte structures, $\overline{X}a_{chl}$ is the average annual input of water column production, $\overline{X}a_{doc}$ is the average annual input from DOC, $\overline{X}a_{b}$ is the average annual input from biofilm, $\overline{X}a_{mb}$ is the average annual input from microbial biomass and $\overline{X}a_{CO2}$ and $\overline{X}a_{CH4}$ are the average annual losses of organic matter from carbon dioxide and methane respectively.

Seasonal wetland carbon budgets can be calculated using Equations 18. An annual carbon budget for each wetland is simply determined by summing the results of the four seasonal budgets.

$$\textit{Equation}\,18:\ OCs_{ST}\ gC = \sum(OCs_{fv} + OCs_{ow} + OCs_{em})$$

Where OCs_{ST} is the whole wetland carbon balance in that season in gC/wetland/year OCs_{fv} is the organic carbon balance in fringing vegetation habitat in gC/wetland/year, OCs_{ow} is the organic carbon balance in the open water habitat in gC/wetland/year, OCs_{em} is the organic carbon balance in the emergent macrophyte habitat in gC/wetland/year.

6.3 RESULTS

A strong seasonal cycle of carbon inputs and losses has been demonstrated in previous chapters with the dominance of summer inputs and losses of carbon and reduced inputs and losses of carbon in the winter period. Tables 6.1, 6.2 & 6.3 demonstrate this seasonal cycle is evident in each of the inputs and losses of carbon for Bokarup Swamp, Kodjinup Swamp and Noobijup Lake respectively. The data used to calculate average seasonal inputs and losses and standard errors are in Appendix 3. Allochthonous litter dominates the carbon sources in all wetlands, being highest in Bokarup Swamp at 251.30 SWU/year and least in Noobijup Lake at 93.21 SWU/year. Annual inputs from emergent macrophytes were dominated by above ground leaf litter fall (ranging from 34.52 to 47.76 SWU/year) with below ground structures providing around one third of the above ground inputs in Bokarup Swamp and Noobijup Lake. Substantially higher inputs from below ground structures in Kodjinup Swamp (42.69 SWU/year) contributed to Kodjinup Swamp having the highest overall input from macrophyte sources. Water column productivity from phytoplankton provided a relatively small source of carbon within each wetland ranging from only 0.34 to 0.68 SWU/year and varied seasonally with higher levels in summer. DOM concentrations also followed the seasonal trends found in litterfall data with highest concentrations in the summer period in all wetlands. As with water column productivity, DOM provided a small pool of carbon with very low values in Bokarup Swamp (1.35 SWU/year) and Noobijup Lake (1.21 SWU/year) but a substantially higher input of 3.45 SWU/year in Kodjinup Swamp. The low levels of productivity within the water column were reflected in the biofilm data, with Bokarup and Kodjinup Swamps having very low annual inputs to the carbon budget from biofilms (4.321 & 1.09 SWU/year respectively). On the other hand, biofilms in Noobijup Lake contributed substantially to the carbon budget (28.18 SWU/year) due to more permanent water levels and a higher density of emergent stems as substrata.

The transformation of carbon inputs into microbial biomass in the surface sediments of each wetland contributed only small amounts of carbon to the annual budget. Values ranged from 0.62 SWU/year in Noobijup Lake to 1.70 SWU/year in Kodjinup Swamp. Losses of organic matter in all wetlands and seasons were dominated by

Table 6.1. Mean (±SE) carbon inputs and losses per SWU standardised to gC/m^2/season for each sampling period in Bokarup Swamp. n/a indicates no standard error was calculated due to insufficient samples for that parameter or season. Autumn has no standard errors as there is only one autumn sample period.

	Winter	***SE***	**Spring**	***SE***	**Summer**	***SE***	**Autumn**	**Annual**	***SE***
Allochthonous litterfall	37.872	*n/a*	43.355	*12.63*	115.830	*23.14*	54.244	251.301	*35.96*
Autochthonous litterfall	8.242	*n/a*	6.780	*0.56*	17.548	*5.06*	8.242	40.813	*4.94*
Macrophyte root biomass	3.185	*n/a*	3.185	*n/a*	3.185	*n/a*	3.185	12.738	*n/a*
Water column production	0.012	*0.01*	0.077	*0.02*	0.316	*0.23*	0.278	0.682	*0.14*
DOM	0.496	*0.15*	0.248	*0.05*	0.543	*0.13*	0.070	1.358	*0.22*
Biofilm	0.000	*n/a*	0.908	*0.36*	3.413	*3.04*	0.000	4.321	*1.61*
Microbial Biomass	0.160	*0.02*	0.233	*0.05*	0.312	*0.03*	0.232	0.938	*0.06*
CO_2 - Unvegetated	1.026	*0.17*	1.754	*N/a*	2.085	*0.35*	2.218	7.083	*0.53*
CO_2 - Vegetated	0.807	*0.13*	1.036	*N/a*	1.014	*0.07*	1.109	3.966	*0.13*
CH_4 - Unvegetated	0.518	*0.06*	0.854	*N/a*	0.899	*0.04*	0.547	2.818	*0.20*
CH_4 - Vegetated	0.569	*0.10*	1.129	*N/a*	1.061	*0.06*	0.871	3.630	*0.25*
Total CO_2	0.917	*0.155*	1.395	*n/a*	1.549	*0.208*	1.663	5.524	*0.329*
Total CH_4	0.662	*0.100*	0.945	*n/a*	0.956	*0.049*	0.828	3.392	*0.137*

Table 6.2. Mean (±SE) carbon inputs and losses per SWU standardised to gC/m^2/season for each sampling period in Kodjinup Swamp. n/a indicates no standard error was calculated due to insufficient samples for that parameter or season. Autumn has no standard errors as there is only one autumn sample period.

	Winter	***SE***	**Spring**	***SE***	**Summer**	***SE***	**Autumn**	**Annual**	***SE***
Allochthonous litterfall	24.772	*n/a*	26.248	*1.48*	70.680	*15.67*	43.408	165.108	*21.35*
Autochthonous litterfall	1.089	*n/a*	8.912	*2.58*	29.681	*6.07*	8.085	47.767	*12.33*
Macrophyte root biomass	10.673	*n/a*	10.673	*n/a*	10.673	*n/a*	10.673	42.690	*n/a*
Water column production	0.000	*n/a*	0.029	*0.02*	0.084	*0.02*	0.018	0.131	*0.03*
DOM	0.110	*n/a*	1.397	*0.90*	1.436	*0.35*	0.515	3.458	*0.65*
Biofilm	0.000	*n/a*	0.350	*0.24*	0.644	*0.16*	0.099	1.093	*0.28*
Sediment microbial biomass	0.284	*0.03*	0.337	*0.08*	0.684	*0.25*	0.401	1.706	*0.17*
CO_2 - Unvegetated	1.344	*0.08*	1.294	*N/a*	1.874	*0.09*	2.022	6.534	*0.36*
CO_2 - Vegetated	1.123	*0.04*	1.787	*N/a*	1.680	*0.21*	1.988	6.578	*0.37*
CH_4 - Unvegetated	0.491	*0.14*	0.717	*N/a*	0.946	*0.02*	0.360	2.514	*0.25*
CH_4 - Vegetated	0.695	*0.01*	1.199	*N/a*	1.316	*0.02*	0.642	3.851	*0.34*
Total CO_2	1.234	*0.06*	1.540	*N/a*	1.777	*0.14*	2.005	6.556	*0.33*
Total CH_4	0.593	*0.07*	0.958	*n/a*	1.131	*0.02*	0.501	3.183	*0.29*

Table 6.3. Mean (±SE) carbon inputs and losses per SWU standardised to gC/m^2/season for each sampling period in Noobijup Lake. n/a indicates no standard error was calculated due to insufficient samples for that parameter or season. Autumn has no standard errors as there is only one autumn sample period.

	Winter	***SE***	**Spring**	***SE***	**Summer**	***SE***	**Autumn**	**Annual**	***SE***
Allochthonous litterfall	21.606	*n/a*	12.798	*7.64*	29.715	*9.67*	29.097	93.216	*7.91*
Autochthonous litterfall	7.958	*n/a*	4.238	*1.87*	16.365	*2.03*	5.967	34.528	*5.37*
Macrophyte root biomass	3.095	*N/a*	3.095	*n/a*	3.095	*n/a*	3.095	12.382	*n/a*
Water column production	0.008	*0.03*	0.042	*0.02*	0.247	*0.09*	0.044	0.341	*0.10*
DOM	0.353	*0.01*	0.394	*0.17*	0.339	*0.09*	0.123	1.210	*0.12*
Biofilm	0.625	*n/a*	1.535	*0.29*	10.140	*7.98*	15.887	28.187	*7.28*
Sediment microbial biomass	0.058	*0.08*	0.126	*0.06*	0.288	*0.06*	0.158	0.629	*0.09*
CO_2 - Unvegetated	0.947	*0.01*	1.430	*n/a*	1.670	*0.14*	1.285	5.332	*0.30*
CO_2 - Vegetated	0.778	*0.09*	0.914	*n/a*	1.047	*0.13*	1.094	3.833	*0.14*
CH_4 - Unvegetated	0.378	*0.02*	0.526	*n/a*	0.584	*0.04*	0.549	2.037	*0.09*
CH_4 - Vegetated	0.677	*0.01*	0.697	*n/a*	0.894	*0.07*	0.840	3.109	*0.10*
Total CO_2	0.863	*0.04*	1.172	*n/a*	1.359	*0.14*	1.189	4.583	*0.20*
Total CH_4	0.528	*0.05*	0.612	*n/a*	0.739	*0.05*	0.694	2.573	*0.09*

atmospheric fluxes of carbon dioxide, with unvegetated habitats contributing substantially more carbon dioxide than vegetated areas. The annual flux of carbon dioxide was lowest in Noobijup Lake (4.58 SWU/year) and highest in Kodjinup Swamp (6.55 SWU/year). The annual flux of methane followed the same seasonal cycle as carbon dioxide with higher exports in summer however, fluxes of methane were higher from vegetated areas. The annual export of methane were generally around half those of carbon dioxide in all wetlands ranging from 2.57 SWU/year in Noobijup Lake to 3.39 SWU/year in Bokarup Swamp.

The calculation of a seasonal and annual carbon budget for each of the major habitat types in each wetland demonstrates that all habitats except one are currently in net gain of carbon (Table 6.4). The exception is the unvegetated area in Bokarup Swamp that is losing organic matter in all seasons at a rate of 2.55 SWU/year. The carbon budgets show that a large proportion of the carbon gain occurs in the summer period, despite the increased exports of organic matter during this period. This seasonality is most pronounced in the fringing vegetation habitat where allochthonous inputs are dominant. The areas of fringing vegetation around the wetland margins have the highest net gain of carbon as they receive substantial input from allochthonous sources. Bokarup Swamp has the highest gain of carbon in this habitat at 303.23 SWU/year with only 8.92 SWU/year exported as carbon gas from these habitats. In comparison, the large area of macrophytes in Bokarup Swamp has substantially lower annual gain of carbon at 50.58 SWU/year. The inputs of allochthonous material to the area of fringing vegetation in Kodjinup Swamp has again resulted in this habitat having a high net carbon gain of 252.22 SWU/year and a minimal loss of 9.74 SWU/year. Kodjinup Swamp has the highest net gain of carbon in the macrophyte habitat with inputs elevated by a large contribution from below ground macrophyte structures. Noobijup Lake has the lowest input from allochthonous sources and correspondingly has the lowest net gain of carbon in this habitat of 163.34 SWU/year despite the lowest export of carbon gases (7.16 SWU/year). Inputs in the macrophyte habitat are increased in Noobijup Lake by the high biomass of biofilms, contributing to the 68.91 SWU/year accumulating in this habitat.

Table 6.4. Mean seasonal and annual organic carbon budgets per SWU for each major habitat type in Bokarup Swamp, Kodjinup Swamp and Noobijup Lake.

Season	**SWU**	**Bokarup Swamp**			**Kodjinup Swamp**		**Noobijup Lake**	
		Fringing	**Unvegetated**	**Macrophytes**	**Fringing**	**Macrophytes**	**Fringing**	**Macrophytes**
Winter	Inputs	49.97	0.67	11.60	36.93	12.05	33.70	11.74
	Losses	1.58	0.92	1.58	1.83	1.83	1.39	1.39
	Total	*48.39*	*-0.25*	*10.02*	*35.10*	*10.22*	*32.31*	*10.35*
Spring	Inputs	54.79	0.56	11.18	47.95	20.30	22.23	9.04
	Losses	2.34	1.39	2.34	2.50	2.50	1.78	1.78
	Total	*52.45*	*-0.84*	*8.84*	*45.45*	*17.80*	*20.44*	*7.25*
Summer	Inputs	141.15	1.17	24.77	113.88	41.77	60.19	30.14
	Losses	2.51	1.55	2.51	2.91	2.91	2.10	2.10
	Total	*138.64*	*-0.38*	*22.27*	*110.97*	*38.86*	*58.09*	*28.04*
Autumn	Inputs	66.25	0.58	11.94	63.20	19.28	54.37	25.15
	Losses	2.49	1.66	2.49	2.51	2.51	1.88	1.88
	Total	*63.76*	*-1.08*	*9.45*	*60.69*	*16.77*	*52.49*	*23.27*
Annual	Inputs	312.15	2.98	59.49	261.95	93.39	170.49	76.07
	Losses	8.92	5.52	8.92	9.74	9.74	7.16	7.16
	Total	*303.23*	*-2.55*	*50.58*	*252.22*	*83.65*	*163.34*	*68.91*

To determine the total net gain or loss of carbon for each habitat area and for the entire wetland basin, the input or loss per SWU was multiplied by the area of each habitat (Section 2.6.4) within each wetland. The results are shown in Table 6.5 and demonstrate the enormous amounts of carbon stored each year in the peat sediments of these wetlands. Bokarup Swamp retains 17546.02 kgC/year with around the same amount contributed from macrophyte and fringing habitats. This wetland has the least residual carbon stored per year of all wetlands and may be due to the large unvegetated area that exports 316.22 kgC/year from the wetland basin. Kodjinup Swamp provides a sink for 27423.59 kgC/year, with almost two thirds of the carbon stored in the macrophyte habitat. The largest sink of carbon of the three study wetlands was Noobijup Lake, which stored 52185 kgC/year within the wetland basin, with three quarters of carbon stored in the extensive macrophyte habitat.

Table 6.5. Annual carbon budget for the area of each major habitat and for the entire wetland basin for Bokarup Swamp, Kodjinup Swamp and Noobijup Lake.

	Inputs (kgC)	Losses (kgC)	Total (kgC)
Bokarup			
Fringing	8958.73	255.89	8702.84
Open Water	369.89	686.11	-316.22
Macrophytes	10774.09	1614.70	9159.39
Total			*17546.02*
Kodjinup			
Fringing	9377.94	348.64	9029.30
Macrophytes	20535.78	2141.49	18394.29
Total			*27423.59*
Noobijup			
Fringing	13298.42	558.12	12740.30
Macrophytes	43540.88	4095.73	39445.15
Total			*52185.45*

6.4 Discussion

The long term accumulation of peat suggests that all of these wetlands have been in net gain of carbon for a considerable period. The construction of an annual carbon budget reveals that each wetland basin is currently a sink for tens of thousands of kilograms of carbon each year. The unvegetated area at Bokarup Swamp that was created by a fire event in the recent past demonstrates the capacity for peatlands to revert from carbon sinks to carbon sources following disturbance. It is the only habitat studied that is a source of carbon, contributing over 300 kgC/year to the global carbon budget and highlights the role of macrophytes not only as a carbon source, but also as an integral part of a functioning system. Alterations to local hydrology, water quality and the management of the surrounding forests have the potential to turn these wetlands from a carbon sink to a carbon source, which may have important local, regional and global consequences.

The rates of accumulation of organic matter in the basins of these wetlands is comparable to many Northern Hemisphere peatland systems. The accumulation of carbon in the macrophyte habitat ranged from 50.58 to 83.65 SWU/year and was dominated by above and below ground inputs from macrophytes. A study of the carbon dynamics in arctic tundra lakes found that benthic and macrophytic production contributed 50% of the input to the annual carbon budget, with 20% from phytoplankton and 30% from allochthonous sources (Ramlal *et al.* 1994). This is supported by Trumbore *et al.* (1999) who constructed a carbon budget for northern boreal peatlands. These wetlands were in net gain of carbon between 31 to 180 gC/m^2/year with the higher range associated with wetlands with the highest proportion of sedge vegetation. Arctic tundra wetlands that were dominated by autochthonous production also retained similar amounts of carbon to the study wetlands (92 gC/m^2/year, Hobbie *et al.* 1998).

The fringing vegetation habitat accumulated carbon at a much faster rate than the macrophyte areas, ranging from 163.34 to 303.23 SWU/year. Inputs of carbon ranging from 489 to 1750 g C/m^2/year have been found in peatland systems that are dominated by allochthonous inputs (Reader & Stewart 1972). However, despite the large input of organic matter, wetlands had a long-term net gain of 26 to 51 gC/m^2/year, losing almost 97% of the inputs through decomposition (Reader and Stewart 1972). The loss of carbon from the study wetlands ranged from 7.16 to 9.74 gC/m^2/year, and is relatively low compared to losses from Northern Hemisphere wetlands (eg. -29.98 gC/m^2/year Rivers *et al.* 1998; 40 to 52 gC/m^2/year Alm *et al.* 1999; 40 gC/m^2/year Morris & Bradley. 1999). The large loss of carbon in some wetlands means that not all peatlands accumulate peat at a constant rate, and others are currently in net loss of carbon. The carbon balance of a temperate poor fen revealed that under present environmental conditions they were losing 145 gC/m^2/year (Carroll & Crill 1997). Rivers *et al.* (1998) displayed the importance of quantifying annual variability in carbon accumulation rates varied from -28.98 to 50.38 gC/m^2/year in circumboreal peatlands depending on the local climatic and hydrological conditions. Studies of raised bogs have shown that accumulation rates can even vary across an individual wetland, with patterns of micro-relief controlling rates of loss or accumulation (Karofeld 1998). The carbon balance in northern peatlands is a balance between losses and gains based on carbon supply, hydrology and climatic conditions (Alm *et al.* 1999; Waddington & Roulet 2000). Despite the relatively small losses of carbon compared to inputs, the alterations of these factors in Australian temperate wetlands may have the same consequences for carbon cycling.

An alteration to the hydrologic regime is the most pronounced form of wetland disturbance, as the hydroperiod is the primary factor controlling their structure and function. Prolonged flooding from increased run-off or the artificial drainage of run-off into wetlands has the potential to affect many aspects of the wetland carbon cycle. Kelly *et al.* (1997) experimentally flooded a boreal forest wetland to 1.3m above its previous water level. The wetland changed from being a small natural carbon sink (6.6 gC/m^2/year) to a large source losing 130 gC/m^2/year to the atmosphere, caused by the death of the aquatic vegetation and increased microbial production of carbon dioxide and methane. The survival of dominant emergent macrophytes in Australian temperate wetlands is also closely linked to inundation regime, being unable to survive inundation of more than 1m for prolonged periods (Froend & McComb 1994). The removal of macrophytes from a wetland severely alters the carbon cycle, as seen in the unvegetated area of Bokarup Swamp being the only habitat having a net loss of carbon from reduced inputs and increased decomposition. In the other habitats, it may be the permanence of water levels at or above the sediment surface that explain the low rates of carbon loss and increased depth of these deposits compared to other peat forming systems.

At the other extreme, drought can lead to the aerobic exposure of organic sediments and increase decomposition rates (Mallik & Wein 1986; Freeman *et al.* 1994). Alm *et al.* (1999) noted that the difference between a raised bog being a source or sink was not methane emissions during inundation, but increased carbon dioxide releases during periods of drought. As in many ecosystems, fire in wetlands often coincides with drought conditions. Peatland fires become possible when natural or artificial drainage lowers the water table for a sufficient period of time. The magnitude of the impact of fire on the physical conditions, biological activity and vegetation recovery of peatlands depends on the timing and intensity of the burn (Eframova and Eframov 1994). Horwitz *et al.* (1998) documented the loss of 8700 cubic metres of peat up to 3800 years old, the removal of overstory vegetation and severe cracking of remaining peat soils as a result of a high intensity fire. Alternatively, no massive exports of sediment carbon were quantified over the two decades following a cool fire from seven boreal forest wetlands (Slaughter *et al.* 1998), although gross fluxes of carbon immediately followed the fire. Pitkanan *et al.* (1999) found that repeated fires slowed down the progress of vertical peat accumulation and resulted in great carbon losses over the long-term. In addition to gross changes in sediment carbon stores, the burning of peat can influence rates of decomposition. Enhanced emissions of methane and carbon dioxide were measured immediately after each event and over a period of years following three controlled burns in Florida wetlands (Levine *et al.* 1990). These data are supported by increased carbon losses from the unvegetated area in Bokarup Swamp, in which the emergent vegetation and up to one metre of surface peat was removed by fire several decades ago.

Inputs from allochthonous sources contributed substantial amonts of organic matter to the margins of the study wetlands. The result is that fires do not have to enter a wetland in order to disrupt the carbon budget. Sizeable proportions of fires ignite naturally, principally by lightning. However, the instances of managed prescription fires in wetland systems for reducing the risk of wildfire, maintaining biodiversity and water quality and waterfowl management is increasing worldwide (Kirby *et al.* 1988). Within the Muir-Unicup region of south-western Australia fire is a natural phenomenon because of summer drought and lightning storms. It is also a management strategy of conservation agencies for the regeneration of logged areas and as a fuel reduction and fire suppression strategy. The majority of wetlands occur within reserves actively managed for fuel reduction prescribed burning, which has the potential to disrupt inputs from allochthonous sources and impact short and long term carbon cycling. The impactof fire on wetland carbon cycles can occur as a direct loss of organic substrate through combustion and compaction, removal of vegetation contributing to peat accumulation and accelerating decomposition through increased aerobic exposure of peat surfaces (Pitkanen *et al.* 1999).

Climate change models all predict higher temperatures and reduced precipitation for vast areas of the world (Hogenbirk & Wein 1991). The most serious effects for wetlands could arise through an increased frequency of summer drought, which could reduce the persistence of waterlogging and therefore compromise the very factor that characterises wetlands. Warmer and drier postglacial periods have been strongly correlated with increased severity and frequency of drought and fire (Johnson & Larson 1991), with future global warming having the potential to cause similar changes in drought and fire regimes (Overpeck *et al.* 1990). However, Hobbie *et al.* (1998) simulated the effects of predicted changes in carbon dioxide and temperature with global warming on a peatland carbon budget. A four to five fold increase was found in the rates of carbon accumulation after 150 years of increased levels, indicating that it is unlikely that warming alone will enhance carbon loss to the atmosphere. Predictions of climate change on wetland habitats are inconclusive and appear dependent on geographical location and wetland type. As such, the impact of predicted climate change on the carbon budgets of the study wetlands cannot be generalised from other studies.

Inputs into the wetland margins were dominated by allochthonous litterfall from tree species such as *Melaleuca* and *Eucalyptus*, whereas the main wetland basin was dominated by above and below ground inputs from emergent macrophytes. The net gain of carbon in the fringing vegetation habitat was up to six times greater than the carbon gain in the macrophyte habitat. This has important implications for the development of these wetlands, as it appears that long-term peat growth involves vertical accumulation in the main basin and a lateral encroachment of the wetland margins. However, rates of lateral encroachment are dependent on, and more susceptible to, the influence of hydrological regime, resulting in different rates of accumulation in the wetland margins to the central basin. Rates of carbon accumulation have been shown to vary in different parts of raised bogs, controlled by fires, hydrological, topographical and edaphic factors (Makila 1997). The processes involved in the vertical accumulation and lateral encroachment of peat in these large basin wetlands has not been described, and may be unique to these wetlands occurring within a forested landscape.

The selection of the method by which a carbon budget is constructed will influence the budget result, temporal scale over which it applies and interpretation of results (Trumbore *et al.* 1999). The use of radiocarbon dated peat profiles to determine long-term rates of accumulation have generally produced lower estimates of carbon accumulation (eg. Kelly *et al.* 1997; Makila 1997; Aucour *et al* 1999). Equally, sources of error that influence the carbon budget are apparent in this study. The major assumption that the atmospheric flux of carbon is the only export precludes any losses through groundwater exchange. Losses from leaching of DOM have been estimated between 3.5 and 8.6 gC/m^2/year in Finnish peatlands (Alm *et al.* 1999). The hydrology of the Muir-Unicup wetlands is complex and relatively unknown. The reliance of each of these wetlands on groundwater is also unknown, resulting in the assumption that each wetland was disconnected from the groundwater and the only losses were atmospheric gas fluxes. The result has the potential for underestimating the loss of carbon from these wetlands.

6.4.1 Conclusion

The use of carbon dating peat profiles to measure carbon accumulation will always demonstrate a net gain of carbon if peat is present, as measurements are derived from the long-term accumulation of carbon. These studies do not elucidate the contemporary processes involved in the accumulation of carbon, nor examine if wetlands are in net gain or loss of carbon under current conditions. For example, Alm *et al.* (1999) measured losses of carbon during an extended summer drought even though annual rainfall was above the long-term average. This highlights the need for information on wetland processes occurring at temporal scales relevant to current conditions as well as carbon dating of sediments to examine long term trends in carbon accumulation. The descriptive model in Chapter 7 combines data from this chapter, which quantifies the current rates of organic matter inputs with palaeoecological data, to estimate long-term rates of peat accumulation in each of the study wetlands.

CHAPTER 7

MODELLING ORGANIC MATTER ACCUMULATION

7.1.1 Peat accumulation models

Organic matter accumulation is a slow process and takes variable lengths of time, and for this reason the historical chronology of peat formation is difficult to measure. The rate at which peat accumulates has been determined for a number of sites in the Northern Hemisphere (eg. Wildi 1978; Clymo 1984; Makila 1997; Karofeld 1998). These estimates have been mainly constructed from measurements of height, weight and age of existing peat cores. Table 7.1 documents some of the models developed to simulate peat accumulation, however these are predominantly for raised bogs and boreal wetlands dominated by *Sphagnum* species in the Northern Hemisphere. A model describing long-term rates of organic matter accumulation and the processes influencing wetland development has not been developed for Australian peatland systems.

Jenny *et al.* (1949) first proposed a model of organic matter accumulation in soils. This model assumed that the final amount of organic matter accumulated in an ecosystem can be calculated from a mathematical equation based on a geometric progression. The basis of the model is that decay is exponential, which assumes a proportion of the original material will always remain. This model of organic matter accumulation has been shown to hold true for numerous peat forming systems (Clymo 1984). Early researchers such as Olsen (1963), Walker (1970), Reader & Stewart (1972) and Jones & Gore (1978) used measurements of organic inputs minus losses from decomposition to develop simple carbon budget models.

Table 7.1 Characteristics of models of peatland development.

Author(s)	Ecosystem	Simulation
Olsen (1963)	English peat bog	Short-term accumulation budget (income – loss)
Walker (1970)	English peat bog	Development of peat storage volume with disturbance from harvesting and fertilisation.
Reader & Stewart (1972)	Manatoba peatland	Short-term accumulation budget (income – loss)
Clymo (1978)	English peat bog	Development of depth/age profiles based on bulk density and age relationships
Jones & Gore (1978)	English peat bog	Development of peat storage volume with disturbance from harvesting and fertilisation (refinement of Walker 1970).
Wildi (1978)	Swiss peat bog	Bog/fen succession based on slope, nutrient and age profiles.
Ingram (1982)	English peat bog	Vertical and lateral expansion of raised bogs.
Clymo (1984)	English *Sphagnum* bog	Sediment carbon accumulation based on organic matter production/supply against long-term decay/compaction.
Charman *et al.* (1994)	Canadian forested peatland	Sediment carbon accumulation based on organic matter production/supply against long-term decay/compaction.
Ramalal *et al.* (1994)	Canadian tundra wetland	Short-term accumulation budget (Income – loss)
Aaviskoo (1995)	Estonian mires	Carbon accumulation/vegetation dynamics and different spatial scales.
Almquist & Foster (1995)	Swedish fens and raised bogs	Sediment carbon accumulation/lateral expansion based on organic matter production/supply against long-term decay/compaction.
Belyea & Warner (1996)	Canadian *Sphagnum* bog	Sediment carbon accumulation based on organic matter production/supply against long-term decay/compaction.

Table 7.1. (continued) Characteristics of peatland development models.

Author(s)	Ecosystem	Simulation
Kelly *et al.* (1997)	Boreal forest wetland	Short-term accumulation budget (Income – loss)
Makila (1997)	Finnish raised bog	Sediment carbon accumulation/lateral expansion based on age/depth relationships.
Karofeld (1998)	Estonian raised bogs	Sediment carbon accumulation based on organic matter production/supply against long-term decay/compaction.
Latter *et al.* (1998)	English pennine peat bogs	Long-term decomposition regressions
Okland & Ohlson (1998)	Scandinavian peat bogs	Age/depth relationships incorporating compaction coefficients
Alm *et al.* (1999)	Finland boreal bog	Short-term accumulation budget (Income – loss) including environmental conditions

It was not until 1978 that Clymo developed a model based on differential equations, using age, bulk density and long-term decay rates to simulate long-term peat accumulation within and across defined functional soil layers in a *Sphagnum* dominated peat bog. According to Clymo's (1984) model, organic matter inputs and decay followed the principles of Jenny *et al.* (1949), however the decay and transfer of organic matter were further quantified for defined peat layers. The concept of two functional soil layers was first used by Ingram (1978), who termed the upper layer the *acrotelm* and the lower layer the *catotelm*. The distinction of the two layers was based on the degree of variability and relative rates of biological and physical processes such as microbial activity, energy and matter exchange, oxygenation and water content. These criteriamake the distinctions between the acrotelm and catotelm definitions applicable to many peat producing systems. Furthermore, the mechanistic representation of organic matter accumulation within the 1978 model of Clymo permits its use in a wider range of peat forming habitats. Long-term rates of organic matter inputs estimated from radiocarbon dates were used to accurately describe the rates and factors influencing long-term peat accumulation in *Sphagnum* peat bogs (Clymo 1984). A better understanding of short-term accumulation rates, particularly in wetland systems where organic matter sources are derived from numerous sources (autochthonous and allochthonous) may be achieved using data derived from present-day carbon budgets.

The model of Clymo (1984) requires detailed knowledge of the stratigraphy of the peat deposit, long-term decay rates and the rates of transfer between two defined peat layers using numerous radiocarbon dates and bulk densities. This study is limited to three radiocarbon dates from one core in each wetland and no data are available on long-term decay rates throughout the profile or the rates of organic matter transfer between the three layers in each peat profile. As such, this chapter can only use data generated from the present-day carbon budget in the simple model of Jenny *et al.* (1949), combined with radiocarbon dates from each wetland, to model the accumulation of organic matter in the study wetlands.

7.1.2 Peat accumulation rates using sediment dating

With a range in excess of 180 years, ^{210}Pb dating is a valuable tool for examining the environmental history of Australia since European settlement (Gale *et al.* 1995). This method is invaluable for establishing the timing of ecological changes, especially in lakes where long-term limnological data are lacking. ^{210}Pb is a naturally occurring radionuclide that has a half-life of 22.6 years (Appleby & Oldfield 1984). The dating of cores requires the estimation of unsupported ^{210}Pb activity (atmospherically derived) and the application of an appropriate dating model (Appleby & Oldfield 1978). The reliability of ^{210}Pb dated sediments in aquatic habitats has been supported through the use of other techniques such as ^{137}Cs (Gerritse *et al.* 1995; Oldfield *et al.* 1995) and pollen analysis (Heijnis *et al.* 1987).

^{210}Pb dating has been extensively used to determine sedimentation rates of lacustrine and other sediments (Brenner *et al.* 1994). Several studies have used ^{210}Pb to successfully evaluate recent peat accumulation rates in Northern Hemisphere ombrotrophic bogs

(Oldfield *et al.* 1979; Richardson 1986; Clymo *et al.* 1990; Oldfield *et al.* 1995) and *Sphagnum* dominated bogs (Kelman-Weider 1994; Novak *et al.* 1994; Belyea & Warner 1996). The use of ^{210}Pb in Australia as a tool for examining sedimentation rates is widespread in wetlands (Smith & Hamilton 1992; Gale *et al.* 1995; Haworth *et al.* 1999), rivers (Wasson *et al.* 1987; Gerritse *et al.* 1995; Wallbrink *et al.* 1998) and estuaries (Gerritse *et al.* 1998). There are fewer Australian studies targeting wetlands with organic soils (eg. Head 1988; Gell *et al.* 1993; Dodson *et al.* 1998).

Obtaining age estimates from deeper sediments allows the examination of long-term trends in sediment accumulation. ^{14}C is a naturally occurring radioisotope with a half life of 5370 years (Rucklidge 1984). The ubiquitous presence of ^{14}C in biological materials (eg. wood, peat, soils, bones, shells) enables carbon to be dated and long-term sedimentation rates to be quantified (Goh 1991). The time frame of the ^{14}C dating technique from 200 to 40 000 years before present spans a period of important global environmental change, making it a useful technique in sediment, climate, hydrological and ecological studies.

^{14}C has been used extensively for dating sediments and determining long-term organic matter accumulation rates in aquatic systems (eg. Martel & Paul 1974; Shepphard *et al.* 1979; Kubiw *et al.* 1989; Meyers & Takemura 1997; Wei *et al.* 1998). Organic sediments provide a reliable dating material, as good agreement has been found between ^{14}C and other dating techniques, and peat is generally formed *in situ* (Geyh *et al.* 1971). This allows radiocarbon dating to be used for determining long-term carbon accumulation rates in these habitats. Radiocarbon dating to examine past changes in rates of net carbon sequestration in boreal peatlands has been used to explore climate trends (Oldfield *et al.* 1997; Karofeld 1998) and hydrological regimes (Nicholson & Vitt 1994; Makila 1997). Long-term carbon accumulation rates in boreal peatlands using ^{14}C analysis were also used to examine the process of raised bog development (Korhola *et al.* 1995).

Although Northern Hemisphere studies dominate this literature, the use of radiocarbon dating in Australian lacustrine sediments has been well documented. Leaney *et al.* (1995) and Cock *et al.* (1999) examined the hydrological history of deep South Australian lakes, relating changes in sedimentation history to past climatic regimes. The age of basal peat deposits in south-eastern Australia wetlands have been documented by Crowley & Kershaw (1994) and Head (1988), accumulation rates of tropical wetland peats using radiocarbon dating were examined by Bell *et al.* (1989) and Macphail *et al.* (1999) determined the chronology of deposits in south-west Tasmanian peat mounds. In south-western Australia, radiocarbon dating has been extensively used to determine the age of peat deposits in wetland systems (eg. Newsome & Pickett 1993; Pickett & Newsome 1997; Dodson & Lu 2000). A recent study by Horwitz *et al.* (1998) in south-western Australia used radiocarbon dating of cores to estimate peat loss from a wetland as a result of an escaped management fire.

Wetland carbon budgets such as those described by Ramlal *et al.* (1994) and Kelly *et al.* (1997) and in Chapter 6 of this thesis quantify net gains or losses of carbon, and are invaluable for assessing the impact of environmental conditions or management regimes on carbon availability. They are generally developed from short-term observations and examine site specific changes from disturbance such as altered hydrology, nutrient enrichment or peat harvesting. Without long term accumulation estimates from sediment dating, these carbon budgets are limited to the interpretation of recent (decadal) accumulation processes as they do not allow for continued *in situ* decomposition or compaction processes. A combination of data quantifying short and long-term processes allows present day carbon budget data to be placed in the context of long-term wetland development.

This chapter uses sediment dating techniques and an organic matter budget to quantify short and long-term rates of organic matter accumulation. Surface sediments are dated using ^{210}Pb with ^{14}C analyses used to examine long-term accumulation rates. The results of the carbon budget for each wetland are then used in conjunction with sediment dates to quantify both short-term and long-term accumulation rates using a simple quantitative model. The development of this model will allow the impact of recent (decadal) and long-term (millennial) environmental changes on wetland organic matter dynamics to be explored.

7.2 METHODS

7.2.1 Sediment dating

Maximum depth to mineral substrate was determined in each wetland by probing with a 4m length of 20mm wooden dowel. A core was taken from the part of the wetland which had the deepest peat deposit. At the chosen site, sediment cores were progressively removed from the one location using a D-section sampler until mineral substrate was reached. Samples were taken in July 1997, when water levels had reached their lowest annual level.

The determination of recent accumulation rates was determined using ^{210}Pb analysis of the surface 20cm of peat. Bokarup and Kodjinup Swamps each had an unconsolidated slurry of organic material at above the sediment surface around 20 cm thick. The sediment surface for the purposes of this study was defined as the point where consolidated surface began. One cm sections of sediment were removed at the following intervals: 0-1, 1-2, 2-3, 3-4, 4-5, 6-7, 9-10, 12-13, 15-16 and 19-20 cm from the sediment surface This represented a compromise between temporal resolution and estimating the depths at which reliable dates may be obtained. Each section was placed in an individually labelled glass vial for ^{210}Pb analysis and stored on ice until returned to the laboratory. The ^{14}C samples were taken from 2cm sections immediately above the Fibric/Hemic and Hemic/Sapric peat delineation in each wetland, and from a 2cm basal section immediately above the mineral substrate. The depths varied according to each wetlands' stratigraphy. Samples were taken at 22, 172cm and 278cm in Bokarup Swamp, 38, 69cm and 132cm in Kodjinup Swamp, and 24, 72cm and 154cm in Noobijup Lake. All samples were oven dried at 90°C until constant weight in a Contherm Series 5 oven housed at Edith Cowan University and returned to a labelled sterile glass.

^{210}Pb analysis was carried out at the Australian Nuclear Science and Technology Organisation (ANSTO) Environmental Radiochemistry Laboratory at the Australian Institute of Nuclear Science and Engineering (AINSE), Lucas Heights facility. Samples were pre-treated to remove fine roots and modern plant material prior to analysis. ^{210}Pb activity was determined by measuring the granddaughter ^{210}Po, which was assumed to be in secular equilibrium with ^{210}Pb. Ground samples of 2.0 g (dry weight) were spiked with ^{208}Po as a yield tracer and leached with hot concentrated acids (HCl), centrifuged and the solid phase removed. Polonium was extracted from the liquid phase using 1% diethylammonium diethyl dithiocarbonate and plated onto polished silver discs at 90°C. The ^{210}Po activity was measured by isotope dilution and alpha spectrometry (using passivated implanted silicon detectors) of the silver source (Gale *et al.* 1995). Calculations were made according to the Constant Initial Concentration (CIC) model. Determination of the supported ^{210}Pb activity was carried out using alpha spectrometry to measure ^{226}Ra peaks following precipitation of a radium-barium sulphate onto a membrane filter. The activity of the supported ^{210}Pb in the sediments was assumed to be in equilibrium with that of ^{226}Ra, whilst total ^{210}Pb activity was taken to equal ^{210}Po activity. The activity of the unsupported ^{210}Pb was thus determined by subtracting the supported from the total ^{210}Pb activity. Sedimentation rates were determined from the slope of the least-square fit for ^{210}Pb excess values plotted versus depth.

Sediment age at a given depth (*tz*) is calculated from the CIC model as follows:

$$tz = \left\{\frac{1}{0.03114}\right\}\left\{\frac{A\circ\,^{210}Pb_{un}}{A\,^{210}Pbun_{z}}\right\}$$

where A° ^{210}Pb*un* is initial excess ^{210}Pb activity and A ^{210}Pb*un* is the excess activity at depth *z*, and 0.03114 is the ^{210}Pb decay constant.

^{14}C analysis was performed at the ANSTO Physics Division at the AINSE Lucas Heights facility. ^{14}C was determined using the Accelerator Mass Spectrometric (AMS) technique. Samples were combusted to CO_2 in an Inconel tube furnace packed with an oxidising agent at 780°C. The gas was then passed through a series of wash bottles to remove impurities and water (Rafter 1965). The CO_2 was converted to graphite pellets using excess H_2 and iron catalyst and packed into a copper rod well. It was then exposed to a Cs-sputter ion beam and ^{14}C, ^{13}C and ^{12}C discriminated and measured by mass spectrometry.

^{14}C ages were calculated as the elapsed time t using the expression

$$t = Tm \ln A_o/A_s$$

where t = age (± error in years before present), Tm as the mean life of ^{14}C, A_o = specific gravity of the oxalic acid standard and A_s = specific gravity of the sample.

7.2.2 Quantitative Model

The model of Jenny *et al.* (1949) was used as the basis of the model to describe the rate of accumulation of the cumulative mass of organic matter (Equation 1). The assumptions of the model are that carbon inputs are constant throughout time and decay is exponential (the half-time for decay is $-(\ln 0.5)/\alpha$), which assumes a proportion of the original material will always remain. The assumptions of Jenny *et al.* (1949) are supported by Latter *et al.* (1998), who concluded that a single exponential curve best described the long-term course of decomposition leading to peat accumulation. The input of organic carbon was calculated using the annual input for the macrophyte habitat in each wetland from Table 6.4. This habitat dominated the basin of each wetland and is the habitat where sediment profiles were dated and depths recorded. Therefore, it is in this habitat that the vertical accumulation of peat will be described using the model.

The annual decay coefficient (α_a) in Equation 1 was derived from Noobijup Lake data as the ^{210}Pb and ^{14}C results indicate that the recent and long-term accumulation rates have not been altered by major disturbance events. The average annual decay coefficient (± standard error) was determined as the coefficient that would generate the same total depth of peat (using Equation 2) after the same period of time as the sediment dating results (± standard error). Therefore, the assumption is that Noobijup Lake represents an undisturbed condition and that the decay coefficient derived is an accurate representation of decay in an undisturbed wetland in this region. Using this assumption, the decay coefficient (± standard error) can be applied to Bokarup and Kodjinup Swamps to test the hypothesis that deviations from the model predictions by the ^{14}C radiocarbon dates are related to disturbance of some form. Disturbances in this sense will be any process or events which lead to different rates of decay or rates of accumulation relative to the control wetland, Noobijup Lake.

The result of Equation 1 is a cumulative mass of organic carbon. This mass needs to be converted to a height increment that incorporates organic and inorganic matter in order to quantify vertical accumulation rates. Bulk density was used to convert the mass of peat accumulation each year to a height using the equations in Plaster (1985). The inputs to Equation 1 are only organic carbon, and as the peat mass contains varying proportions of organic and inorganic material with depth it needs to be corrected so that a height increment incorporates both peat components. A profile of bulk density and percent carbon values was constructed for each wetland from the points in the profile where sediment dates were obtained. The bulk density and carbon content values were plotted against dated points in the profile for each wetland and an equation derived that described the change in bulk density with depth. Data used to generate the equations are in Table 7.2.

$$\textit{Equation}\,1:\; x = \frac{P_a}{\alpha_a}\left\{1 - \mathrm{EXP}^{-\alpha_a t}\right\}$$

Where x is the cumulative mass of organic carbon per m^2, P_a is the rate of supply of organic carbon per m^2 determined from the carbon budget, α_a is the decay coefficient and t is the time in years.

The rate of annual vertical peat accumulation for the macrophyte habitat in each wetland is calculated using Equation 2. This equation calculates the annual height increment (X) based on the carbon content and bulk density value derived for that year. The annual input of organic matter (Pa) in year 1 is calculated from the carbon budget. Pa values for year 2 onwards are calculated as the remaining undecayed mass from the previous year (i.e. year 2 Pa is the result of (x) from Equation 1 in year 1, year 3 Pa is the result of (x)

from Equation 1 in year 2 and so on). Cumulative height increment is calculated by summing the *X* values for the desired run-time.

Table 7.2. Age (years BP), depth (cm), percent elemental carbon and bulk density (gm^3) of samples from a peat profile in Bokarup Swamp, Kodjinup Swamp and Noobijup Lake.

	Age (years BP)	Depth (cm)	% Carbon	Bulk Density (gm^3)
Bokarup Swamp				
Surface	0	0	97.33	190
Fibric Peat	270±50	25	96.72	655
Hemic peat	4490±50	172	73.19	880
Sapric Peat	5570±60	278	50.00	965
Kodjinup Swamp				
Surface	0	0	95.55	225
Fibric Peat	700±55	25	91.65	665
Hemic peat	850±40	92	89.67	805
Sapric Peat	3100±50	134	67.99	1130
Noobijup Lake				
Surface	0	0	90.22	320
Fibric Peat	990±55	5	88.37	1075
Hemic peat	6060±60	72	47.03	1405
Sapric Peat	8430±60	154	35.03	1510

The equations that best describe the change in bulk density with depth are:

Bokarup Swamp: $y = 86.69 \ln(t) + 184.93$, $R^2 = 0.9933$.

Kodjinup Swamp: $y = 152.82 \ln(t) + 238.65$, $R^2 = 0.939$.

Noobijup Lake: $y = 222.14. \ln(t) + 303.22$, $R^2 = 0.9968$.

The equations that best describe the change in percent carbon content with depth are:

Bokarup Swamp: $0.9983\ e^{(-0.0001\,t)}$, $R^2 = 0.8728$.

Kodjinup Swamp: $0.9765\ e^{(-0.0001\,t)}$, $R^2 = 0.9869$.

Noobijup Lake: $0.9429\ e^{(-0.0001\,t)}$, $R^2 = 0.993$.

$$Equation\,2:\ x = \frac{\left\langle \frac{P_a}{\alpha_a}\left\{1 - EXP^{-\alpha_a t}\right\}\right\rangle \bullet BD_a}{C_a}$$

Where x is the annual height increment of peat (cm) per m^2, P_a is the annual rate of supply of organic carbon per m^2 determined from the previous year, α_a is the annual decay coefficient, t is the the time in years, BD_a is the dulk density in g/m^3, C_a is the fraction of elemental carbon in the peat.

7.3 RESULTS

7.3.1 ^{210}Pb analysis

^{226}Ra activities in Bokarup Swamp are fairly uniform, ranging from 0.576 ± 0.04 dpm/g to 0.428 ± 0.03 dpm/g, suggesting that the mineral structure of the soil is unchanged and the samples came from the same soil horizon (Table 7.3). With the exception of the surface sediment section (0-1cm) the ^{210}Po activities fall in the range 0.578 ± 0.03 dpm/g to 0.448 ±0.03 dpm/g which is consistent with the level expected for supported ^{210}Pb (as indicated by the corresponding level of ^{226}Ra). This indicates that there is negligible excess ^{210}Pb present in the core. The ^{210}Po activity in the two upper most slices is only slightly above the corresponding ^{226}Ra activity, suggesting a small amount of ^{210}Pb excess in surface sediments (Figure 7.1). With the lack of a number of ^{210}Pb activities in a temporal sequence, it is not possible to obtain a sedimentation rate from this core.

As with Bokarup Swamp, ^{226}Ra activities in Kodjinup Swamp are fairly uniform, ranging from 1.746 ± 0.15 dpm/g to 1.144 ± 0.10 dpm/g, suggesting that these samples came from the same organic soil horizon (Table 7.4). ^{210}Po activities also had little variability, ranging from 1.641 ±0.07 dpm/g to 1.146 ± 0.06 dpm/g, with maximum activity at 9 to 10 cm below the surface. These ^{210}Po data are similar to the ^{226}Ra data, which is reflected in the negligible excess ^{210}Pb within the core (Figure 7.2). A sedimentation rate from this core was not possible.

^{226}Ra activities in Noobijup Lake were of a similar magnitude to Bokarup Swamp, ranging from 1.007 ± 0.10 dpm/g to 0.462 ± 0.06 dpm/g. ^{210}Po activities decreased with depth, ranging from 3.057 ± 0.09 dpm/g at the surface to 0.547 ± 0.01 dpm/g in the 20 cm section (Table 7.5). A slight elevation in ^{226}Ra activity occurred in the 6-7 cm sediment section leading to a corresponding increase in ^{210}Po activity in the same sample. The surface sediments of Noobijup Lake displayed a clear exponential decrease in excess ^{210}Pb with depth (Figure 7.3). The CIC derived sedimentation rate is $0.12 cm.year^{-1}$, resulting in an estimation of 162.7 ± 21.9 years BP for the 19-20 cm section (Table 7.6).

Table 7.3 Mean ^{226}Ra and ^{210}Po activities (dpm/g ± SE) from the sediment surface to 19-20 cm depth in Bokarup Swamp.

Sample Depth (cm)	^{226}Ra dpm/g	^{210}Po dpm/g
0-1	0.534 ± 0.05	0.731 ± 0.01
1-2	0.428 ± 0.03	0.523 ±0.02
2-3	0.521 ± 0.05	0.512 ± 0.05
3-4	0.576 ± 0.04	0.476 ± 0.03
4-5	0.529 ± 0.04	0.476 ± 0.02
6-7	No result	0.578 ± 0.03
9-10	0.515 ± 0.04	0.537 ± 0.07
12-13	No result	0.474 ±0.02
15-16	0.517 ± 0.05	0.448 ± 0.03
19-20	0.438 ± 0.03	0.453 ± 0.01

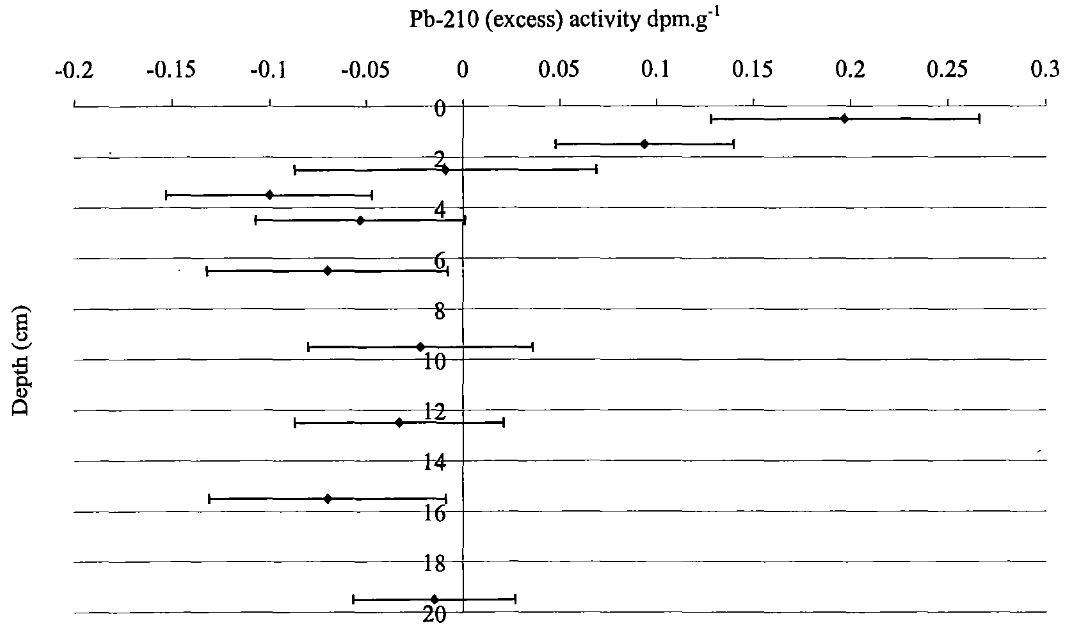


Figure 7.1. Mean excess Pb^{210} activity (dpm/g ± SE) in sediments from surface to 19.5 cm depth at Bokarup Swamp.

Table 7.4. Mean ^{226}Ra and ^{210}Po activities (dpm/g ± SE) from the sediment surface to 19-20 cm depth in Kodjinup Swamp.

Sample Depth (cm)	^{226}Ra dpm/g	^{210}Po dpm/g
0-1	1.243 ± 0.11	1.568 ± 0.05
1-2	1.144 ± 0.10	1.476 ± 0.06
2-3	1.628 ± 0.13	1.454 ± 0.06
3-4	1.360 ± 0.12	1.304 ± 0.05
4-5	1.600 ± 0.13	1.431 ± 0.05
6-7	1.331 ± 0.12	1.371 ± 0.05
9-10	1.746 ± 0.15	1.641 ± 0.07
12-13	1.365 ± 0.13	1.143 ± 0.05
15-16	1.716 ± 0.14	1.371 ± 0.05
19-20	1.181 ± 0.09	1.146 ± 0.06

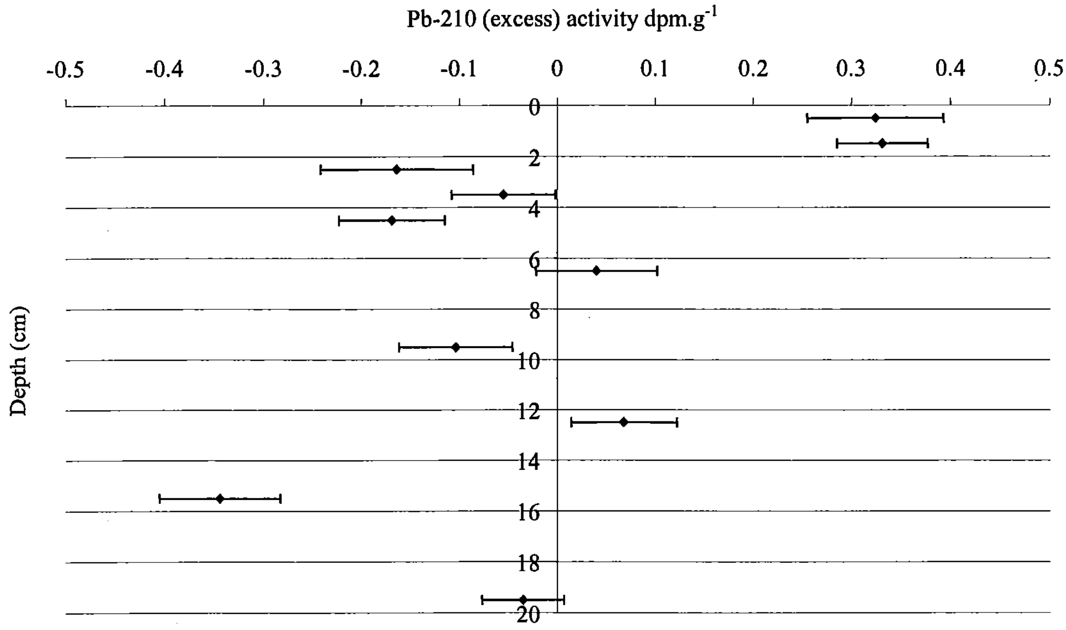


Figure 7.2. Mean excess Pb^{210} activity (dpm/g ± SE) in sediments from surface to 19.5cm depth at Kodjinup Swamp.

Table 7.5. Mean ^{226}Ra and ^{210}Po activities (dpm/g ± SE) from the sediment surface to 19-20 cm depth in Noobijup Lake.

Sample Depth (cm)	^{226}Ra dpm/g	^{210}Po dpm/g
0-1	0.631 ± 0.08	3.057 ± 0.09
1-2	0.627 ± 0.08	2.530 ± 0.09
2-3	0.644 ± 0.05	2.222 ± 0.07
3-4	0.741 ± 0.07	1.766 ± 0.07
4-5	0.603 ± 0.06	1.633 ± 0.06
6-7	1.007 ± 0.10	1.543 ± 0.05
9-10	No result	0.741 ± 0.03
12-13	0.462 ± 0.06	0.591 ± 0.01
15-16	No result	0.634 ± 0.03
19-20	0.806 ± 0.08	0.547 ± 0.01

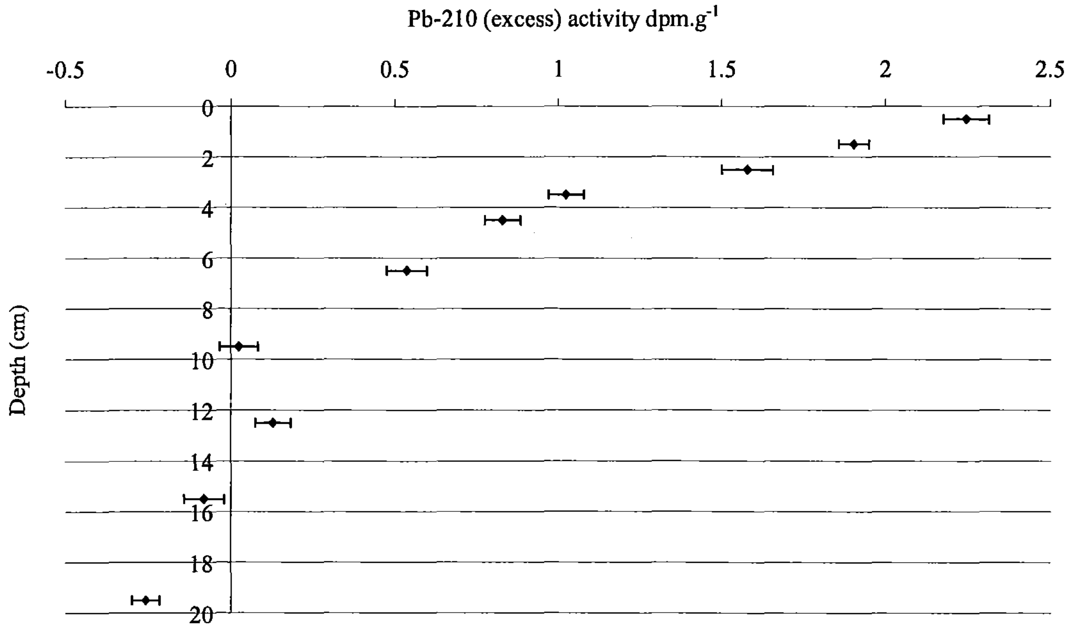


Figure 7.3. Mean excess Pb^{210} activity (dpm/g ± SE) in sediments from surface to 19.5cm depth at Noobijup Lake.

Table 7.6. CIC calculated dates (year ± SE) and calendar dates (year ± SE) for sediment sections from the sediment surface to 19-20 cm depth in Noobijup Lake.

Sample Depth (cm)	CIC year	Calendar year	SE (years)
0-1	4.2	1992	4.2
1-2	12.5	1984	4.5
2-3	20.9	1976	5.0
3-4	29.2	1968	5.7
4-5	37.5	1959	6.5
6-7	54.2	1943	8.3
9-10	79.2	1918	11.3
12-13	104.3	1893	14.4
15-16	129.3	1868	17.6
19-20	162.7	1835	21.9

7.3.2 ^{14}C analysis

Radiocarbon dates from sediment profiles have indicated considerable variability in the age of sediments between wetlands. Kodjinup Swamp, with the shallowest peats, had the youngest sediment deposits at 3100 ± 50 years BP at the base of the profile (Figure 7.4). The deepest organic deposits were found at Bokarup Swamp, however their age of 5570 ± 60 years BP at 278 cm was surpassed by Noobijup Lake (8430 ± 60 years BP at a depth of 154 cm). The uppermost sediment date derived from AMS ^{14}C is consistent with ^{210}Pb dates and suggests a slowing of the accumulation rate with depth from the surface in Noobijup Lake. ^{210}Pb analysis dated sediments at 20 cm were dated at 162.7 ±21.9 years BP compared to a ^{14}C date of 990 ± 55 years BP at 25 cm from the same profile. Sediment dates at the Fibric/Hemic and Hemic/Sapric peat delineation show sediment accumulation rates in these wetlands have not been constant, with zones of rapid sedimentation evident within each profile.

Sedimentation rates have been calculated for each profile and for sections within each profile using AMS ^{14}C dates (Table 7.7). All rates are calculated using the sediment surface as 0 years B.P. Bokarup Swamp has the highest sedimentation rate from the

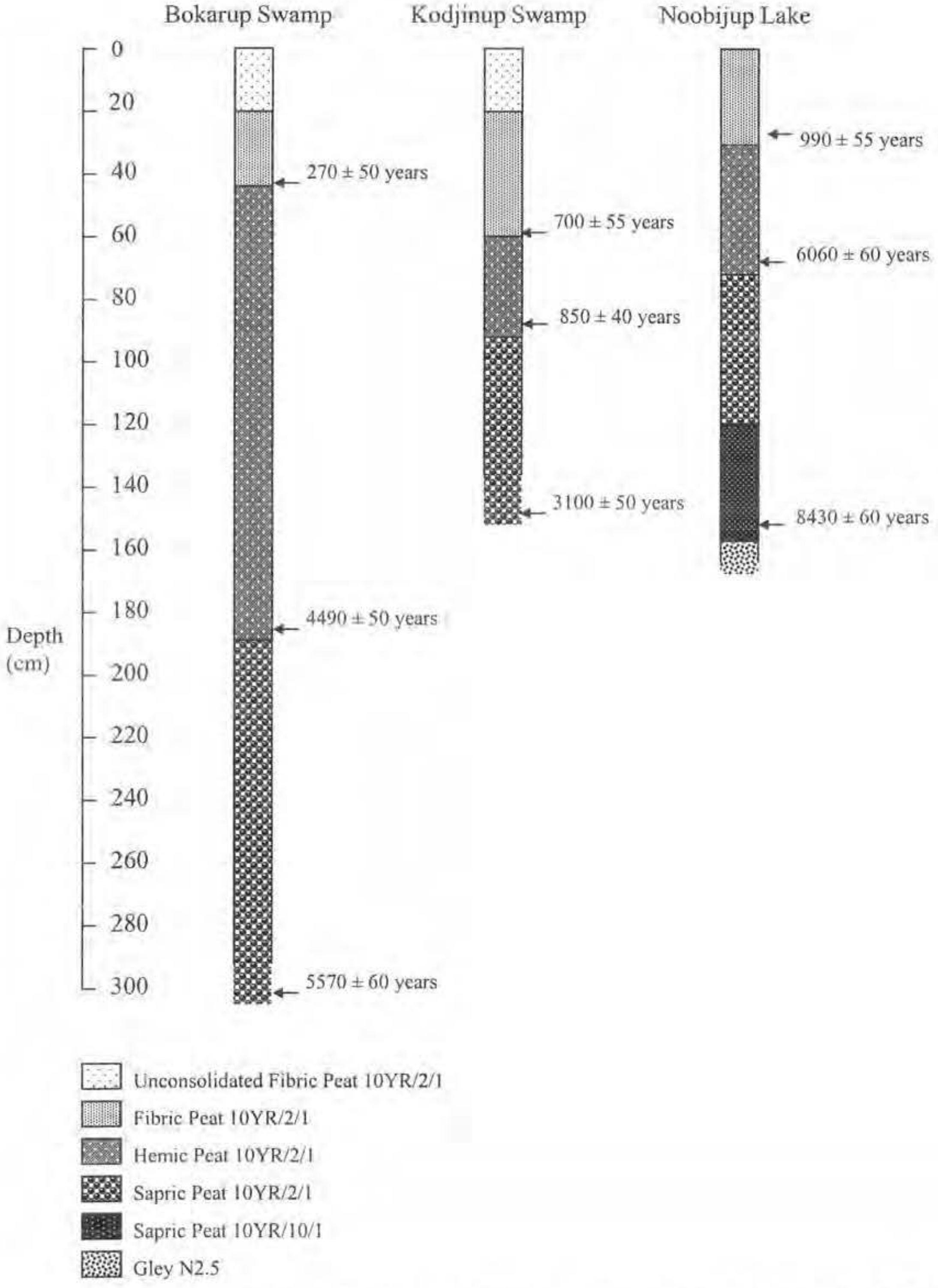


Figure 7.4. Sediment profiles showing major sediment classifications and C^{14} age (years BP) at known depths at Bokarup Swamp, Kodjinup Swamp and Noobijup Lake.

Table 7.7. ^{14}C calculated sediment age (years B.P. ± SE) and sedimentation rate (± SE) for sediment profiles from Bokarup Swamp, Kodjinup Swamp and Noobijup Lake.

Wetland	Sediment Profile Depth (cm)	Sediment Profile Age (years B.P.)	Sedimentation rate (cm per year)
Bokarup Swamp	0-22	270±50	0.081 ± 1.3 x 10^{-2}
	22 – 174cm	4220 ± 50	0.035 ± 4.2 x 10^{-3}
	174 – 288cm	1080 ± 60	0.107 ± 6.0 x 10^{-3}
	0 – 278cm	5570 ± 60	0.052 ± 5.0 x 10^{-4}
Kodjinup Swamp	0 - 38	700 ± 55	0.054 ± 4.0 x 10^{-3}
	38 – 69cm	150 ± 40	0.206 ± 4.0 x 10^{-3}
	69 – 134cm	2250 ± 50	0.028 ± 2.6 x 10^{-4}
	0 – 134cm	3100 ± 50	0.043 ± 9.9 x 10^{-4}
Noobijup Lake	0-25	990 ±55	0.025 ± 1.1 x 10^{-4}
	25 – 72cm	5070 ± 60	0.009 ± 1.4 x 10^{-5}
	72 – 154cm	2370 ± 60	0.034 ± 9.4 x 10^{-4}
	0 – 154cm	8430 ± 60	0.018 ± 1.3 x 10^{-4}

surface sediment to the base of the profile (0-278 cm) at 0.052 ± 5.0 x 10^{-4} cm/year. If one core in each wetland is representative of whole wetland accumulation rates, these dates indicate organic matter accumulation in the surface sediments of Bokarup Swamp is rapid, with the rate of accumulation fastest between 4490 and 5570 years BP (0.107 ± 6.0 x 10^{-3} cm/year) and the slowest in the hemic layer (0.035 ± 4.2 x 10^{-3} cm/year). As with Bokarup Swamp, the surface sedimentation rate was rapid in Noobijup Lake, with the most rapid accumulation in the Sapric layer between 6060 and 8430 years BP (0.034 ± 9.4 x 10^{-4} cm/year) and slowest in the Hemic peat (0.009 ± 1.4 x 10^{-5} cm/year in the surface horizon. The rates of accumulation in Noobijup Lake were consistently the slowest of all wetlands. (Table 7.7). Kodjinup Swamp displayed the opposite trend to the other wetlands with a substantial increase in sedimentation rates towards the present. The deep Sapric layer had the slowest rate of 0.028 ± 2.6 x 10^{-4} cm/year with the Hemic peat horizon having the fastest accumulation rate found in all profiles sections of 0.206 ± 4.0 x 10^{-3} cm/year. Higher rates of peat accumulation such as those in the Sapric peat layer of

Bokarup Swamp and Kodjinup Swamp may be the result of factors such as increased organic matter supply or altered hydrology leading to a reduction in the rates of peat decomposition. Alternatively, truncations in the profile of Kodjinup Swamp may indicate a large scale disturbance such as the erosion of sediment layers by fire.

7.3.3 Model output

An average annual decay coefficient of 4.71 x 10^{-5} was calculated using data from Noobijup Lake. When used in the model, this decay coefficient produced a peat depth of 154.000 cm after 8430 years. The ^{14}C date at 8430 years had an error of ± 60 years. This was used to calculate the error for the model by calculating the decay coefficient required to generate a peat depth of 154.000 cm in Noobijup Lake between 8370 and 8490 years. The error for the decay coefficient was ± 6.4 x 10^{-6}.

The application of the annual decay coefficient and the model's assumptions of constant carbon inputs and exponential decay produced a curve with an asymptote at 154cm depth in Noobijup Lake (Figure 7.5). The model predictions closely resemble the ^{210}Pb accumulation rates for the first 10 to 12 cm of the profile (around 100 years), but then deviate away from the remaining ^{210}Pb dated depths (Table 7.8). Model predictions significantly differ from the two ^{14}C dated points (990 ± 55 years BP and 6060 ±60 years BP), overestimating accumulation rates by almost double.

As with Noobijup Lake, the model accurately describes the rate of organic matter accumulation in the surface sediments of Bokarup Swamp, however, long-term predictions severely underestimate the total depth after a 5570 year simulation (Figure 7.6). The model predicts that after 270 years, 19.92cm of peat has accumulated, which is in close agreement to the ^{14}C date of 270 years at 22cm (Table 7.8). At 4490 years, the model slightly underestimates peat accumulation compared to the ^{14}C dated depth, but the curve is approaching its asymptote.

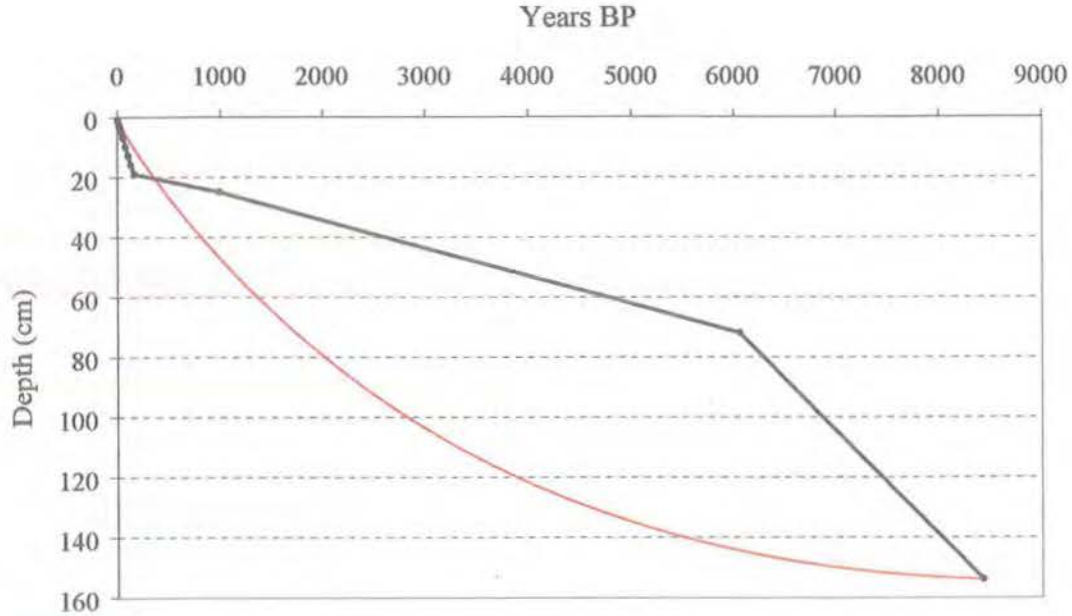


Figure 7.5 Combined ^{210}Pb and ^{14}C dates (black line) from known depths in the profile and the predicted peat depth (red line) over time from the model at Noobijup Lake.

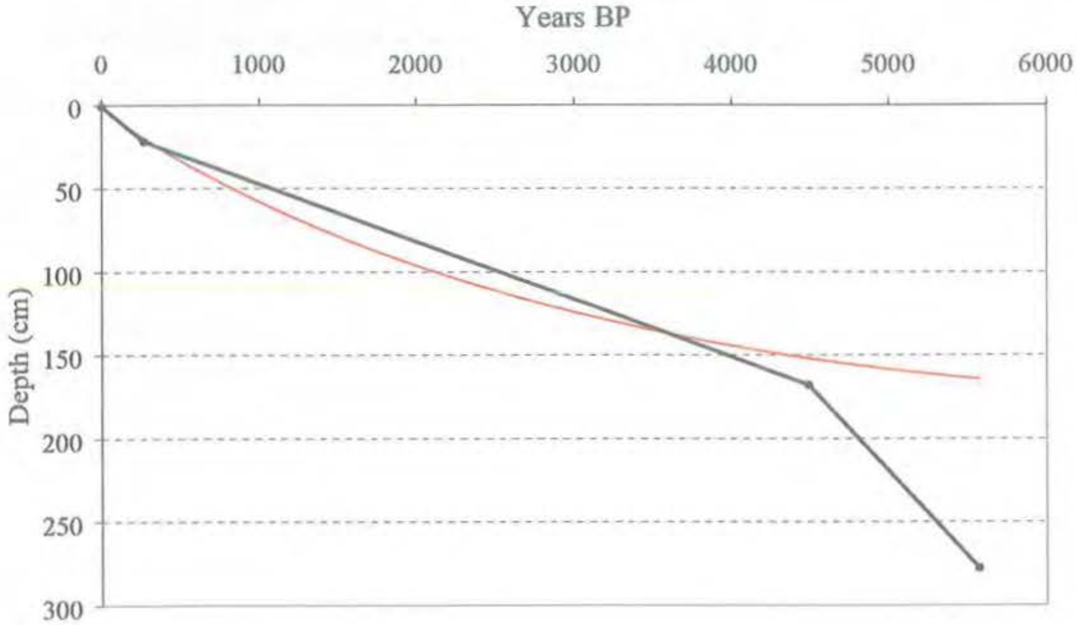


Figure 7.6 ^{14}C dates (black line) from known depths in the profile and the predicted peat depth (red line) over time from the model at Bokarup Swamp.

Table 7.8 Comparison of $^{210}Pb/^{14}C$ sediment dated depth (cm ± SE) and model predicted depth (cm ± SE) for $^{210}Pb/^{14}C$ dated sediment age (years BP± SE) for Noobijup Lake, Bokarup Swamp and Kodjinup Swamp.

Sediment Age (years BP ± SE.)	$^{210}Pb/^{14}C$ Dated Depth (cm) ± SE.	Model predicted depth (cm) ± SE.
Noobijup Lake		
4.2 ± 4.2	0.5 ± 0.5	0.51 ± 0.0
12.5 ± 4.5	1.5 ± 0.5	1.19 ± 0.0
20.9 ± 5.0	2.5 ± 0.5	1.87 ± 0.0
29.2 ± 5.7	3.5 ± 0.5	2.44 ± 0.0
37.5 ± 6.5	4.5 ± 0.5	3.05 ± 0.0
54.2 ± 8.3	6.5 ± 0.5	4.15 ± 0.0
79.2 ± 11.3	9.5 ± 0.5	5.63 ± 0.1
104.3 ± 14.4	12.5 ± 0.5	7.17 ± 0.1
129.3 ± 17.6	15.5 ± 0.5	8.59 ± 0.2
162.7 ± 21.9	19.5 ± 0.5	10.51 ± 0.3
990 ± 55	25 ± 1.0	46.79 ± 0.5
6060 ± 60	72 ± 1.0	144.48 ± 0.7
8430 ± 60	154 ± 1.0	154.00 ± 0.8
Bokarup Swamp		
270 ± 50	22 ± 1.0	19.92 ± 0.0
4490 ± 50	172 ± 1.0	151.93 ± 0.5
5570 ± 60	278 ± 1.0	164.31 ± 0.6
Kodjinup Swamp		
700 ± 55	38 ± 1.0	56.82 ± 0.0
850 ± 40	69 ± 1.0	66.39 ± 0.1
3100 ± 50	134 ± 1.0	165.31 ± 0.4

The final predicted depth based on current inputs and using the decay coefficient derived from Noobijup Lake is 164.31 ± 0.06 cm after 5570 years. This compares to the ^{14}C date of 5570 ± 60 years BP derived from a depth of 278 cm, a difference of around 114 cm of peat depth.

The model produced an average accumulation rate of 0.029 $gC/m^2/year$ compared to the overall accumulation rate of 0.052 $gC/m^2/year$ generated by the radiocarbon dates. This indicates that either decay rates in the past were much slower or rates of organic matter input were substantially higher than current rates in order to accumulate the additional 114 cm of peat. For instance, a depth of 278 cm of peat can be achieved after 5570 years by changing the average input to 105.46 $gC/m^2/year$ using the described decay coefficient, bulk density profile and carbon content profile for Bokarup Swamp. A decay coefficient small enough to generate a peat depth of 278 cm after 5570 years based on current inputs could not be quantified.

Kodjinup Swamp is the shallowest and has the most recent deposits of the three wetlands. Unlike Bokarup Swamp, the model prediction is an overestimate of peat accumulation indicating current input rates are higher than those in the past, the decay coefficient is too small or peat has been eroded from the profile (Figure 7.7). The model predicts a peat depth of 165.31 ± 0.04 cm after 3100 years compared to a depth of 134cm ^{14}C dated to 3100 ± 50 years, a difference of around 30cm. The most obvious feature of the ^{14}C dates is the truncated profile, giving the upper most date of 700 ± 55 years BP at 38 cm, 850 ± 40 years is found at 69 cm and 3100 ± 50 years BP at the base of the profile, a difference of 31 cm. The rapid increase in deposition between 850 and 700 years BP represents either an error in the ^{14}C dates, an erosional event or a period of exceptional productivity and deposition of organic matter.

The model can be used to predict the impact of erosional events based on current conditions. The model predicts that the depth of peat at 700 years BP would be around 56.82 cm, compared to the 38 cm shown by the ^{14}C date, a difference of around 19 cm of peat depth. The 700 year old peat occurring at a shallower than predicted depth and an

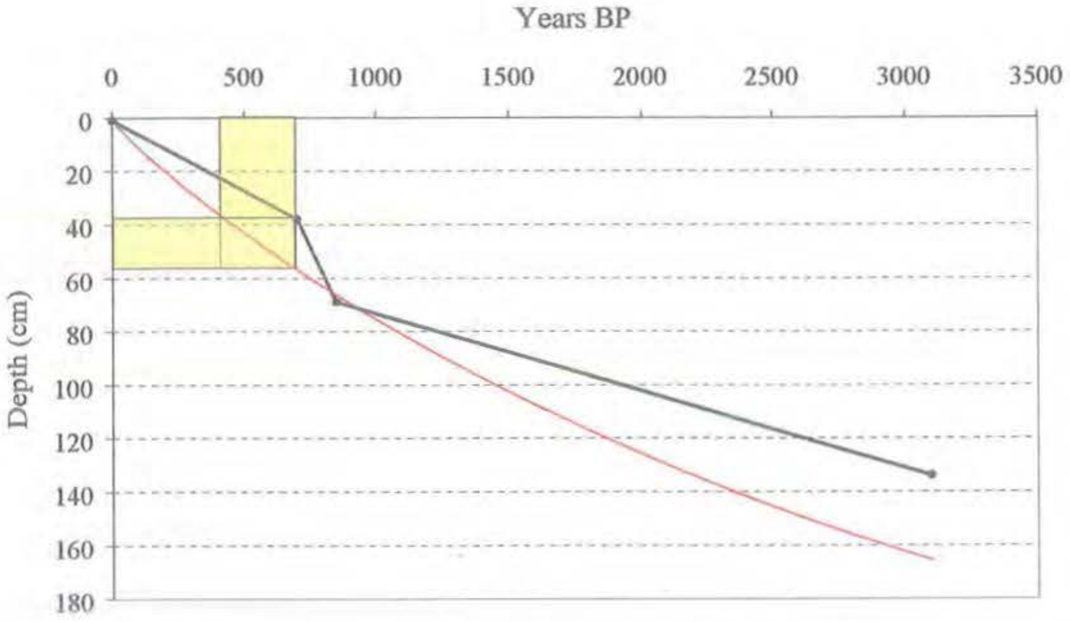


Figure 7.7 ^{14}C dates (black line) from known depths in the profile and the predicted peat depth (red line) over time from the model at Kodjinup Swamp. Coloured areas represents the range and time periods of projected organic matter losses.

overestimate of peat accumulation by the model compared to the ^{14}C dates indicate that a disturbance event, most probably a fire, may have removed a large volume of peat from the profile. The model predicts that 38cm of peat takes around 430 years to accumulation, compared to the 700 ± 55 years for the same depth using the ^{14}C date, a difference of up to 325 years. From the modelled data and ^{14}C dates it can be hypothesised that between 21 to 30 cm and 215 to 325 years of peat has been eroded. The sharp increase in the rate of accumulation between 700 and 850 years BP indicates the fire may have occurred around 850 years BP, the increase due to increased inputs following firing or the remobilisation/redistribution of peat within the profile.

The model can be used to predict the asymptote, or maximum height of peat attainable under specified rates of organic matter supply and decay. This is possible for Kodjinup Swamp where the model has not produced an asymptote after a run time equivalent to the oldest carbon date. The model predicts that under current condition, the peat depth in Kodjinup Swamp would reach an asymptote at around 217 cm at an age of 6300 years. So with a current peat depth of 134 cm (3100 years BP) and a maximum water depth of around 1m, it can be hypothesised that in another 3200 years the wetland basin will be almost completely filled with organic matter if conditions remain relatively constant.

7.4 DISCUSSION

The development of a simple, descriptive model based on sediment dates, contemporary organic matter budgets and sediment characteristics has produced predictions of rates of sediment organic matter accumulation that allow an examination and interpretation of processes affecting wetland development. A decay coefficient was derived from Noobijup Lake and used within the model to examine the rates of organic matter accumulation in Bokarup and Kodjinup Swamps. Parameters within the model such as run-time, rates of organic matter supply and decay can be altered to simulate organic matter accumulation under different environmental conditions. These simulations can be used to examine the impact of altered wetland hydrology, changes in organic matter supply or water quality and erosional events such as fire on organic matter accumulation rates.

7.4.1 Model assumptions

The model used to predict the long-term accumulation of organic matter in the sediments of these wetlands is based on several critical assumptions. The use of a single, long-term decay coefficient derived from one wetland assumes that this rate is representative of similar surrounding systems. It assumes that the profile of Noobijup Lake is relatively undisturbed and that the sediment dates derived from ^{210}Pb and ^{14}C techniques are accurate.

Several papers summarise the evidence for and against the validity of ^{210}Pb based chronologies in organic soils (see review in Oldfield *et al.* 1995). ^{210}Pb dates in sediments have been corroborated by lamination counting (Bollhoffer *et al.* 1994), pollen analytical techniques (Oldfield *et al.* 1979; Heijnis *et al.* 1987; Gale *et al.* 1995) and moss increment counts (El-Daoushy *et al.* 1982). However, limitations to the resolution of these techniques and the presence of numerous contaminants in the sediment often make recent peat deposits difficult to date using this method (Belyea & Warner 1996). The uneven ^{210}Pb chronology for Bokarup and Kodjinup Swamp compared to Noobijup Lake highlights the potential problems of using ^{210}Pb dating in organic soils. Oldfield *et al.* (1995) have suggested that the variability of wetland surface waters and the associated drawdown of water through the peat profile and reduced residence time may lead to the uneven distribution of ^{210}Pb in surface peat sediments. Bokarup and Kodjinup Swamps both experienced the most variable surface water levels and had periods of no surface water during this study and these factors outlined may in part explain the poor ^{210}Pb chronology from these wetlands. However, the presence of an unconsolidated sediment layer at the surface of the profile in Bokarup and Kodjinup Swamps (and not in Noobijup Lake) indicate that the surface sediments in these wetlands are mobile, which may have led to the redistribution of ^{210}Pb within the surface sediments. Benoit & Hemond (1990) and Stevenson *et al.* (1990) were also unable to obtain a chronology for wetland sediments due to the remobilisation of ^{210}Po and ^{210}Pb from erosion events.

Many authors have documented striking discrepancies between the rate of surface peat growth and the average rate of peat growth over millennia (eg. Clymo 1970; Lyndholm & Vasander 1990; Rochefort *et al.* 1990). ^{14}C analysis has been extensively used for dating sediments to determining long-term organic matter accumulation rates in aquatic systems (eg. Martel & Paul 1974; Shepphard *et al.* 1979; Kubiw *et al.* 1989; Korhola *et al.* 1995; Meyers & Takemura 1997; Wei *et al.* 1998). Organic sediments provide a reliable dating material (provided contaminants are removed), as good agreement has been found between ^{14}C and other dating techniques, and peat is generally formed *in situ* (Geyh *et al.* 1971). The use of Accelerator Mass Spectrometry (AMS) radiocarbon dating in this study has further increased the accuracy of the dates used to derive the decay coefficient. AMS requires significantly less mass compared to conventional radiocarbon dating and produces less error in estimated dates (Vance & Telka 1998). The small error of ±60 years for an estimated age of 8430 years BP for Noobijup Lake highlights the accuracy of the technique.

Radiocarbon dates in this study were taken from three points from a single core in the deepest peat deposits of each wetland. This assumes that dates derived from each core and their position in the profile are representative of the entire wetland basin from which it was taken. It therefore assumes that the physical and biological characteristics have been spatially uniform throughout the development of the wetland. The high costs associated with radiocarbon dating have resulted in the literature being dominated by studies that extrapolate peat accumulation rates from a single core from the deepest deposits within the wetland. This assumption has been examined in several separate studies. The spatial representativeness of peat profiles was examined using multiple cores to date basal peats in south-eastern Australian wetlands (Head 1988). Two cores from equivalent depths had dates of 6800 ± 90 years and 6710 ± 100 years. Makila (1997) found the highest rates of peat accumulation from the centre of a concentric raised bog using 79 ^{14}C samples from across the peatland. Oldfield *et al.* (1997) tested the accuracy of AMS radiocarbon dating against annually laminated lake sediments and found the ^{14}C measurements consistently overestimated sediment age. Age discrepancies were thought to have arisen from the resuspension and focussing of older organic material into the deepest part of the lake basin. The process of sediment focussing may result in the rates of peat accumulation determined for this study being overestimated. Although this study assumes one core is representative of the accumulation rates for each wetland basin, it increases its accuracy by having the rates of organic matter input and decomposition determined independently of the radiocarbon dates.

Sediment dates derived from numerous studies of Australian wetland systems provide good agreement with the dates found in the Muir-Unicup wetland. Gell *et al.* (1993) successfully used ^{210}Pb chronology to date recent organic deposits from a tea tree swamp in south-east Victoria. Head (1988) used ^{14}C radiocarbon dating to examine organic matter accumulation in south-west Victorian swamps, dating the oldest deposits at 6000 years BP. Basal sediments (3m) in Tordit-Garrup Lagoon and Poorginup Swamp (two wetlands in the Muir-Unicup system) were dated to 5720 ± 320 years BP and 8300 ± 500 years BP respectively as part of an environmental impact study for a proposed peat mine (Magnet Industries 1993). Byenup Lagoon, also in the Muir-Unicup system, has been dated at around 4800 years BP in a recent palynological study (Dodson & Lu 2000). Nearby wetlands with organic sediments have been dated at 5600 ± 60 years BP at a depth of 92 to 95 cm (Horwitz *et al.* 1998) and 4380 ± 130 years BP at 328 to 331 cm below the surface (Newsome & Pickett 1993). Loch McNess (a Swan Coastal Plain wetland dominated by *B.articulata*) was also dated by Newsome & Pickett (1993) and found to have basal organic deposits (405 to 407 cm) 8910 ± 400 years BP and shallow organic deposits (135 to 137 cm) 1370 ± 200years BP. The successful application of these techniques and comparable results from similar systems combined with the lack of obvious truncations in the chronology from Noobijup Lake provides a justification for the use of the sequence of dates from this wetland to develop a decay coefficient representative of a relatively undisturbed wetland.

The decay coefficient for this model (4.71×10^{-5}) was derived using radiocarbon dates from known depths, as long-term decay coefficients for these peat deposits were unavailable. Estimates of decomposition have been inferred from short-term observations (1-2 years) and generally represent an overestimate of decomposition from the whole profile (Gorham 1991). Decomposition rates for organic litters in agricultural soils have been documented for 20 years (Sorensen 1974), 10 years (Jenkinson 1977) and 8 years (Ladd *et al.* 1985). Latter *et al.* (1998) provide the only example of long-term decomposition in aquatic systems (23 years). These studies, although considered long-term in a contemporary sense, are more representative of recent decay in the context of soils that are over 8000 years old. Alternatively, artificial substrata (cellulose filter paper, unbleached cotton paper) inserted at different depths of a peat profile have been used to examine the *in situ* long-term decomposition of organic matter (Clymo 1963; Heal 1974; Heal *et al.* 1978). Decay coefficients of 0.003 for blanket bogs and 0.015 for peat podzols were derived by Heal *et al.* (1978), but produced underestimates of peat depth when used in the model developed in this thesis. Decay coefficients (derived using radiocarbon dates from known depths), for Northern Hemisphere bogs systems with similar environmental conditions ranged from 1.1×10^{-4} to $6.5 \text{x} 10^{-5}$ (Clymo 1984). Clymo (1978) also used a very small decay coefficient (1.0×10^{-5}) to describe decay in the permanently anoxic catotelm of *Sphagnum* bogs. This range of values encompasses the decay coefficient of 4.71×10^{-5} developed from Noobijup Lake.

The use of a simple descriptive model and a single decay coefficient produces an asymptotic curve of predicted peat depth. This curve accurately predicts the depth of organic matter in the surface horizon (circa 0-100 years) and the overall depth of the deposit compared to dating techniques in Noobijup Lake. However, the curve does not accurately represent the accumulation rates throughout the whole profile, with model predictions overestimating accumulation rates by almost double for much of the profile. The stratigraphy of these organic deposits shows the presence of three distinct layers with well defined boundaries common to each wetland (Figure 7.4). The model proposed by Clymo (1984) estimates rates of organic matter accumulation in Northern Hemisphere peat bogs within and across such defined functional soil layers. Organic matter is added to the acrotelm (upper layer) at a constant rate, and a constant proportion of all material in this layer decays each year. A small amount of this material survives its residence in the acrotelm and is transferred to the thickening catotelm (lower layer). A much smaller but constant proportion of all the material in the catotelm decays each year. This model accurately predicted rates of peat accumulation compared to radiocarbon dated profiles. Belyea & Warner (1996) proposed the application of a decay constant that varies with depth within the acrotelm. This would allow a more realistic simulation of the gradual transition from rapid, variable processes to slow constant ones in the catotelm. Incorporating local, fine temporal scale changes into the model using a variable decay coefficient reduces the applicability of the model to other peat forming systems. This type of model is only applicable where the environmental history of the wetland has been well documented.

The model of Clymo (1984) uses rates of organic matter input and decay based on radiocarbon dates and describes the transfer of organic matter across two peat layers. Using present day inputs generated from a carbon budget to describe the peat accumulation across three defined layers would be 'mathematically challenging'. The model would require substantially more detailed spatial and temporal data about the characteristics of the peat deposit and the ^{14}C dated chronology of the profile.

7.4.2 Chronology, model predictions and wetland development

If all the assumptions outlined hold true, then the model predictions accurately represent the accumulation rates of peat in these wetlands. The model predictions of an underestimate of peat height in Bokarup Swamp and an overestimate of peat height in Kodjinup compared to ^{14}C dates indicate that environmental conditions and rates of organic matter supply and/or decay have been highly variable in the past. The ^{14}C dates for Bokarup Swamp and Noobijup Lake display a consistent pattern of an initial phase of rapid accumulation at the base of the profile (sapric layer), followed by a slower rate of accumulation in the middle (hemic layer) of the profile and a rapid surface deposition rate. This pattern of organic matter accumulation is similar despite these wetlands having had their origins nearly 3000 years apart. Kodjinup Swamp displays a distinctly different pattern of accumulation, with a slow rate of accumulation in basal sapric deposits, followed by an extremely rapid rate of hemic and surface deposition of organic matter. This may be a result of disturbance to the profile. Differences in the rates and patterns of organic matter accumulation in each wetland may be due to altered local and regional environmental conditions leading to changes in decay and deposition rates or discrete events that led to rapid and substantial erosion or deposition of organic matter.

Long-term rates of organic matter accumulation taken over the whole profile in these wetlands ranged from 0.018 ± 1.3×10^{-4} cm/year in Noobijup Lake, 0.043 ± 9.9×10^{-4} cm/year in Kodjinup Swamp to 0.052 ± 5.0×10^{-4} cm/year in Bokarup Swamp based on depth of organic sediments and radiocarbon dates. This range of values is generally lower than those estimated from other recent Australian studies; 0.072 cm/year for Boggy Lake and 0.045 cm/year for Loch McNess in south-western Australia (Newsome & Pickett 1993); 0.084 cm/year for Long Swamp in coastal south-east Australian (Head 1988); 0.299 cm/year in a tropical wetland (Bell *et al.* 1989); 0.235 cm/year for a coastal Victorian wetland (Crowley & Kershaw 1994). Accumulation rates in Northern Hemisphere systems are more similar to those found in the Muir-Unicup wetlands with values ranging from 0.025cm/year for a Canadian forested peatland (Charman *et al.* 1994); 0.045 cm/year for a Canadian Sphagnum bog (Belyea & Warner 1996); 0.018

cm/year in a Swedish swamp (Sergestrom *et al.* 1996); 0.056 cm/year in a Finnish raised bog (Makila 1997). The review of decay coefficients has shown that decomposition is severely reduced in these wetlands and it is unlikely the low rates of vertical accumulation are due to excess organic matter degradation and loss. Clearly, the long-term rates of organic matter supply to the sediment in these wetlands are low compared to other Australian systems and more comparable to Northern Hemisphere bog and swamp habitats. The presence of high levels of dissolved organic matter, acidic sediments and surface waters, exceptionally low phosphorus concentrations and highly reduced sediments may all contribute to low organic matter inputs in these wetlands.

The uses of palaeoclimatic analogues has the potential to contribute significantly to the understanding of climate change (De Deckker *et al.* 1998), however, little is known of the palaeoclimatic record of south-western Australia. On coastal plains, transgression and regression to the sea corresponding to expanding and contracting polar ice masses have set the starting dates for peatland development to the current Holocene period, at around 12 000 years BP (Kershaw & Nansen 1993). In south-western Australia the available palaeoclimate data are sparse and contradictory. Early palynological work by Churchill (1968) in Boggy Lake (100km south of the Muir-Unicup wetlands) indicated marked fluctuations in rainfall through the mid to late Holocene in this region. Specifically it was hypothesised that the period 4000 to 7000 years BP experienced climates wetter than present. More recent research based on fossil molluscs (Kendrick 1977) and ostracods and foraminifera (Yassini & Kendrick 1988) in the Swan River Estuary near Perth, concluded that the mid Holocene was a period of reduced winter flooding and regional aridity. This is supported by Semeniuk (1986) who suggested the period 7000 to 2800 BP was more arid than contemporary conditions based on the degree of calcrete formations in coastal sands near Perth. The similarities in the profiles of organic matter accumulation in Bokarup Swamp and Noobijup Lake, despite discrepancies in radiocarbon dates, infer that climate change has not had a large impact on rates of organic matter accumulation in these wetlands. The recent study of a Holocene sequence in Byenup Lagoon in the Muir-Unicup hypothesised that an increase in effective rainfall in the mid Holocene (around 4800 years BP) initiated the continuous part of the sediment record (Dodson & Lu 2000).

They suggest that since that time, changes are most likely due to local effects such as fire and the interaction of species rather than climate shifts.

In the most extensive palynological study in the south-west region, Newsome & Pickett (1993) revisited Churchill's site at Boggy Lake in the far south-west and investigated Loch McNess (a swamp dominated by *B.articulata*) north of Perth. Churchill's hypothesis of a wetter than present mid Holocene could not be supported in Boggy Lake due to the poor resolution of *Eucalyptus* pollen, an over-reliance of ratios from two species and an incomplete understanding of the ecological tolerances of key taxa. A more recent investigation into *Eucalyptus* pollen morphology by Pickett & Newsome (1997) has increased the resolution of pollen likely to be found in Holocene sequences, however, they were still unable to support Churchill's claims of climate change. The palynological record from Loch McNess suggests that vegetation changes during the Holocene have been minor, with the greatest change being in the non terrestrial taxa such as Cyperaceae and Restionaceae. Changes observed were consistent with normal patterns of hydroseral development as the wetlands infilled and increased the areas of habitat accessible to aquatic vegetation (Newsome & Pickett 1993). There is considerable contradiction in the palaeoclimatic conclusions drawn from studies in south-western Australia. Research on nearby and similar organic profiles have concluded that climate has played little part in wetland development and that local environmental conditions have dominated the processes of organic matter accumulation.

7.4.2.1 Bokarup Swamp

The model predictions for Bokarup Swamp indicate that the current rate of organic input (50.58 gC/m^2/year) generates over 1 m less organic sediments than quantified using radiocarbon dates for the same period of time. Simulated decreases in decay coefficients to retard decomposition and favour accumulation were unable to produce the required peat depth, leading to the hypothesis that increased inputs rather than decreased decomposition have prevailed in the past. The model was used to derive an input of 105.46 gC/m2/year needed to accumulate 278 cm of organic matter in 5570 years, over double the current input since the wetland's initiation. The high organic matter content of the sediments and the lack of layers of inorganic sediment indicate that Bokarup Swamp has been continually vegetated and supports the hypothesis that increased organic inputs are responsible for the more rapid accumulation. The continuous profile of organic matter accumulation infers reasonably stable conditions in this wetland for around the past 5500 years.

Plates 2.1a/b show a lunette on the eastern side separating Bokarup Swamp from another smaller wetland. The lunette is thought to have formed from the wind erosion of basal sediments from the main wetland (Semeniuk & Semeniuk 1997). Dodson & Lu (2000) found similar patterns of erosion and weathering in Byenup Lagoon, suggesting that up until around 4800 years BP, this region was influenced heavily by westerly winds. The deposition of sediments on the easterly side of Bokarup Swamp, which ceased around the same time, again supports the hypothesis of continuous peat deposition since that time.

If Bokarup Swamp contains a profile that is predominantly organic and uninterrupted by inorganic sedimentation, then past accumulation rates are due to increased organic inputs. The recent use of regression modelling by Latter *et al.* (1998) and Okland & Ohlson (1998) to examine decomposition and compaction processes associated with long-term peat accumulation, has allowed differential rates of accumulation to be determined for specific species contributing to peat formation. The rapid phase of accumulation in the early stages of wetland development common to both Bokarup Swamp and Noobijup Lake may be due to increased inputs, but also increased inputs from more refractory sources. The carbon budget showed that inputs at the wetland margin were over five times higher than in the macrophyte dominated basin (Chapter 6) and dominated by *Melaleuca* litter (Chapter 2). The pollen record from Byenup Lagoon shows that *Melaleuca* species have been the dominant understorey vegetation associated with wetlands in this area since the mid to late Holocene (around 5000 years BP) (Dodson & Lu 2000). The higher rates of organic matter accumulation in the past may therefore be a result of increased inputs from fringing species. The dense macrophyte communities also currently limit the distribution of submergent macrophytes. Models of hydroseral succession developed for the Northern Hemisphere suggest submergent macrophytes contribute significantly to the sedimentation in the initial stages of wetland development (Tallis 1983). In the early stages of wetland development and organic matter accumulation, water levels may have been such that submergent macrophytes played a more important role in the carbon dynamics of these wetlands. Macrofossil remains of plant tissue were not apparent and no palynology has been done from these cores to reconstruct the dominant taxa involved in organic matter accumulation. Accumulation rates in the past may therefore have been due to increased inputs from any of submergent macrophytes, emergent macrophytes and/or littoral tree species such as *Melaleuca*.

Clearly, contemporary rates of organic matter supply are reduced from those in the past. At present, Bokarup Swamp has one of the highest levels of surface water salinity of the wetlands in the Muir-Unicup system (Chapter 2; Storey 1998). The wetland may be showing elevated salinities either because it is receiving saline run-off from cleared catchments, or it is showing long-term accumulation of salt as a result of progressive effects of evaporation and/or concentration. The extensive stands of *B.articulata* do not appear to be as 'healthy' as in other wetlands showing distinct signs of prolonged stress such as leaf discolouration and necrosis of leaf tips (also noted by Storey 1998). The decline of *B. articulata* in Lake Towerrinning (a wetland in the Western Australian wheatbelt) was attributed to increased salinities from agricultural clearing (Froend & McComb 1991). Historical evidence shows that from the 1850's to the early 1900's, Bokarup Swamp was used for the watering of stock throughout the year, indicating that water quality decline is a relatively recent phenomenon associated with agricultural clearing.

Stresses placed on the emergent macrophytes by a reduced water table may also lead to the decline in plant vigour and therefore a reduced organic matter contribution to the sediments. Maximum water levels of only 40 cm and no surface water present for six months of the year may stress the *B.articulata* community. The shallow maximum water depths indicates that the level of organic sediments is approaching that of the surrounding landscape, and that reduced surface water levels may be an expected part of the late stages of the seral development of Bokarup Swamp. In order for understorey species to become established within the wetland basin, surface water levels must be reduced by an increasing depth of organic sediments, to the detriment of the macrophyte communities. This successional pathway has been observed in many Northern Hemisphere wetlands (see reviews in Moore & Bellamy 1974; Wetzel 1975; Tallis 1983) but has not been examined in Australian temperate wetlands. The increase in salinity of the local surface and groundwater may exacerbate the decline in macrophyte productivity and prevent the continued accumulation of organic matter in the sediments of Bokarup Swamp.

7.4.2.2 Kodjinup Swamp

The model prediction of an overestimate of organic matter accumulation compared to basal radiocarbon dates and an anomalous chronology leading to a different accumulation pattern to the other wetlands suggests that the process of accumulation has been disturbed in Kodjinup Swamp. The model predicts a peat depth of around 30cm deeper after 3100 years and that the 700 and 850 year dated sediments should appear around 19cm higher in the profile compared to radiocarbon dates. One hypothesis is that a severe fire removed a large proportion of the organic matter and exposed the surface of the sapric peat. The removal of the upper layers of the sapric peat would explain the apparent slow initial accumulation rate compared to the other wetlands. The apparent rapid increase in deposition between 850 and 700 years BP may represent the remobilisation of sediments following rewetting. Eframova & Eframov (1994) documented the occurrence of low intensity below ground peat fires that burned substantial volumes of peat while leaving surface deposits in tact. Such a fire in Kodjinup Swamp may have led to the spatial redistribution of organic sediments and an anomalous chronology. This hypothesis can be tested in the furure by examining the macrofossil records of peat cores.

The presence of a layer of unconsolidated peat at the surface of Kodjinup Swamp that failed to generate a reliable ^{210}Pb chronology supports the hypothesis that the sediments in this wetland have been influenced by fire event(s) in the recent past. The vegetation associations in Kodjinup Swamp also show a proliferation of Bracken Fern (*Pteridium esclentum*) in this wetland, a species known for its occurrence following fire. This species was not found at the other wetlands. There was, however, no evidence of macrofossil charcoal in the profile, which is indicative of past fire events (Patterson *et al.* 1987). In the development of the methods for fossil charcoal analysis, Clark (1988) found that the interactions between vegetation, topography, weather and fire intensity influenced charcoal formation. The absence of macrofossil charcoal does not preclude the presence of microfossil charcoal which requires microscopic examination and was not performed on these sediments. The lack of charcoal in an obviously disturbed profile indicates that the fire event would have been of high intensity, resulting in the complete combustion of sedimentary organic matter (Fransden 1991). Numerous cores from locations across the wetland would be needed to examine the occurrence and distribution of remnant pedastals (sensu Horwitz *et al.* 1998).

An alternative to the hypothesis of disturbance by fire, is that the peat chronology is correct and the decay coefficient is too small, resulting in Kodjinup Swamp having a period of exceptionally high productivity leading to a deposition rate five times the long-term average. This would require the sediments of Kodjinup Swamp to accumulate 31 cm of organic matter in 150 years. As the review of accumulation rates in other Australian systems has shown, accumulation rates such as this are possible in highly productive and nutrient rich systems. However, this pattern is not evident in the other wetlands and such sustained productivity and litterfall from allochthonous or autochthonous sources is unlikely. Kodjinup Swamp does not have any direct drainage channels into the wetland and so it is also unlikely that organic matter was transported from within the catchment resulting in focussed deposition in the wetland basin.

Kodjinup Swamp is the shallowest and has the most recent deposits of the three wetlands studied. Semeniuk & Semeniuk (1997) hypothesised the occurrence of circular through to irregular shaped basins represented the geomorphic evolution where creeks geomorphically degrade to become broad valley flats which in turn clog to form irregular shaped basins (such as Noobijup Lake - Section 2.3.3). During intermittent climatic cycles, sedimentary processes result in the basins becoming excavated, ringed by beach ridges and finally circular (such as Bokarup and Kodjinup Swamps - Section 2.3.1 and 2.3.2 respectively). The radiocarbon dates from the three wetlands refute this hypothesis with Noobijup Lake being the oldest and having the most irregular shaped basin. The progression from irregular to circular wetland is more complex in these organic rich basins, where autogenic processes play a central role in wetland development. The model can be used to predict the trajectory for wetland development under a range of scenarios. For example, under current conditions of organic matter supply and decay, the peat depth in Kodjinup Swamp would reach an asymptote at around 217 cm at an age of 6300 years BP. With a current peat depth of 134 cm (3100 years BP) and a maximum water depth of around 1m, it can be hypothesised that in another 3200 years the wetland basin will be almost completely filled with organic matter. However, this trajectory of wetland development can be easily altered by changes in rates of supply and decay of organic matter through deterioration of water quality such as increased salinity or nutrients, alteration to local hydrology or direct losses of organic matter through erosional events such as fires.

7.4.3 Summary

Short-term studies examining wetland carbon budgets provide limited interpretation of long-term accumulation processes as they do not allow for continued *in situ* decomposition, nor use sediment characteristics in model predictions. Alternatively, ^{14}C radiocarbon dating has been used to estimate the average input of organic matter supply to model long-term rates of peat accumulation. The model developed in this thesis uses both contemporary rates of carbon supply generated from organic matter budgets and ^{210}Pb and ^{14}C sediment dating techniques to quantify short and long-term peat accumulation rates. The application of a decay coefficient derived from Noobijup Lake and applied to the other wetlands' results in model predictions and simulations in these wetlands being independent of radiocarbon dates. The assumption of a constant rate of organic matter supply to peat formation based on carbon budget data allows hypotheses about the impact of environmental change on accumulation rates to be generated from predictions based on constant, contemporary conditions. The use of organic matter bulk density data allows any compaction occurring with depth in the profile to be incorporated into the model. A correction for carbon content with depth also allows changes in inorganic sedimentation or selective carbon decay to be incorporated into the model. Based on model predictions for Noobijup Swamp, the accuracy of this model lies in the predictions of recent accumulation rates (up to 100 years) and the overall depth of the organic matter deposit.

Based on the assumptions of constant organic matter supply and exponential decay the model generates an underestimate of peat height in Bokarup Swamp and an overestimate of peat height in Kodjinup compared to ^{14}C dates. This indicates that environmental conditions and rates of organic matter supply and/or decay have been highly variable in the past. The model predictions for Bokarup Swamp indicate that the current rate of organic input generates over 1m less peat than quantified using radiocarbon dates for the same period of time. The model was used to determine that over double the current rate of organic matter input since the wetlands' initiation was required to generate the sufficient peat depth. In Kodjinup Swamp, the model prediction of an overestimate of organic matter accumulation compared to basal radiocarbon dates and an anomalous chronology suggests that the process of accumulation has been disturbed. It is hypothesised that fire related disturbance(s) over the last 3000 years have resulted in the redistribution of sediments within the peat profile and the formation of an unconsolidated layer of peat at the sediment surface in this wetland.

Parameters within the model such as run-time, rates of organic matter supply and decay can be altered. This allows the trajectory of wetland development to be examined under different environmental conditions, such as altered rates of supply and decay of organic matter, deterioration of water quality such as increased salinity or nutrients, alteration to local hydrology or direct losses of organic matter through erosional events such as fires. Model predictions can therefore be used in determining the impact of catchment management on the process of peat accumulation in these wetlands.

CHAPTER 8

SYNTHESIS

Carbon cycles, wetland development and management recommendations

8.1 Summary

This thesis examined the cycling of organic matter in three shallow (<1 m) wetlands (Bokarup Swamp, Kodjinup Swamp and Noobijup Lake) with deep peat deposits in the Miur-Unicup region of south-western Australia. Each wetland had a different recent history of disturbance from fire and altered drainage. Water quality of the wetlands is also decreasing, with rises in regional groundwater and wetland salinity levels. The impacts of these disturbances on wetland processes and development are unknown, and therefore the sustainability of these ecosystems under current management practices needs to be addressed.

Dominant inputs (Chapter 3) and losses (Chapter 4) of organic matter were quantified, and the role of the dominant sources of organic matter in wetland food webs examined (Chapter 5). Sources and sinks of organic matter were used to construct a seasonal and annual carbon budget for each wetland (Chapter 6). Empirical data from the carbon budgets, sediment dating (^{210}Pb and ^{14}C) and sediment characteristics such as peat bulk density and organic content from each wetland were used to build a simple, descriptive model of long term rates of organic matter accumulation in these wetlands (Chapter 7). This thesis provides the only examples of a quantitative carbon budget and a descriptive, predictive model of long-term peat accumulation rates for Australian wetland systems.

Sources and losses of organic matter were dominated by a strong seasonal cycle. Peak rates of inputs and losses occurred during the summer periods of each year and coincided with the period of maximum wetland water levels and temperatures. Emergent macrophytes (predominantly *Baumea articulata*) dominated the organic matter supply in each wetland basin through the contribution of litterfall and below ground structures. Losses of organic matter (expressed as carbon dioxide and methane atmospheric flux) were relatively low compared to other wetland systems (see review in Kiene 1991), and may be a result of reduced microbial activity from highly anoxic organic sediments. The importance of this microbial activity to system function was evident in wetland foodwebs (through $\delta^{13}C$ and $\delta^{15}N$ analysis), with the detrital litter (mainly of macrophytic origin) hypothesised to be a primary source of energy in these wetlands.

The annual carbon budget demonstrated that each wetland basin is currently a sink for tens of thousands of kilograms of carbon each year. The budget also highlighted the potential for disturbance events (such as fire) to transform wetland areas from carbon sinks to carbon sources. The development of a simple, descriptive model of peat accumulation rates also demonstrated that short-term erosional events and long-term changes to rates of organic matter supply and decay have led to variable rates of peat accumulation between wetlands in the Muir-Unicup region.

8.2 The importance of ecosystem processes

One of the primary factors controlling the formation of organic sediments is the suppression of the aerobic decay of plant material. In Bokarup Swamp, Kodjinup Swamp and Noobijup Lake, dissolved oxygen concentrations at the soil-water interface were consistently less than 1 mg/L, even with water depths as low as 10 cm. Diurnal profiles of water column DO and temperature indicated that a high and persistent benthic oxygen demand was driving sediment and water column anoxia. The high benthic oxygen demand from sediment microorganisms is dependant on a continued supply of organic matter as a substrate for respiration. The microbial decomposition of this material in turn reduces DO concentrations and favours the organic matter accumulation. The deep peat deposits in each wetland indicate that the conditions conducive to peat accumulation have been persistent for several thousand years. The exposure of surface peats to aerobic processes through altered wetland hydrology can accelerate the decomposition of organic matter and alter rates of accumulation. If organic sediments are to continue to accumulate in the wetlands of the Muir-Unicup region it is essential that existing peat deposits remain permanently inundated in order to maintain the anoxic sediment conditions necessary for peat accumulation.

The accumulation of peat is also reliant on the supply of organic matter to wetland basins. The contribution of carbon inputs from allochthonous sources is substantial in the margins of these wetlands, with inputs exceeding those from emergent macrophytes in all seasons. This has important implications for the development of these wetlands, as it appears that long-term peat accumulation involves vertical accumulation in the main basin and a lateral encroachment of the wetland margins (Chapter 6). However, rates of lateral encroachment are dependent on, and more susceptible to, the influence of hydrological regime, resulting in different rates of accumulation in the wetland margins to the central basin. This is evidenced by shallower peat deposits in the wetland margins of all the study wetlands, indicating the wetting and drying cycle experienced by this habitat is accelerating organic matter decomposition. The processes involved in the lateral accumulation of organic matter have not been described in this study due to limited knowledge of decomposition rates in the wetland margins and no available radiocarbon dates. Differences in the rates of organic matter inputs and losses need to be quantified in for all macrohabitats occurring in wetland basins if the process of wetland development is to be determined.

Emergent macrophytes, particularly *B.articulata*, dominated the carbon supply in each wetland through the contribution of leaf litter and below ground structures. Macrophytes contributed highly refractory particulate organic matter to sediments, provided a source of DOM, which may have contributed to low water column productivity and provided a colonisable substratum for biofilms. The results of the stable carbon and nitrogen analyses demonstrate the importance of macrophyte organic matter in the foodwebs of these wetlands as a source of organic matter for detrital microflora (Chapter 5). The litterfall from emergent macrophytes therefore not only provides the primary resource for peat accumulation in the wetland basins, it is also central to the functioning of wetland foodwebs by providing an organic substrate for detrital microorganisms.

Emergent macrophytes also exerted a strong influence on the transformations and losses of organic matter in these wetlands. They provided an important source of methanogenic substrate and enhanced the atmospheric flux of the methane. Methane flux rates were significantly higher through emergent vegetation indicating *B.articulata* acts as a conduit for gas transport from the sediments to the atmosphere. Conversely, rates of carbon dioxide flux were higher from unvegetated sediments, which may have resulted from the aerobic consumption of methane by methanotrophic bacteria in surface sediments or in the water column (Chapter 4). The transport of methane to the atmosphere through emergent vegetation is an important process, as it removes methane from saturated sediments and creates an aerobic rhizospere for methanotropic bacteria. The stable isotopes study hypothesised that detrital microorganisms (such as methanotrophic bacteria) were an important energy source in these wetlands. The balance between these two processes is therefore crucial to wetland function and is reliant on a hydrologic regime that sustains macrophyte communities.

Emergent macrophytes dominate the pathways of organic matter sources, sinks and transformations in Bokarup Swamp, Kodjinup Swamp and Noobijup Lake. The maintenance of emergent macrophyte communities is therefore paramount to sustain fundamental wetland processes. Altered wetland hydrology leading to prolonged flooding or drought in excess of plant tolerances may lead to a decline in productivity and subsequent reduction in organic matter inputs. Recent changes to water quality in the Muir-Unicup region may also result in changes to organic matter supply. Rising salinity levels as a result of catchment agricultural practices in many of the wetlands in this system may reduce plant vigour. Equally, high levels of phosphorus from agricultural runoff may increase macrophyte productivity. Froend & McComb (1994) have described the tolerances for *B.articulata* to changes in water quantity and quality. The maintenance of water quality and quantity in the Muir-Unicup region must be addressed to ensure the continued supply or organic matter important to short and long-term wetland processes.

A strong seasonal cycle dominated wetland physico-chemistry and organic matter inputs, transformations and losses in all wetlands. Allochthonous and autochthonous inputs of organic matter peaked during the summer periods of each year and corresponded to the timing of maximum organic matter decomposition rates. This period of increased organic matter inputs and losses coincided with the period of maximum wetland water levels and temperatures. The coincidence of these processes is important, as the difference between inputs and losses of organic matter control the rate of peat accumulation. There was approximately a six-month lag (taking into account the sampling interval) between maximum rainfall and maximum water levels. The result is a suite of wetlands with highly seasonal water levels that are deepest in the warmer summer periods, an uncommon feature in south-west Australian wetlands. High water levels during this period may be important for providing the low benthic oxygen conditions at the time of the highest organic inputs and therefore favouring the accumulation of peat. The presence of the physico-chemical conditions most conducive to peat accumulation coinciding with peak organic matter inputs has not been noted in the Australian limnological literature. The fact that the co-occurrence of these conditions occur in a limited geographic region may be the predominant reason explaining the occurrence and distribution of peat deposits in south-western Australia.

8.3 Disturbance and rates of organic matter accumulation

The deep organic sediments in the basins of the Muir-Unicup wetlands suggest that they have all been in net gain of carbon for a considerable period. A carbon budget quantifying whether Australian wetland systems are a net source or sink of carbon had not been previously constructed. The development of an annual carbon budget for shallow, macrophyte dominated wetlands has demonstrated that each wetland basin is currently a sink for tens of thousands of kilograms of carbon each year. These wetland types are geographically restricted in south-western Australia and therefore become important in both regional and global carbon cycles, sequestering enormous quantities of carbon in their peat deposits. The unvegetated area in Bokarup Swamp created by a fire event, however demonstrates the capacity for these wetlands to revert from carbon sinks to carbon sources following disturbance. It is the only habitat studied that is a source of carbon, contributing over 300 kgC/year to the global carbon budget and highlights the role of macrophytes not only as a carbon source, but also as an integral part of a self-perpetuating, functioning, homeostatic system. Increases in the periods of no surface water, loss of macrophytes from decreased water quality and the fire management of the surrounding forests also have the potential to accelerate decomposition, and turn these wetlands from a carbon sink to a carbon source. The consequences of these disturbances extend well beyond the boundaries of these wetlands, as they can affect local, regional and global carbon cycles.

The development of a simple, descriptive model (based on data from organic matter budgets, sediment dates and sediment characteristics) has produced predictions of rates of sediment organic matter accumulation (Chapter 7). The model predictions for Bokarup Swamp indicate that past long-term rates of organic matter supply would have needed to be over double the present rates in order to accumulate the current depth of peat. At present, Bokarup Swamp has one of the highest levels of surface water salinity of the Muir-Unicup wetlands and the lowest imput of organic matter from macrophytes. The extensive stands of *B.articulata* do not appear to be as 'healthy' as in other wetlands showing distinct signs of prolonged stress such as leaf discolouration and necrosis of leaf tips. Maximum water levels of only 40 cm and no surface water present for six months may contribute to the decline in plant vigour caused by decreasing water quality. The shallow maximum water depths indicate that the level of organic sediments is approaching that of the surrounding landscape, and that reduced surface water levels would be an expected part of the late stages of the seral development of this wetland. The increase in salinity of the local surface and groundwater may exacerbate the decline in macrophyte productivity to the point where rates of organic matter decomposition exceed inputs. If this were to occur, Bokarup Swamp would not reach the terminal stages of wetland development.

The model prediction of an overestimate of organic matter accumulation compared to basal radiocarbon dates and an anomalous chronology suggest that the process of peat accumulation has been disturbed in Kodjinup Swamp. It was hypothesised that a severe fire event(s) removed a large proportion of the sediment organic matter. Peat fires can cause the direct loss of organic substrate through combustion and compaction, remove vegetation contributing to peat accumulation and accelerate decomposition through increased aerobic exposure of peat surfaces (Pitkanen *et al.* 1999). Altered hydrology leading to increased drought conditions and the occurrence of wetlands approaching the late stages of seral succession will mean they may be more susceptible to disturbance from fire. The impact from short-term disturbances such as fire on peat accumulation rates and will therefore depend on the peat conditions (primarily moisture content) and the timing and frequency of fire events.

The model can also be used to predict the trajectory for wetland development under a range of scenarios, providing information on short and long-term wetland processes. The predictive power of the model permits the simulation of different scenarios and allows for thresholds critical to continued peat formation to be identified. The ability of the model to predict the long-term impacts of current or simulated environmental conditions is an important component in identifying environmental conditions that may cause impacts on rates of peat accumulation that are not apparent in the short-term. The monitoring of environmental conditions and rates of organic matter supply and decay, and simulating the long-term impact on organic sediment could provide a valuable tool for assessing the impact of current and proposed management on wetland function and development.

8.4 Wetland development and management recommendations

8.4.1 Water quality and quantity

Altered wetland physico-chemistry is the greatest threat to the biogeochemistry of the Muir-Unicup wetlands. A myriad of land management practices and management options adopted in this region have led to substantial changes in water quality and quantity since the Muir-Unicup region was opened to large-scale agriculture in the 1970's. Extensive networks of surface water drainage channels have been constructed within the catchment to remove saline overland flow from agriculturally productive land into nearby rivers and wetlands. While this does prevent the localised salinisation of individual wetlands, the threats to the functioning of the Muir-Unicup wetlands from periodic drought through water diversions have not been established. The results from this thesis demonstrate that drying phases lead to increased aerobic decomposition and losses of organic matter, and may result in a long-term reduction in peat accumulation. Dry phases also increase the risk of short-term disturbances from fire, which can severely alter the trajectory of wetland development. Equally, extended periods of inundation can reduce macrophyte vigour and affect the long-term rates of organic matter supply. The drainage system constructed through Kodjinup Swamp Nature Reserve, for example, has reduced the local catchment by two thirds, resulting in Kodjinup Swamp drying out for the first time on record immediately following the drain construction. The issue of drainage needs to be addressed, as diverting water into and away from wetlands can have important ecological consequences. Further research outlining the impacts of flooding frequency, timing and duration on wetland function would provide a basis for a management regime to ensure sufficient water quality and quantity to sustain aspects of ecosystem function.

Extensive plantations of Blue Gums (*Eucalyptus globulus*) and *Pinus radiata* have been recently established throughout the catchment on land considered unsuitable for traditional agriculture (crops and grazing). Many of these plantations cover hundreds of hectares immediately adjacent to wetland reserves. The role of these plantations in reducing the level of the regional groundwater is important, however, their impact on localised groundwater drawdown and hence wetland water levels is unknown. The saturation of peat deposits in the Muir-Unicup wetlands has been identified as a critical component in maintaing the physico-chemical conditions conducive to peat accumulation. Equally, the impact on water levels following plantation harvests is unknown, and has the potential to lead to severe increased water depths through localised rises in the groundwater table. Although only short-term, this impact may reduce macrophyte productivity or even cause their death. This thesis has demonstrated the central role of macrophytes in the ecological processes of these wetlands, and quantified the detrimental impact of their loss to long-term wetland development and function. Reasearch into the impact of these extensive plantations on local and regional groundwater levels would provide for management strategies that minimised detrimental impacts on wetland function from altered hydrology.

8.4.2 Fire

Due to the high moisture content afforded by the organic deposits and their location in basins, the Muir-Unicup wetlands have probably not been affected by fire to the same extent as the surrounding vegetation. As such, these systems may be considered refugia from fire for many species of flora and fauna. Equally, the lack of obvious impacts of past fire events in many of the Muir-Unicup wetlands does not preclude their current susceptibility to damage from fire.

Within the Muir-Unicup region fire is a natural phenomenon because of frequent summer drought and lightning storms. Fire is also a management strategy of conservation agencies for the regeneration of logged areas and as a fuel reduction and fire suppression strategy. The Muir-Unicup catchment contains a diverse mosaic of peat-floored wetlands with different physico-chemistries and rates of peat accumulation, and of considerably different ages and stages in seral development. The susceptibility of each wetland to disturbance from fire will therefore differ depending on past and current wetland conditions. The silvicultural practice of rotational prescription burning therefore cannot be applied homogeneously to a landscape that is heterogeneous in nature (Wardell-Johnson & Horwitz 1996). In order to preserve areas with highly organic sediments that are sensitive to fire, detailed maps need to be constructed detailing their distribution. Once identified, the moisture content of individual organic deposits need to be assessed to determine their vunerability to fire at time of the prescription burn. Fire regimes need to be developed for the Muir-Unicup region that recognise the mosaic of wetland types and provide a diversity of 'prescriptions', which include a regime of fire exclusion. A regime targeted to a specific vunerable habitat will allow for representative wetlands to continue to develop and accumulate peat without anthropogenic disturbance from fire, while retaining a mosaic of wetlands with a range of developmental stages, ages and intrinsic characteristics.

8.4.3 Conclusion

To quantify the rates of organic matter accumulation in wetland systems, and predict their future response to environmental change, we need to consider the management of these systems at various spatial and temporal scales. This research has demonstrated differences in physico-chemistry, rates of organic matter supply and decay, foodweb structure and short and long-term rates of peat accumulation between Bokarup Swamp, Kodjinup Swamp and Noobijup Lake in the Muir Unicup region of south-western Australia. These differences are evident despite the fact that these wetlands all contain peat-floored basins dominated by the same species of emergent macrophyte and are in close proximity to each other within the same catchment. It has also been shown that these wetlands are in different stages of seral development as a result of differeing ages of the peat deposits and exposure to disturbance events. Without quantitative data describing the contemporary ecological processes as well as estimates of long-term rates of organic matter accumulation, we have somewhat optimistic expectations when trying to predict the effects of environmental change on wetland development.

The Muir-Unicup wetlands are vulnerable to large-scale disturbance from human activity that can affect short and long-term fundamental wetland processes. The preservation of wetlands in small isolated pockets of forest surrounded by cleared agricultural land may not ensure the long-term survival of these systems. Disturbance is a key process in the development of wetland systems, and the active prevention of disturbance may also lead to the disintegration of many wetland processes. Management of these systems requires landscape scale planning over long-term time frames (decades to centuries). Palaeoecological techniques combined with contemporary process data provide a valuable baseline from which to judge the present situation and argue for a long-term landscape scale management and conservation policy. Such management would result in a landscape where key processes involved in wetland development are allowed to operate without undue hindrance from anthropogenic disturbance.

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APPENDIX 1- TAXONOMIC LISTS FOR VEGETATION TRANSECTS

Bokarup Swamp.

		Transect 1			Transect 2			Transect 3		
FAMILY	Species	A	B	C	A	B	C	A	B	C
ZAMIACEAE	*Macrozamia riedlei*	x			x			x		
DILLENIACEAE	*H. hypercoides*				x			x		
	H. racemosa							x		
DROSERACEAE	*Drosera pallida*				x			x		
	D. penicillaris				x			x		
EPACRIDACEAE	*Leucopogon capitillaris*				x			x		
MIMOSACEAE	*A.extensa*				x			x		
	A.heuglelii				x			x		
	A.pulchella				x					
PAPILIONACEAE	*Bossiaea linofolia*				x			x		
	Davesia sp1				x			x		
	Isotropis cuneata				x					
PROTEACEAE	*B. littoralis*				x			x		
	H. prostrata				x			x		
	Synaphea spinulosa				x			x		
THYMELAEACEAE	*Pimelia sulphurea*				x			x		
MYRTACEAE	*Eucalyptus calophylla*	x			x			x		
	E. rudis	x			x			x		
	Hypocalymma sp3				x					
	Melaleuca raphiophylla					x	x		x	x
	M.densa					x	x		x	
ASTERACEAE	*Asteridia pulverulenta*				x			x		
	Craspedia sp1				x			x		
XANTHORRHOEACEAE	*xanthorrhoea preissii*				x			x		
ANTHERICACEAE	*Chamaescilla corymbosa*				x			x		
	Sowerbaea laxiflora				x			x		
IRIDACEAE	*Ixia sp1*				x					
ORCHIDACEAE	*Caladenia flava*				x					
HAEMODORACEAE	*Conostylis setigera*				x			x		
	Tribonanthes violacea				x					
HYDROCHARITACEAE	*Vallisneria gigantea*		x			x	x		x	x
MENYANTHACEAE	*Villarsia sp.*		x			x	x		x	x
CYPERACEAE	*Baumea articulata*		x			x	x		x	x
	Schoenoplectus validus						x			x
Species Richness		2	3	0	27	5	6	22	5	5

Kodjinup Swamp

		Transect 1				Transect 2			Transect 3		
FAMILY	Species	A	B	C	D	A	B	C	A	B	C
DENNSTAEDTIACEAE	*Pteridium esculentum*	x	X								
ZAMIACEAE	*Macrozamia riedlei*	x	X			x			x		
STERCULIACEAE	*Thomesia sp*					x					
DROSERACEAE	*D. penicillaris*	x				x			x		
EPACRIDACEAE	*Leucopogon capitillaris*					x			x		
	L. propinea					x			x		
MIMOSACEAE	*A.heuglelii*	x	X			x			x		
	Acacia saligna	x							x		
PROTEACEAE	*B. littoralis*	x	X	x		x	x		x		
	Isopogon sp 1					x			x		
	Lambertia sp1	x				x					
MYRTACEAE	*Baeckea sp1*					x			x		
	Eucalyptus calophylla	x				x			x		
	E. rudis	x				x			x		
	Hypocalymma sp1	x				x			x		
	Hypocalymma sp2					x			x		
	Kunzea recurva								x		
	Melaleuca raphiophylla			x	x		x			x	
	M.densa	x		x			x				
GOODENIACEAE	*Scaevola sp1*	x				x			x		
XANTHORRHOEACEAE	*xanthorrhoea preissii*	x				x			x		
ORCHIDACEAE	*Caladenia flava*					x			x		
HAEMODORACEAE	*Conostylis setigera*					x			x		
HYDROCHARITACEAE	*Vallisneria gigantea*			x	x		x	x		x	x
MENYANTHACEAE	*Villarsia sp.*			x	x		x	x		x	x
CYPERACEAE	*Baumea articulata*			x	x		x	x		x	x
Species Richness		13	4	6	4	18	6	3	18	4	3

Noobijup Lake

		Transect 1				Transect 2			Transect 3			
FAMILY	Species	A	B	C	D	A	B	C	A	B	C	D
ZAMIACEAE	*Macrozamia riedlei*	x	x			x	x		x	x		
DILLENIACEAE	*Hibbertia amplexicaulis*	x	x			x	x		x			
	H. racemosa	x							x			
DROSERACEAE	*Drosera pallida*	x	x			x	x		x	x		
	D. penicillaris	x	x			x	x		x	x		
EPACRIDACEAE	*Leucopogon capitillaris*	x				x			x			
PITTOSPORACEAE	*Sollya heterophylla*	x							x			
MIMOSACEAE	*A.pulchella*	x				x	x		x			
PAPILIONACEAE	*Kennedia sp1*	x	x						x	x		
PROTEACEAE	*Banksia latifolia*	x	x			x	x		x			
	Dryandra nivea	x	x			x	x		x	x		
	Hakea lissocarpha	x				x	x					
	H. prostrata	x				x						
	H. ruscifolia					x	x					
	Synaphea spinulosa	x				x			x			
MYRTACEAE	*Baeckea sp1*	x				x	x		x	x		
	Eucalyptus calophylla	x				x			x			
	E. rudis		x				x			x		
	Hypocalymma sp1	x				x						
	H.angustifolium		x			x						
	Melaleuca raphiophylla		x	x			x	x				
	M.densa						x					
EUPHORBIACEAE	*Phyllanthus calycinus*								x			
RUTACEAE	*Boronia spathulata*	x							x			
APIACEAE	*Xanthosia heuglii*	x				x	x		x			
GOODENIACEAE	*Scaevola sp1*	x					x					
ASTERACEAE	*Craspedia sp1*	x				x			x			
	Ursinia sp1	x				x			x			
XANTHORRHOEACEAE	*xanthorrhoea preissii*	x	x			x	x		x			
ANTHERICACEAE	*Chamaescilla corymbosa*	x							x			
	Thysanotus manglesianus	x							x			
ORCHIDACEAE	*Caladenia flava*	x	x			x	x		x	x		
	C.heuglii	x	x			x	x		x	x		
HAEMODORACEAE	*Conostylis setigera*	x	x			x	x		x	x		
HYDROCHARITACEAE	*Hydrilla verticillata*			x				x			x	
	Vallisneria gigantea			x				x			x	
MENYANTHACEAE	*Villarsia sp.*			x				x			x	
CYPERACEAE	*Baumea articulata*			x	x			x			x	x
	B.arthrophylla				x			x				x
Species Richness		28	14	5	2	23	19	6	25	10	4	2

APPENDIX 2 - RAW DATA FROM PHOSPHOLIPID PRELIMINARY EXPERIMENT

Replicate	0-15cm µg PO4	*running s.d.*	15-30cm µg PO4	*running s.d.*	30-45cm µg PO4	*running s.d.*
1	38.82		23.55		12.15	
2	52.75	*9.85*	36.05	*8.84*	18.88	*4.76*
3	42.56	*7.21*	34.93	*6.92*	13.98	*3.48*
4	57.98	*8.87*	35.49	*5.99*	12.76	*3.05*
5	43.15	*7.98*	40.61	*6.33*	18.27	*3.15*
6	52.87	*7.53*	26.64	*6.43*	14.90	*2.82*
7	52.26	*7.05*	32.76	*5.87*	17.66	*2.74*
8	61.98	*8.06*	42.16	*6.35*	19.66	*2.93*
9	39.79	*8.31*	37.16	*6.03*	22.22	*3.43*
10	47.66	*7.85*	38.27	*5.82*	12.86	*3.46*
11	59.37	*8.08*	25.99	*6.12*	13.41	*3.40*
12	63.28	*8.61*	43.19	*6.42*	16.43	*3.24*
13	55.47	*8.34*	28.76	*6.36*	15.67	*3.11*
14	52.44	*8.34*	32.15	*6.36*	21.29	*3.11*
15	57.20	*7.87*	39.47	*6.07*	16.93	*3.18*

APPENDIX 3 - RAW DATA USED IN CARBON BUDGET CALCULATIONS.

Bokarup Swamp (g/m^2)

	Winter		Spring		Summer			Autumn
	Jul-95	Jul-96	Sep-95	Oct-96	Dec-95	Feb-96	Jan-97	Apr-96
Allochthonous litterfall	nd	37.872	52.302	34.408	129.777	128.596	89.117	54.244
Autochthonous litterfall	nd	8.242	6.381	7.179	20.473	20.473	11.699	8.242
Macrophyte roots/rhizomes	3.185	3.185	3.185	3.185	3.185	3.185	3.185	3.185
Water column production	0.009	0.015	0.091	0.062	0.353	0.532	0.062	0.278
DOC	0.393	0.600	0.213	0.284	0.473	0.702	0.454	0.070
Biofilm	nd	0.000	0.649	1.166	5.860	0.000	4.381	0.000
Microbial Biomass	0.142	0.178	0.197	0.269	0.327	0.341	0.269	0.232
CO2 - Open water	0.903	1.150	nd	1.754	1.696	2.182	2.377	2.218
CO2 - Macrophytes	0.710	0.903	nd	1.036	0.931	1.073	1.036	1.109
CH4 - Open water	0.472	0.564	nd	0.854	0.896	0.947	0.854	0.547
CH4 - Macrophytes	0.497	0.641	nd	1.129	0.991	1.064	1.129	0.871
Total CO2	0.807	1.026	nd	1.395	1.314	1.628	1.707	1.663
Total CH4	0.591	0.733	nd	0.945	0.914	1.010	0.945	0.828

Kodjinup Swamp (g/m^2)

	Winter		Spring		Summer			Autumn
	Jul-95	Jul-96	Sep-95	Oct-96	Dec-95	Feb-96	Jan-97	Apr-96
Allochthonous litterfall	nd	24.772	25.197	27.299	78.185	81.195	52.660	43.408
Autochthonous litterfall	nd	1.089	7.084	10.740	33.692	32.661	22.691	8.085
Macrophyte roots/rhizomes	10.673	10.673	10.673	10.673	10.673	10.673	10.673	10.673
Water column production	0.000	0.000	0.013	0.045	0.069	0.079	0.105	0.018
DOC	0.105	0.115	0.759	2.035	1.837	1.304	1.167	0.515
Biofilm	nd	0.000	0.175	0.526	0.637	0.482	0.813	0.099
Microbial Biomass	0.309	0.259	0.276	0.398	0.440	0.671	0.940	0.401
CO2 - Open water	1.286	1.402	nd	1.294	1.836	1.805	1.981	2.022
CO2 - Macrophytes	1.091	1.156	nd	1.787	1.466	1.687	1.887	1.988
CH4 - Open water	0.390	0.591	nd	0.717	0.931	0.936	0.970	0.360
CH4 - Macrophytes	0.686	0.704	nd	1.199	1.298	1.303	1.346	0.642
Total CO2	1.188	1.279	nd	1.540	1.651	1.746	1.934	2.005
Total CH4	0.538	0.647	nd	0.958	1.115	1.119	1.158	0.501

Noobijup Lake (g/m^2)

	Winter		Spring		Summer			Autumn
	Jul-95	Jul-96	Sep-95	Oct-96	Dec-95	Feb-96	Jan-97	Apr-96
Allochthonous litterfall	nd	21.606	18.201	7.395	33.983	36.527	18.636	29.097
Autochthonous litterfall	nd	7.958	2.914	5.563	17.366	17.700	14.027	5.967
Macrophyte roots/rhizomes	3.095	3.095	3.095	3.095	3.095	3.095	3.095	3.095
Water column production	0.006	0.011	0.024	0.059	0.203	0.184	0.353	0.044
DOC	0.364	0.343	0.272	0.516	0.446	0.281	0.290	0.123
Biofilm	nd	0.625	1.328	1.742	3.026	8.612	18.783	15.887
Microbial Biomass	0.052	0.063	0.079	0.172	0.219	0.295	0.350	0.158
CO2 - Open water	0.955	0.940	nd	1.430	1.510	1.791	1.708	1.285
CO2 - Macrophytes	0.713	0.843	nd	0.914	0.899	1.176	1.067	1.094
CH4 - Open water	0.361	0.394	nd	0.526	0.550	0.569	0.633	0.549
CH4 - Macrophytes	0.686	0.668	nd	0.697	0.812	0.965	0.906	0.840
Total CO2	0.834	0.892	nd	1.172	1.205	1.483	1.388	1.189
Total CH4	0.524	0.531	nd	0.612	0.681	0.767	0.770	0.694

APPENDIX 4 - PERCENT ORGANIC CARBON VALUES FOR DOMINANT ORGANIC MATTER SOURCES DETERMINED BY IRMS.

	Summer	*S.E*	Autumn	*S.E*	Winter	*S.E*	Spring	*S.E*
Bokarup Swamp								
Biofilm unvegetated	18.37	*0.04*			15	*0.445*	7.74	*1.94*
Biofilm vegetated					14.42	*1.86*	8	*0.57*
B.articulata leaves	35.6	*0.16*			28.9	*1.37*	28.46	*2.11*
B.articulata roots	33.7	*2.29*			27.24	*2*	16.9	*0.43*
B.preisii leaves	33	*1.9*			36.07	*1.87*	23.13	*2.36*
B.arthrophylla leaves	29.35	*0.8*			42.63	*1.82*	25.48	*4.1*
Nymphoides sp.	34	*0.31*			32.43	*0.097*	23.3	*2.68*
Triglochin sp.	37.36	*1.15*			37.35	*2.6*	30.65	*3.9*
M.raphiophylla	37.7	*0.51*			43.42	*1.16*	30.2	*2.9*
E.rudis	40.7	*0.39*			42.7	*1.5*	26.97	*0.2*
Kodjinup Swamp								
Biofilm vegetated	25.3	*0.6*			24.7	*1*	18.97	*1.7*
B.articulata leaves	38.2	*2*			33.81	*0.58*	25.11	*6.32*
B.articulata roots	33	*6.3*			29.8	*0.94*	23.88	*1.66*
Nymphoides sp.	26.5	*6.6*			26.48	*1.7*	22.59	*5.69*
Triglochin sp.	28.9	*0.47*			36.38	*3.44*	21.16	*9.2*
M.raphiophylla	40.9	*0.6*			36	*2.1*	33	*7.6*
E.rudis	41.75	*0.4*			37.9	*2.1*	29.19	*4.17*
Noobijup Lake								
Biofilm vegetated	25	*1.4*	17.38	*0.09*	11.3	*0.92*	13.14	*2.21*
B.articulata leaves	35	*0.43*	28.2	*1.58*	37.61	*0.56*	28.35	*0.29*
B.articulata roots	34.2	*0.5*	27.89	*0.5*	33.1	*1.76*	26.52	*0.77*
B.arthrophylla leaves	38.8	*0.37*	40	*1.2*	35.86	*0.46*	29.8	*0.53*
Nymphoides sp.	45.5	*0.64*	25	*2.48*	37.78	*3.05*	31.79	*3.68*
Triglochin sp.	33.3	*0.45*	30.2	*2.57*	39.84	*2.1*	45.98	*1.29*
Myriophyllum sp	39.6	*0.9*	31.97	*1.58*	43.38	*3.96*	44.87	*0.29*
M.raphiophylla	49.8	*1.2*	30.6	*0.33*	57.27	*5.79*	40.37	*0.78*
E.rudis	58.4	*6.78*	37.97	*4.93*	57.67	*2.21*	41.12	*0.14*