Factors affecting the recruitment of riparian vegetation on the Ord and Blackwood Rivers in Western Australia

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FACTORS AFFECTING THE RECRUITMENT OF RIPARIAN VEGETATION ON THE ORD AND BLACKWOOD RIVERS IN WESTERN AUSTRALIA.

Neil Pettit (Bachelor of Applied Science, Master of Philosophy)
School of Natural Sciences
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25 May 2000

This Thesis is presented for the degree of Doctor of Philosophy at Edith Cowan University.
ABSTRACT

This thesis provides baseline information on the ecological processes involved in the recruitment and regeneration of riparian vegetation. As there has been a paucity of basic ecological studies on riparian vegetation in Australia, the project is broad in scope, and gives a general picture of the factors influencing the regeneration of riparian vegetation and provides a starting point for more detailed work. The project focuses on factors determining recruitment events and the life history traits of particular species on a river in the cool temperate zone of south western Australia (Blackwood River) and on a river in the dry tropics of the Kimberley region of north-western Australia (Ord River). By studying two contrasting river systems in different climatic zones, the influence of the physical environment and biotic factors on vegetation persistence and recruitment in the riparian zone can be distinguished. This will contribute to providing an ecological basis for the rehabilitation and management of riparian vegetation in these types of systems.

The structure of the vegetation on the Blackwood River consists of an overstorey dominated by *Eucalyptus rudis*, with a shrub understorey at ungrazed sites and with annual species dominant in areas grazed by livestock. On the Ord River there is a much more diverse overstorey and a species-poor understorey dominated by perennial grasses. Fencing to exclude stock, or to at least manage grazing, is a fundamental step towards achieving rehabilitation of degraded riparian sites where recruitment may be severely limited. Exclosure experiments on the Blackwood River show little improvement in recruitment after three years, with only minor increases in the occurrence and cover of native species. Establishment of these species may be difficult with the increase in abundance of exotic grasses and annual herbs which has occurred as a result of the absence of grazing. These results are however for the short-term and a much longer period is required to look at the vegetation dynamics and successional processes of these sites. In the riparian zone, regeneration of the vegetation from soil seedbanks is important for annual species of herbs and grasses but of only minor significance for perennial species. For perennial species, particularly the overstorey, direct seedfall from existing vegetation occurs, and enhanced dispersal by floating downstream with flood debris is a consequential recruitment mechanism. Hence, reproductive phenology of the four species monitored in this study appears to be well adapted to the hydrological regime on the respective rivers. Position in the riparian landscape where seedlings manage to establish is strongly related to environmental conditions that provide adequate moisture but protect seedlings from flooding.

Historical flow records can be used to develop an understanding of the natural flow regime for a particular river which can then be related to patterns of vegetation development in terms of...
reproductive phenology, seedling establishment and population structure, as well as plant community patterns in the riparian zone. Variability in natural flow regimes, as a disturbance, can therefore be used in conjunction with other abiotic and biotic factors in developing a model of vegetation dynamics for the riparian zone. For example, the regime of intermittent high frequency large flood disturbances on the Ord River prevents the establishment of stable states of the vegetation and the ecosystem is characterised by long periods of transition between short-lived stable states. This riparian ecosystem is thus driven by physical (allogenic) processes rather than by vegetation successional (autogenic) processes. In contrast, lower energy seasonal flooding on the Blackwood River allows mature stands of trees to develop throughout the river profile. Recruitment is continual, although species can also respond to large flood events. This disturbance regime results in long periods of stable states with short periods of transition. The vegetation is thus subject to longer periods of autogenic processes and, because of lower frequency flooding disturbance, shorter periods of allogenic processes. These results highlight the effect of the different fluvial regimes of the two rivers on the respective vegetation dynamics. Management of the riparian vegetation should therefore take into account the frequency and rate of change in the vegetation and that disturbed states and long periods of transition between states, particularly on the Ord River, are part of the natural process. This would suggest that altering the natural flow regimes, such as through river regulation, would have significant effects on riparian vegetation dynamics.

This work has relevance to all aspects of riparian zone vegetation, including management of natural systems unaffected by man-made disturbances, for systems affected by stock grazing, for areas requiring rehabilitation and on regulated rivers. It highlights the importance of fluvial processes to riparian vegetation and indicates that understanding the natural flow regime of a target river is a critical first step in the management of riparian vegetation and in the planning of riparian zone rehabilitation. Where the riparian zone is highly modified, through, for example, livestock grazing and/or weed invasion, natural regeneration of the riparian vegetation may be a long term process. If intervention, such as replanting, is appropriate, care should be taken that species selected are adapted to particular site conditions, such as flooding regime, landscape position and river geomorphology.
Declaration

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

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Neil Pettit
25 May 2000
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CHAPTER 1

INTRODUCTION

Understanding the ecological processes in river systems is acknowledged as fundamental to sound management of river systems in Australia (Lovett & Price 1999; Pen 1999) and elsewhere (Decamps 1993; Malanson 1993; Naiman & Bilby 1998). This thesis provides baseline information on the ecological processes involved in the recruitment and regeneration of riparian vegetation. As there has been a paucity of basic ecological studies on riparian vegetation in Australia, the project is broad in scope, giving a general picture of the factors influencing the regeneration of riparian vegetation and providing a starting point for more detailed work. The project focuses on factors determining recruitment events and the life history traits of particular species on a river in the cool temperate zone of south-western Australia (Blackwood River) and on a river in the dry tropics of the Kimberley region of north-western Australia (Ord River). By studying two contrasting river systems in different climatic zones, the influence of the physical environment and biotic factors on vegetation persistence and recruitment in the riparian zone can be distinguished. This will contribute to providing an ecological basis for the rehabilitation and management of riparian vegetation in these types of systems.

Definition

Riparius is the Latin word meaning “of or belonging to the bank of the river” and therefore “riparian” refers to the biotic communities living along streams (Naiman et al. 1998). The riparian zone can be thought of as the interface between terrestrial and aquatic systems and often contains sharp gradients in environmental and community processes (Naiman et al. 1998). Riparian environments are recognised as being highly productive and a key component of the landscape (Bunn 1993; Malanson 1993). However, what constitutes the riparian zone is not always clear. There are several definitions that can be applied, the efficacy of each depending on the purposes for which it is used. The legislative definition traditionally used in many areas
of Australia usually defines the riparian zone as a strip 20 to 40 metres wide along the banks of a river or stream. In natural systems, this is not very useful as river ecosystems rarely fit neatly within these boundaries. A landform definition includes the area between low-flow level of the water course and the highest point of transition between the channel and the floodplain. However, in many rivers the floodplain is an integral part of the riparian zone. A definition based on differences in the vegetation is clearly not adequate because of the many varied plant communities that can make up the riparian zone. A definition based on riparian functions would therefore be the most useful and would describe that part of the landscape which exerts a direct influence on stream channels and on the aquatic ecosystems within them and which in turn is affected by the geomorphology of the stream channel and flow.

In the field the transition to the riparian zone is often easily recognised by changes in the vegetation as it becomes more dense and lush and has a different suite of species in both the overstorey and understorey. The distribution of plant communities is mainly influenced by tolerance to waterlogging, which is itself determined by micro-topography and soil type, particularly sediment build-up from flooding (Malanson 1993). In a generalised riparian zone, along a transect perpendicular to the stream, the vegetation may consist of several distinct zones. The littoral zone is the area between the summer low and winter high water marks which consists of aquatic floating, submerged and emergent macrophytes. Immediately above this are the stream or levee banks which are formed after the deposition of sand during flooding. These areas are usually well-drained and contain species which are not highly tolerant of waterlogging. Away from the levee banks is the floodplain, the width of which may vary greatly from virtually absent in deeply incised stretches of rivers to tens of kilometres wide on low relief plains. Plant communities on the floodplain vary and usually exhibit some tolerance to periodic inundation. Within the floodplain old abandoned river channels may periodically fill with water or contain permanent water. These areas may also have distinct vegetation communities which resemble lentic wetlands. In deeply incised stretches of the river, riparian vegetation can be restricted to the stream bank with dryland vegetation coming right up to the
top of the bank. Such areas, in view of the previous functional definition, should be regarded as part of the riparian zone.

The core of riparian ecosystems is the zone between unflooded (upland) and continuously submerged (aquatic) areas (Nilsson et al. 1993). The upland boundary often coincides with the lower limit of particular upland species which cannot tolerate even short periods of flooding. Hydrologic, geomorphic and ecological processes interact to form the riparian landscape (Malanson 1993) and the riparian zone can be described as the three dimensional zone of direct interaction between terrestrial and aquatic ecosystems (Gregory et al. 1991). Dimensions of the riparian zone of influence for specific ecological processes are determined by unique spatial patterns and temporal dynamics. In this study, the area treated as the riparian zone for both study rivers generally encompassed from the low water mark at summer base flow levels to the beginning of the floodplain, where there is usually a change of slope and the vegetation is affected by flooding only very occasionally.

Importance of Riparian Vegetation

The vegetation within the riparian zone performs an important ecological function for in-stream processes (Bunn 1993). Trees on the river edge provide shade which can reduce primary productivity through the reduction of light and also reduce water temperature (Bayly & Williams 1981; Bunn 1993). This effect is implicit in the river continuum concept whereby, largely because of shading, heterotrophic processes pre-dominate and macroinvertebrate fauna are dominated by shredder, collector and to a lesser extent predator species (Vannote et al. 1980; Williams 1983). The process of limiting primary productivity by shading is particularly important in maintaining the health of rivers which drain predominantly agricultural land, where there can be high inputs of nutrients (particularly N and P) into the river from surface and groundwater flows (Peterjohn & Correll 1984; Chauvet & Decamps 1989). Streamside vegetation also contributes carbon to the water through leaf litter and other woody material (Davies 1994). However, in Australia, the sclerophyllous leaves of most streamside trees break down very
slowly and are shed in small numbers throughout the year, thus limiting nutrient input by this means. The leaf litter can also be high in tannins which stain the water, reducing light penetration and thus limiting photosynthesis (Campbell 1993).

Riparian vegetation provides a diversity of habitats for in-stream fauna that are important in maintaining biodiversity. This can be in the form of leaf litter and fallen branches as well as whole trees which can create 'riffle' zones, an important habitat for stream macroinvertebrates (Malanson 1993). Other riparian vegetation, such as aquatic submerged, floating and emergent macrophytes can provide a wide variety of habitats (Bunn 1993; Bunn et al. 1999). Large woody debris plays a significant ecological role in the colonisation and establishment of many plant species on the floodplain and in the river channel in areas of sediment deposition (Naiman et al. 1998; Pen 1999, Lovett & Price 1999). It also has an important geomorphic role in the development of channel morphology (Rutherfurd et al. 1999).

Off-stream riparian vegetation can provide many different habitats for terrestrial fauna. It contributes to higher species diversity and abundance of flora in the riparian zone as it forms an ecotone between the different plant communities (Wissmar & Swanson 1990; Nilsson et al. 1993; Bretschko 1995). The riparian zone may not strictly fit the definition of an ecotone however (see Risser 1993) and may be better described as a transition zone between aquatic and terrestrial habitats.

Many animals prefer the moist, productive riparian habitat to adjacent upland areas (Leach & Edge 1994). The high levels of natural disturbance and the great diversity of habitat formed by these corridors of natural vegetation makes them very important for regional biodiversity (Naiman et al. 1993). The importance of the riparian zone for wildlife habitat becomes particularly significant in fragmented landscapes in a matrix of cleared agricultural land. Riparian corridors have been considered useful for connecting isolated remnant patches of native vegetation (Watson 1991) as well as in facilitating the movement of avian fauna, affecting regional biodiversity (Knopf & Samson 1994). Species diversity and abundance of avian and
mammalian fauna has been shown to be greater in riparian corridors than in the surrounding landscape (Decamps et al. 1987; Crome et al. 1994). Insectivorous birds, sheltering and nesting in riparian vegetation, are important in controlling populations of herbivorous insects which are potentially harmful to agriculture and native plants (Loyn 1987). Riparian systems can be key elements in the landscape as they are usually interspersed throughout the landscape, are high in species richness and are corridors for the flow of nutrients, energy and species (Nilsson & Jansson 1995).

Riparian vegetation is also important in buffering the flow of nutrients and sediment from the catchment into the river system. Sediment and nitrate concentrations in a river in the United States were reduced by up to 90% in water flowing through riparian areas, with less effective removal of phosphorus (Gilliam 1994). Riparian vegetation is also considered a good short-term filter for removing N, P, Ca and Mg flowing from upland areas, thus protecting water quality (Lowrance et al. 1984). The wet soils of the riparian zone, together with the vegetation, can have an effective nitrate buffering capacity with a 30 metre wide buffer reported as being sufficient to remove all nitrates seeping through in the groundwater (Pinay & Decamps 1988; Pinay et al. 1993). Streamside vegetation is also an important buffer, reducing agricultural runoff of N and P into the river on the south coast of Western Australia (Weaver & Reed 1998).

Rivers are naturally high energy systems, especially in periods of high flow such as during floods, and consequently some erosion is a natural occurrence. However, without riparian vegetation high levels of bank erosion can occur. This can have in-stream and off-stream impacts such as increased turbidity from increased sediment loads and greater flooding of surrounding land due to destruction of stream levee banks which help to contain the water within the stream channel (Thorne 1990). Riparian vegetation can limit channel erosion and down-cutting by reducing the tractive force of flowing water, protecting the bank from direct impacts and by inducing deposition of sediments (Malanson 1993). Accumulation of sediment promotes the establishment of vegetation which in turn tends to reduce near-bank velocities and tractive forces, reducing erosion and increasing deposition of sediment (Thorne 1990). The accumulation of
woody debris also contributes to the deposition of sediment. These sites of deposition are also important for the recruitment of riparian vegetation (Nanson & Beach 1977). Bank stability is maintained by the roots of perennial vegetation which provide a stable base for binding the soil and holding the bank in place (Pen 1999). Large roots of trees anchor the river bank and the roots and rhizomes of perennial understorey vegetation, such as shrubs and sedges, hold the surface soil in place between these larger roots. Subsidence of the bank can occur if perennial vegetation is missing, particularly if the soil is wet, and the bank can collapse under its own weight (Thorne 1990). Vegetation is particularly important in reducing damaging effects when the river is in flood, by reducing the velocity and spread of floodwaters and, through evapotranspiration, reducing bank wettness (Pen 1999).

Many riparian habitats are subject to one or more forms of external disturbance such as land clearing, livestock grazing and trampling and increased fire frequency. In most cases, these disturbances interfere with the natural processes of plant recruitment and regeneration of riparian vegetation, eventually resulting in the disappearance of these communities as mature trees die. This can threaten the long-term sustainability of the whole river and riparian ecosystem.

**Impacts on Riparian Vegetation**

In most countries, changes to land use in river catchments has had a major detrimental impact on riparian zones. Activities include industrial and urban pollution (Jeffries & Mills 1990) and agriculture and forestry (Abido 1985; Shah & Thames 1985; Fleischner 1994). In Australia, riparian zones are regarded as the most degraded natural resource zones (CEPA 1992).

Clearing of land adjacent to the riparian zone can result in rising watertables causing stress and even death of the vegetation through permanent waterlogging and/or salinity (Peck 1978; Busch & Smith 1993). Groundwater under cleared agricultural land can be high in nutrients, particularly nitrates, which can flow into the riparian zone and the river itself, causing
eutrophication (Pinay & Decamps 1988). Surface water flows from agricultural land can also cause problems by carrying nutrients into the riparian zone, particularly where this land has been fertilised for crops or carries livestock (Lowrance et al. 1984; Weaver & Reed 1998). High levels of nitrates in the water may also result in acidification of waterways, impacting on in-stream macroinvertebrates and other fauna (Jeffries & Mills 1990).

High nutrient levels combined with high rates of disturbance and the large edge to area ratio of riparian zones make them particularly vulnerable to invasion by exotic plants. In woodlands in the wheatbelt of Western Australia these factors, together with livestock grazing, have led to invasion by exotic species and the disappearance of natives (Scougall et al. 1993). In the riparian zone in Australia the replacement of native plants, usually by soft-leaved exotics which break down quickly adding to nutrient inputs, can drastically alter in-stream ecology (Pidgeon & Cairns 1981; Pen 1999).

Some of the most serious degradation of the riparian zone is caused by livestock. Livestock, usually cattle or sheep, can have direct impacts such as destruction and trampling of vegetation. They can cause erosion (by trampling streambanks), compaction of the soil, an increase in nutrient levels (both in-stream and in the soil) as well as increased stream turbidity (Askey-Doran & Pettit 1999). In many rivers in the agricultural and pastoral zones of Australia, livestock have free access to the riparian zone for summer watering and grazing. In the Kimberley region of north-western Australia, cattle overgrazing of the native vegetation has caused major erosion and siltation problems in many rivers (Williams et al. 1996). In addition to the loss of native species and reduction in cover, increases in nutrient levels and disturbance of the soil surface, livestock can also promote invasion by weeds (usually annual ruderal species) and bring about changes in vegetation structure (Fleischner 1994). In many semi-arid areas, livestock tend to congregate in the riparian zone as this area is the most productive and may be the only source of water and shade. Livestock affect stream morphology, stream-side vegetation, shape and quality of the water column and the structure of stream bank soil and have been implicated in the reduction of trout numbers in many U.S. rivers (Fleischner 1994). Grazing by livestock severely
restricts recruitment of most riparian plants, particularly that of overstorey species, mainly by grazing of new seedlings. Livestock can also cause changes to the soil (e.g. compaction and erosion) and promote the introduction of competing weeds (Kauffman et al. 1983). This leads, in the long term, to profound changes in the structure of riparian vegetation and to consequent impacts on stream ecosystems.

Fencing to exclude stock, or to at least manage grazing, is a fundamental step towards achieving rehabilitation of degraded riparian sites. Whether grazing needs to be excluded completely will depend on the type of community and the extent of existing degradation. In environments that have had a long history of grazing, and where the vegetation has adapted to this form of disturbance, the exclusion of livestock may result in deleterious changes to the vegetation structure such as invasion of woody plants and reduction in species diversity (Milchunas & Lauenroth 1993). Experiments on grazing exclusion in riparian vegetation have shown a reduction in species richness and an increase in plant cover (Kauffman et al. 1983). These studies advocate management of grazing in riparian zones so that grazing is excluded for some period of the year, or in particular years, to allow the vegetation to recover and recruitment to take place. In the winter rainfall areas of Australia, exclusion of grazing for the summer period only, when most damage to the vegetation and the stream bank occurs, may be enough to prevent further degradation (L. Pen, Water and Rivers Commission, pers comm). However, successful recruitment of many plant species may be episodic and rely on the coincidence of several factors such as winter flooding, early receding of floodwaters corresponding with seedfall and summer rainfall. Recruitment opportunities limited by the necessity for the accordance of particular environmental conditions, such as disturbance and climate, have been documented in other plant communities (Wellington & Noble 1985a; Enright & Lamont 1989) and allowing intermittent grazing may interfere with the 'window of opportunity' for recruitment. Predicting which particular species are most affected by livestock grazing and which species are likely to return after stock exclusion is important in planning for the rehabilitation of degraded riparian areas. This may depend on particular traits of individual species such as life form, ability to resprout after defoliation, seed production, seed dispersal strategies, seed dormancy and the ability to
form a seedbank. Abiotic factors are also important, such as microtopography and 'safe sites', waterlogging, seasonal drought, soil types and climatic factors. In a study on remnant woodlands, life form and reproductive strategy were both important in determining species persistence under livestock grazing disturbance (Pettit et al. 1995).

Altered fire regime is another impact within riparian zones that may have detrimental effects on regeneration. In areas of native vegetation wildfires would probably have occurred historically from time to time and, as for upland vegetation, many plants in the riparian zone may require a disturbance such as fire to provide gaps for recruitment (Kellman & Tackaberry 1993) and to stimulate seed release (Lamont et al. 1991) and germination (Shea et al. 1979). In managed areas, prescribed fires for fuel reduction or to stimulate new growth of edible species may be too frequent, resulting in the loss of many native species and an increase in weeds (Busch & Smith 1993), or fire may be too rare to stimulate adequate recruitment of native riparian species.

At least 70% of the world's freshwater flows are regulated (Petts 1984). In regulated rivers, altered flow regimes and flooding patterns can restrict regeneration opportunities and cause changes to species composition and structure in the riparian zone (Stromberg 1993; Decamps et al. 1995; Walker et al. 1995). On the Murray River in eastern Australia changes in degree, frequency and season of flooding has resulted in the lack of recruitment of *Eucalyptus camaldulensis* (Dexter 1978; Bren & Gibbs 1986). Dams can act as dispersal barriers and cause fragmentation of continuous river populations into small isolated areas. Reduced water-level fluctuations in regulated rivers can also reduce the area of the riparian zone (Nilsson et al. 1997).

**Significance of Study**

To preserve the riparian landscape, consideration should be given to conservation of the whole catchment, including the maintenance of the hydrological regime as well as managing energy, materials and species flows (Malanson 1993). Restoration usually has the objective of restoring a
system to a previous state that is self-sustaining through natural processes (Werner 1990). This goal is difficult to achieve both practically and because the nature of the pre-degraded state may not be known or current conditions may not support a return to that state. The maintenance of an altered community that fulfils appropriate ecological functions within the riparian ecosystem, such as acting as a nutrient trap, is more achievable (Hobbs & Norton 1996). Rehabilitation is thus directed at developing a vegetation community that is reasonably stable and allows natural recruitment, and the cessation of processes that contributed to the initial degradation.

In many rivers in the south-west of Western Australia, such as the Blackwood River, rising salinity can affect re-establishment of plants. Careful selection of salt tolerant species and various site amelioration methods are required to improve establishment (Pettit & Froend 1992). For rehabilitation of these saline sites attention should also be paid to upland recharge areas which are the source of rising saline groundwater in the valley bottom and the riparian zone (Peck 1978).

Ecology-based studies on the regeneration of plant communities have been carried out for many types of plant communities including grasslands (e.g. Grime & Hillier 1992; McIntyre et al. 1995), heath (e.g. Bell et al. 1982) and forest (e.g. Bell & Koch 1980) as well as lentic wetlands (e.g. van der Valk 1981; Boutin & Keddy 1993; Hills et al. 1994). However, little work has been done specifically on riparian vegetation (e.g. Nilsson et al. 1994) and especially not in Australia (e.g. Dexter 1978; Bren & Gibbs 1986; Bren 1992; Roberts 1993). In many areas of Australia, such as in the Blackwood River catchment in south-west Western Australia, there is a high level of community interest in restoration of rivers. However, there is a lack of ecologically-based knowledge of the processes of regeneration within the riparian vegetation. In order to manage these systems knowledge of those ecological processes that are important for regeneration of the riparian vegetation is required. This thesis will contribute to this understanding by providing specific knowledge of the riparian vegetation of two rivers in Western Australia and by
developing some general principles on riparian vegetation recruitment that can be more generally applied.

An overall aim of this project is to provide baseline information on the processes involved in the recruitment and regeneration of riparian vegetation. Large scale disturbances, such as high water flows and flooding, are likely to be important factors in the dynamics of riparian communities. Therefore a general hypothesis for this thesis is that the fluvial regime has a strong influence on the vegetation dynamics of the riparian vegetation on these rivers. As a means to understanding the extent of this influence, the ecology of the riparian vegetation on two rivers with contrasting fluvial regimes are compared. In addition, congeneric species occurring on each river, selected for detailed study, are functionally similar and therefore can help clarify the adaptations of each to the particular fluvial regime.

Specific aims are to:

- Describe the riparian vegetation community on the two rivers and the environmental factors that affect their distribution in the riparian zone as well as the relative importance of different life form groups.
- Characterise the river fluvial regime and channel morphology of the two rivers and the relationship of these with the riparian vegetation.
- Describe the effects of two significant disturbances on the riparian vegetation, livestock grazing and fire, and the response of the vegetation to relief from grazing.
- Investigate the sources of seed available for the regeneration of the riparian vegetation, including timing of seed production and seed release, dispersal of seed and the existence of a soil seedbank.
- Examine the mechanisms of seedling recruitment in the riparian zone, including the temperature requirements for germination, survival and establishment of seedlings in the field and the adaptation of seedlings of riparian species to flooding.
• Develop a model of vegetation dynamics for each river based on examination of the population structure and spatial distribution of selected species in the riparian zone and their relationship to river hydrology.

• Outline management implications based on the results described in this thesis.

The thesis aims to establish the link between the fluvial regime and vegetation dynamics on these rivers. This will contribute to providing an ecological basis for the rehabilitation and management of riparian vegetation in these types of systems.

**Thesis Outline**

The thesis is structured to consider at community level riparian vegetation on both rivers and from this, particular species (*Eucalyptus rudis* and *Melaleuca rhaphiophylla* on the Blackwood River and *E. camaldulensis* and *M. leucadendra* on the Ord River) have been selected for more detailed investigation of population structure and ecology and the influence of environmental factors on recruitment. Chapter 2 provides a background for regeneration processes of riparian vegetation considered in later chapters. It explores the linkages between hydrologic, geomorphic and ecological processes in the riparian zone. This includes a discussion of river processes, particularly in an Australian context; related aspects of vegetation theory; vegetation regeneration, including restoration ecology and plant life history traits; and seed and seedling establishment, as well as vegetative regeneration. Previous studies and current knowledge of riparian vegetation regeneration are also summarised. A detailed description of the two study rivers and their environments is given in Chapter 3, including sections on climate, hydrology, geology, soils, vegetation and land use. The next six chapters are structured to address the six specific aims outlined above. Chapter 4 provides a general description of the vegetation in the riparian zone at the study sites on the Blackwood and Ord Rivers. This includes examination of patterns of species richness and diversity of the plant communities in the riparian zone as well as exploring the key functional groups in terms of life form and species origin. Chapter 5 details the relationship between historical river flows and the riparian vegetation. Historical flow records can be used to develop a picture of the variability of the natural flow regime which can then be
related to patterns of vegetation development and plant community zonation in the riparian zone. Chapter 6 is an assessment of the effects of livestock grazing on riparian vegetation and of the initial response of communities to the exclusion of livestock after long term grazing. This includes examining the effects livestock grazing has had on the floristics of sites on the Blackwood and Ord rivers, particularly the effect on species richness and diversity, structural changes in terms of life form and seedling establishment and continued recruitment of particular species. The effects of fire on riparian vegetation will also be examined in this chapter. Chapter 7 investigates the potential sources of seed that are available for recruitment in riparian communities, through considering the diversity and abundance of the soil seedbank and whether this changes with topographic position and distance from the river, the fate and longevity of seed of specific species (and therefore their likelihood of entering the soil seedbank). The spectrum of propagule dispersal types and the role of flood debris as a potential source and means of dispersal of plant propagules in the riparian zone will also be investigated. In addition, this chapter documents the reproductive phenology of the two target species on each river. Chapter 8 examines the influence of temperature on seed germination and the survival and growth of seedlings of the four target species in the particular riparian environments of the Ord and Blackwood Rivers. This includes determining the optimum temperature requirements for germination of seed of these species and the conditions likely to allow successful early establishment of seedlings. The adaptation of the target species to various degrees of flooding is also determined. In Chapter 9 the population structure of the target species is examined. This is done by recording the size class structure of these species on different river reaches and their spatial variation within the riparian zone. This can be used to assess the population stability and successional trends or vegetation dynamics of these species (Veblen 1986). The final chapter (Chapter 10) brings the various elements of this study to a synthesis and discusses various aspects of recruitment patterns and vegetation dynamics in riparian vegetation on the Blackwood and Ord rivers. Management implications of this work will also be discussed in this chapter.
CHAPTER 2

THE RIPARIAN ZONE AND VEGETATION DYNAMICS: A REVIEW

This chapter provides a background to the regeneration processes of riparian vegetation considered in later chapters. It explores the linkages between hydrologic, geomorphic and ecological processes in the riparian zone. This includes a discussion of river processes, particularly in an Australian context; related aspects of vegetation dynamics; vegetation regeneration (including restoration ecology and plant life history traits); seed and seedling establishment; and vegetative regeneration. Previous studies and current knowledge of riparian vegetation regeneration are also summarised. The concluding section discusses how these relate to the specific questions addressed in this thesis.

River Processes

Riparian zones are shaped by spatial and temporal patterns of hydrology and geomorphology as well as by terrestrial and aquatic ecosystems (Gregory et al. 1991). The geomorphic structure of the riparian zone results from the interaction of landform geology, climate and hydrology as well as from inputs of materials from adjacent hill slopes and vegetation. Geomorphic effects therefore create a mosaic of stream channels and floodplains within the valley floor (Gregory et al. 1991), the functions and relationships of which are summarised in Figure 2.1. These processes modify the riparian zone and exert their influence over various time scales, ranging from regular events to much less frequent episodic events. Different types and scale of physical disturbance, along with landforms and hydrology, can determine the structure and dynamics within the riparian zone (Wissmar & Swanson 1990). Spatial scales can also vary widely from local deposition or erosion to local channel shifts or whole catchment flooding. Hierarchical classification of spatial scales for river channels would include geomorphic province, watershed and valley segment at higher scales, down to channel reach and pool and riffle zones at smaller...
scales (Montgomery & Buffington 1998). Within the river zone, scale-dependent relationships between biological, geomorphic and hydrologic features and ecological processes also exist (Walker et al. 1995). These include macro-habitat, which relates to the whole river ecosystem and flow regime; meso-habitat (at the community or population level) which is related to flow history; and micro-habitat at the organism level.

The structure of riparian environments can also be considered from various aspects within the landscape including longitudinal (e.g. from headwaters to river mouth), transverse (river profile) and internal (including reaches, pools, riffles, meanders and backwaters) (Malanson 1993). In a characteristic river system, the longitudinal pattern usually begins with small (first order) streams at high elevations in the landscape at the headwaters of the catchment. These streams tend to be fast flowing and erosive. At lower elevations the river slows down and meanders across a plain before entering the sea. This lower section can be subject to flooding and is usually an area of deposition where more material is deposited than eroded (Bayly &

![Diagram of river processes influencing riparian vegetation](image)

**Figure 2.1**: Summary of river processes influencing riparian vegetation (adapted from Gregory et al. 1991).
Williams 1981). As the gradient of a river decreases the bed materials become finer, so that while source streams tend to have gravel beds, mobile beds of silt and sand are found at the river mouth. River morphology comprises many different features and at different scales which provide a variety of habitats. These features include channel form (comprising width, depth, slope, roughness, velocity and discharge) and channel pattern. The formation of these features is influenced by regional geology, climate and sediment transport in the form of erosion and deposition. Within the river channel are pool, run and riffle zones which are influenced by, and which in turn influence, water flow. These pool and riffle sequences tend to alternate along the river (Jeffries & Mills 1990). River bends are major sites of erosion and deposition as material is eroded from the outside of the bend and deposited on the inside. In many rivers these depositional areas (point bars) provide a major substrate on which primary succession of riparian vegetation communities can take place (Malanson 1993).

In floodplain rivers, along a cross-section perpendicular to the channel, several zones can be discerned, influenced mainly by microtopography and groundwater, that provide different habitats for various biotic communities. The littoral zone, that area between the seasonal normal high and low water levels, provides a habitat that is subject to long periods of inundation and high levels of disturbance. The levee bank is immediately adjacent to the river channel. Here rising floodwaters lose velocity and deposit sediment, creating an area of slightly higher elevation and higher nutrient levels. The floodplain, which is subject to intermittent flooding, is developed by sediment deposition and can be of variable width and made up of several terraces of different elevation. Terraces are generally considered to be old floodplain levels which have become redundant as the river has incised into the landscape and, through meandering, created new floodplains at a lower level. Finally, 'abandoned' channels occur on the floodplain, usually parallel to the existing channel, which may have standing water for long periods and can behave much like lentic wetlands.

The river processes considered important for structuring riparian vegetation include water flow, water level fluctuation, sediment transport (deposition and erosion), litter transport and seed
dispersal (Nilsson et al. 1993). Distribution and composition of riparian plant communities reflect mainly fluvial disturbances but also some non-fluvial disturbances such as fire or wind. Geomorphic surfaces provide a physical template for the development of riparian communities (Gregory et al. 1991). The flood pulse concept (Junk et al. 1989) acknowledges the connection of the river to its floodplain which may result in several successional stages in vegetation development (Ward & Stanford 1995). The flood pulse provides a recharge of nutrients to the floodplain via deposition which can result in productivity benefits. It can also lead to a recharge of soil water which can be important for the survival of many riparian plant species on semi-arid and arid rivers (Roberts 1993).

The existing models of rivers have been predominantly derived from studies of northern hemisphere rivers and, although they can be applied to Australian lotic systems, there are features of many Australian rivers that are unique (Williams 1983). Other than for the eastern seaboard, the two major characteristics of the Australian environment that influence lotic systems, are aridity and the flaness of the terrain. The arid climate not only results in very low average total annual runoff compared with other countries but also in a low percentage of annual precipitation as runoff (apart from rare large events). This has led to large river basins and relatively long rivers with low annual flows, such as the Murray-Darling River in eastern Australia (Bayly & Williams 1981). There is also wide variation in seasonal and annual river flows. This is evident in most rivers in southern Australia but is most pronounced in the northern rivers (Walker et al. 1995). In these areas, rivers carry very large volumes of water in the wet season after the monsoon rains but can be reduced to a series of pools in the dry season, with a great deal of annual variability. In Australia, large floods tend to be of greater magnitude than those of other continents, with 100 year flood levels ten to twenty times the magnitude of mean annual flood levels, compared with two to four times for other parts of the world (Lovett & Price 1999). As erosive power of flow increases disproportionately with increasing discharge, 100 year floods are extremely powerful agents for landscape change (Lovett & Price 1999). Where river basins are draining arid and semi-arid areas of the continent, rivers may be dry most of the time and only flow after a large episodic rainfall event (Walker et al. 1995). The lack of relief over
most of Australia results in many rivers, such as the Murray-Darling, having very low gradients. As a consequence, short areas of erosion occur in the upper reaches and extensive areas of deposition occur in the lower reaches, which can lead to high turbidity (Williams 1983). Many Australian rivers, especially those draining low rainfall areas, have high salinity levels by world standards (Williams 1983). The fringing vegetation on Australian rivers also contributes to an ecology which is different from most northern hemisphere rivers. In Australia, most riparian vegetation is evergreen. Leaves are shed throughout the year, usually with a pulse in summer, instead of all at once at a particular time of year, as do deciduous trees (Pen 1999; Bunn et al. 1999). The leaves that are shed are harder, more sclerophyllous and take longer to break down and many contain chemicals that stain the water, thus affecting in-stream ecology and productivity (Pidgeon & Cairns 1981; Bunn 1988).

Plant Ecology

Vegetation dynamics

The riparian zone experiences a naturally high level of disturbance, both in frequency and intensity, due mainly to the flow of water and flooding (Malanson 1993). The high level of disturbance can result in a mosaic of successional communities (Kallida & Puhakka 1988). Therefore, a study of the natural recruitment of riparian vegetation needs to consider the processes of vegetation dynamics under natural disturbance regimes. Furthermore, the rehabilitation of degraded areas usually follows successional pathways and sound knowledge of these processes is necessary for successful planning and implementation of the re-establishment of vegetation (Werner 1990).

Vegetation dynamics usually refers to the ways in which vegetation may change over time and incorporates the concepts of succession and plant community. It involves the successive nature of the development of plant communities over time, including the interaction of populations in uniform environments (van der Maarel 1988). Vegetation dynamics can be viewed in terms of
temporal scales, ranging from short-term through to long-term changes, as well as on several spatial scales including individual patches, communities, landscapes and bioregions. The plant community has three major components relating to species response to habitat; interaction between species; and chance and random processes both in the environment and in populations (Noy-Meir & van der Maarel 1988).

Earliest theories of succession developed by Clements (1916) see (Glenn-Lewin & van der Maarel 1992) were based on the idea that plant communities develop in sequence to reach a climax stable community after some perturbation. Others stressed the importance of individual responses of species to the environment and to chance events following disturbance (Gleason 1927; Egler 1954). More recent discussion on ecological succession has considered that physical stresses on plants and competition for resources between plants are the main mechanisms determining the course of succession (Drury & Nisbet 1973). A model proposed by Connell and Slatyer (1977) suggested three mechanisms for succession which included elements of these earlier theories. These were facilitation or 'relay' floristics, where earlier species modify the environment so that later successional species can establish; tolerance, where different species evolve different strategies or life history traits for exploiting available resources; and inhibition, where species resist the invasion of competitors and the first occupants prevent the establishment of later colonisers until they are damaged or die and thus release resources. These mechanisms differ mainly in the way later species establish. The facilitation model is most likely to apply in primary succession where the substrate has not been influenced by species beforehand, whereas tolerance and inhibition models will apply to secondary succession (Connell & Slatyer 1977). Connell and Slatyer (1977) emphasised the importance of competition in the succession process and in the determination of species composition. Competition between species for limited resources was also considered critical for species composition and succession in the resource ratio hypothesis, where the ratio of limiting resources is important rather than a single resource (Tilman 1986). This hypothesis suggested that community composition is largely influenced by limiting resources and that patterns of succession will change with relative availability of these resources.
The initial floristic composition model proposed that many species which initially establish may not necessarily give way to other species later in the successional sequence but may become dominant themselves (Egler 1954). Evidence of this has been reported after fire in forests in eastern Australia (Purdie & Slatyer 1976). This model may also apply in the jarrah forest of south-western Australia due to the predominance of resprouter species in the vegetation (Bell & Heddle 1989). In the high disturbance riparian zone, where vegetative resprouting is probably very significant, this initial floristic composition model may also apply.

Models of succession are difficult to apply to spatially heterogeneous ecosystems such as the riparian zone and the concept of ecosystem stability has been suggested (Fischer 1990). This concept allows the ideas of disturbance, stability and resilience to be directly incorporated into the description of vegetation dynamics. Rather than unidirectional succession, dynamics within vegetation communities may result in a series of patches made up of transitions between more or less stable states mediated by disturbance, climate or management (Hobbs 1994). Different vegetation types within an area may thus not be predictable by current environmental factors and species interactions only, rather the present state is the result of a particular history of disturbance, climatic factors and/or management. The regeneration phase and longevity of the vegetation can be critical in determining the stage and rate of transition states. For example, a tree-dominated community, where there is little or no recruitment, would take a long time to change because of the long-lived nature of the trees, unless they are killed by some disturbance. Hobbs (1994) suggested that a synthesis of qualitative transition state models (i.e. Westoby et al. 1989) with the quantitative, statistical Markov models (Hobbs 1983) could be used in a geographical information system (GIS) to predict landscape scale changes to vegetation due to disturbance. State and transition models have been suggested as a tool for rangeland management (Westoby et al. 1989; George et al. 1992), and as an alternative to linear succession, to allow for different vegetation community composition (states) depending on the transitions. Management can be used in conjunction with natural disturbances to direct vegetation composition to a desired
Large scale disturbances, such as high water flows and flooding, are likely to be important factors in the dynamics of the riparian community. Flood induced disturbance may instigate the transition from stable states of plant composition and population structure. Recruitment, establishment and survival of riparian trees is thought to be closely tied to the hydrological regime (Barnes 1985; Bradley & Smith 1986; Wissmar & Swanson 1990; Johnson 1994; Naiman et al. 1998) and there is obviously a strong link between river processes and the dynamics of riparian vegetation. The dynamics can vary longitudinally along the river as well as laterally and are a function of geomorphology, vegetation history and vegetation life history strategies (Naiman et al. 1998). The interaction of plant life history processes and the physical processes of rivers can determine the typical patterns of vegetation colonisation, establishment and succession. For example, for many riparian species seed dispersal coincides with seasonal retreat of floodwaters, when moist sediments are exposed which enhance germination and colonisation (Johnson 1994; Naiman et al. 1998). Floods can affect vegetation patterns by destroying and subsequently excluding plants, by creating new areas for colonisation and by forming elevational gradients where plants show varying tolerance to flows and sediment movement (Wissmar & Swanson 1990). High frequency flooding can keep vegetation in an early stage of succession (Naiman et al. 1998). How fluvial processes can affect vegetation life history patterns can be assessed by gathering information on magnitude, frequency and duration of flows. Patterns of these flows will influence successional stages of the vegetation. For example, where flooding disturbances are chronic to frequent, riparian forests are young, as vegetation patch development is continually reset and remains in stand initiation and exclusion successional stages (Wissmar & Swanson 1990). In environments with low magnitude, seasonally predictable floods the vegetation is likely to be more stable and hence more developed. Floodplain succession is therefore an interaction between stochastic flood events and life history traits as well as the extent, intensity and timing of flooding, which determines patterns of vegetation colonisation. Lateral patterns of the riparian vegetation can also occur, with vegetation of low terraces and
floodplains mostly influenced by factors such as moisture gradients and flooding tolerance. On higher terraces and slopes the vegetation is more influenced by biotic factors such as competition and herbivory. Heterogeneity of soils and habitat and microtopography are also important influences on riparian vegetation dynamics.

**Restoration ecology**

As discussed earlier, the majority of riparian zones in Australia have suffered some form of degradation (CEPA 1992). Discussion of restoration ecology is therefore appropriate when considering the recruitment of native species in the riparian zone. Characteristics of the natural ecosystem that need to be considered in restoration ecology include composition, structure, pattern, heterogeneity, function and resilience (Hobbs & Norton 1996). In restoring a degraded ecosystem, removal of the factors causing the degradation is the essential first step. The likely success of natural regeneration once these factors have been removed will depend on how they have affected ecosystem function (Brown & Lugo 1994). If the degradation stress has affected only biotic components of the ecosystem, such as through the removal of the vegetation, then removal of this stress may result in fairly rapid recovery without further management intervention (Allen et al. 1994). However, if the degradation stress has affected the resource base or ecosystem processes, such as the soil or hydrology, restoration may be more difficult (Milchunas & Laurenroth 1995). Hobbs and Norton (1996) identified a number of key processes that need to be considered in ecosystem restoration. These included identifying degrading processes, developing methods to reverse the degradation, determining realistic goals, developing observable measures of success, developing practical techniques and communicating results. The restoration of degraded systems to some desired state (whatever this may be) in ecological terms also requires the re-initiation of successional processes by accelerating biotic change (Luken 1990). The identification of factors important in recruitment of riparian species will provide important information in developing a restoration framework for degraded riparian systems.
Plant life-history traits

Modelling succession and species composition using life form, life history traits, functional groups or vital attributes has been widely used. These models are usually developed for particular habitats or types of disturbance and, as generalisations to describe succession, they may be oversimplified (Brown 1992). Noble and Slatyer (1980) devised a qualitative model of vegetation dynamics in habitats disturbed by fire, characterising the plants into three life history groups with certain attributes important in succession. Using the interaction between categories (groups) they could predict changes in composition and dominance of species following disturbance. The three categories were method of persistence and arrival after disturbance; ability to establish and grow in a developing community; and time taken for species to reach critical life stages. This model has obvious application in a study of grazing disturbance and provides a basis for discussing the role of disturbance frequency in community types such as the riparian zone. In communities which are subject to more than one recurring disturbance, such as grazing and flooding, then more than one vital attribute may be appropriate for each species. Where a community is subject to a continuous disturbance, such as grazing (which prevents reproduction) Noble and Slatyer (1980) predicted that plants in all but two categories of attributes would become locally extinct. That is, only those species with widely dispersed seeds and those species with the ability to withstand disturbance with little harm, as well as having widely dispersed seed, would be able to survive in the long term.

Plant strategies in response to disturbance have been described to explain species co-existence for plant species of the British Isles (Grime 1979). This scheme suggests that vegetation develops as a result of equilibrium between competition, stress and disturbance where disturbance is the destruction of extant growth by outside factors (e.g. fire), stress is the reduction in rate of growth by outside forces causing a shortage of resources (e.g. aridity) and competition is limitation to growth through shortage of resources due to capture by other plants (Grime et al. 1986). This system distinguishes plants into three main groups (Grime 1980):

1) **Competitors**: capable of high productivity, vegetative expansion and usually flowering each year after maximum vegetative production.
2) **Stress tolerators**: slow growing, with long life histories and for which onset of flowering is usually delayed and intermittent.

3) **Ruderals** (disturbance tolerators): usually small annual herbs with dormant seeds, short life histories and early flowering.

Identification of the different strategies among plants within a community can be useful in providing a means of predicting the community response to continued disturbances such as grazing. For example, this scheme predicts that under a regime of high stress and high disturbance, no strategy exists to allow plants to survive and therefore no vegetation is possible. This situation may occur in riparian areas that are continuously grazed. These plant functional strategies were applied to regularly disturbed riverine wetland ecosystems in which competition and stress tolerance were found to be the most important traits (Hills *et al.* 1994). Grime’s plant strategies have been criticised as being too simplistic and too specific to British grasslands (Glenn-Lewin & van der Maarel 1992).

Life history traits have been used to predict species response to fire in Australia (Gill 1981) and the effect of fire on sandplain species in Western Australia (Bell *et al.* 1982). Reproductive strategies of plants that occur in the riparian zone are not well understood (Malanson 1993) but may be important for predicting the outcome of succession in this highly disturbed zone. Classification of plants by life history strategies can be useful in predicting riparian vegetation succession (Naiman *et al.* 1998). Naiman *et al.* (1998) categorised plant species according to their strategy in coping with flooding disturbance as invaders, endurers or resisters. A model for predicting the outcomes of succession in wetlands has also been developed using three key life history traits (van der Valk 1981). These traits include life span (annual, perennial and vegetative perennial), propagule longevity in the seedbank and propagule establishment requirements. This model relies on using the composition of the seedbank to predict the vegetation composition after a disturbance. Many other attempts to classify vegetation communities into functional groups in order to predict the outcome of changes have been made. For example, herbaceous wetland plant traits were selected that reflected function and included ruderals, matrix species and interstitial species (Boutin & Keddy 1993). Grouping plants into life
and growth form groups has also been used (Rodolfo & Sala 1993; McIntyre et al. 1995), as have reproductive and regeneration characteristics (Cowling et al. 1994), to help describe successional processes and species co-existence in plant communities. Grime and Hillier (1992) have suggested that accurate predictions of plant communities can be made with a good theoretical framework of regenerative functional types for a flora.

Disturbance

Natural disturbance and patch dynamics are important concepts in plant ecology when determining the structure and function of communities. Disturbance is considered to be important in maintaining species diversity by creating gaps in vegetation that has exploited most of the resources and, through competition, excluded other individuals (Abugov 1982). The creation of patches through disturbance allows germination and establishment of new individuals which may be of different species. In the riparian zone, patch dynamics may allow the continuous recruitment of individuals between infrequent large scale disturbances such as flooding. Disturbance reduces the dominance of a site by established plants and, by altering the availability of light, water and soil nutrients, creates openings for colonisation and growth of new individuals not necessarily of the same species (Canham & Marks 1985). Patch dynamics may be defined as the internal dynamics generated by patterns of natural disturbance and subsequent patterns of succession (Pickett & Thompson 1978). The first three forms of vegetation dynamics detailed by van der Maarel (1988), that is, fluctuation, gap dynamics and patch dynamics, describe the types of processes that make up this definition of patch dynamics. These different terms relate mainly to the size of disturbance and the subsequent size of patches created. For example, fluctuations are considered on the level of the individual plant and gap dynamics may result from the death of an individual plant, resulting in the opening up of the area to light, thus affecting plants in the immediate vicinity.

A plant's ability to exploit patches will depend on reproductive traits, such as the ability to expand vegetatively, seed dispersal, the ability to form a seedbank and also to exploit increased resources quickly (Sousa 1984). The natural disturbance regime will determine the size, density
and temporal frequency of patches and the range in temporal and spatial distribution of patches may allow the calculation of the natural disturbance regime within a community (White & Pickett 1985). How disturbance shapes community structure will depend on the frequency, magnitude, predictability and type of disturbance (Sousa 1984). In the riparian zone, naturally high levels of disturbance can cause stream migration, and erosion and deposition are continually destroying and creating new sediment substrate which allows colonisation by plants (White 1979). Disturbances such as fire, flooding and drought are very important for the recruitment of salmon gum (*Eucalyptus salmonophloia*) in woodlands in the wheatbelt of Western Australia (Yates *et al.* 1994) and flooding is essential for river red gum (*Eucalyptus camaldulensis*) recruitment on the Murray River in eastern Australia (Dexter 1978; Bren & Gibbs 1986). Small scale disturbance has been shown to be influential in maintaining species diversity in mediterranean old fields (Lavorel *et al.* 1994), in wetland communities (McIntyre *et al.* 1988) and in temperate grasslands and herbaceous vegetation in eastern Australia (McIntyre & Lavorel 1994; McIntyre *et al.* 1995).

Many river systems (including the ones studied here) are subjected, at least for some part of their length, to livestock grazing. This has serious consequences for riparian systems in terms of loss of native species through grazing pressure, prevention of seedling recruitment and the replacement by better adapted exotic weeds and pasture species, resulting in a change of structure and species composition. Livestock, through trampling, can cause compaction and soil erosion, thus changing the physical properties of the soil. With the exclusion of livestock grazing, recovery of the native vegetation can be prevented by competition from exotic species (such as annual grasses) and changed soil properties, even where propagules of native species are available. Effects of livestock on the riparian zone have been reported in North America (Kauffman *et al.* 1983; Armour *et al.* 1994), documenting changes to the structure and composition of the riparian vegetation, and for other landscapes in Australia (Wilson 1990) but there has been little work specifically on the riparian zone in Australia.
Seed and Seedling Ecology

Once disturbance has created gaps in the vegetation for recruitment of new individuals, successful recruitment will depend on particular reproductive traits and the seed ecology of particular species (Canham & Marks 1985). Factors that are important in successful regeneration include abiotic factors such as the creation of ‘safe’ sites for seeds and favourable climatic conditions. Important biotic factors include ability to reproduce vegetatively, production of seed, timing of seed release, dispersal mechanisms of seed, seed dormancy and the ability to create a soil seedbank as well as germination requirements of seed and requirements for seedling establishment.

The regeneration niche theory (Grubb 1977) proposes that replacement of species is primarily driven by the biotic and physiochemical heterogeneity of the environment. Therefore the variable environment may provide new niches and determines whether there is a place for the co-existence of species. This regeneration involves vegetative and reproductive parts of plant life histories, the relative importance of each depending on the type of community. Grubb (1977) proposed five processes important for the regeneration of plants, including production of seed, dispersal, germination, establishment of seedlings and the development of the mature plant. These elements incorporate the factors which are considered important in the differentiation of the regeneration niche. These can be usefully applied to regeneration traits of species within the riparian zone.

The production of seed is obviously critical for successful recruitment of species which have no ability to resprout vegetatively (obligate reseeders). Timing of seed production and seed fall is also very important to ensure that seed is released at times of most favourable conditions, such as after receding floodwaters when fresh soil is exposed (White 1979), soil moisture levels are high (Roberts 1993) and there is peak abundance of seed vectors (Willson 1992). Production of large numbers of seeds may reduce the impact of seed predators (Ashton 1979; Wellington & Noble 1985a) and can also compensate for low seed germination rates (De Steven 1991).
One aspect that can influence the coexistence of species in plant communities is propagule dispersal traits (Levin 1976). The development of seed dispersal syndromes has been influenced by the probability of finding a 'safe' site, avoidance of sibling interaction and the avoidance of seed predators (Willson 1992). Dispersal to a safe site is particularly important for species that have no capacity for seed dormancy. The determination of dispersal spectra can be useful in identifying the relative advantage of different dispersal types in particular habitats (Willson 1992). In riparian landscapes, Malanson (1993) described three main vectors of seed dispersal including air, water and animals, with seven sub-groups. The relative importance of different seed dispersal types may change in various parts of the river with greater occurrence of wind dispersal at the headwaters and animal dispersal being more important in the lower reaches (Malanson 1993). In fragmented landscapes with narrow riparian corridors, wind dispersal of fugitive species may become more prevalent. In rivers in Sweden, floodwaters carrying seed greatly extended the dispersal range of wind-dispersed species, dependent on the ability of the seed to float and the length of time they could float (Skoglund 1990). In fact, the long hairs on a seed which appear to aid in dispersal by wind may also increase ability to float which may be the prime means of dispersal (Herrera 1991). Floating time can also be important for dispersal distance with larger, heavier seeds establishing closer to the point of release (Nilsson et al. 1991b).

To understand the role of the seedbank in vegetation dynamics Thompson (1992) suggested that it is necessary to estimate the buried seed density, measure seed production and seed ‘rain’ and also determine the source of colonists. The seedbank should also be examined at different times of the year in order to assess seasonal differences and to separate the long term seedbank from the transient (Grime 1979). Soil seed storage is an important aspect of natural regeneration (Onans & Parsons 1980). Species with seeds which remain dormant in the soil have the advantage over resprouting species of being able to remain viable for a very long time. Seeds of herbaceous species such as Digitalis purpurea and Hypericum paletrium have been found to remain viable in the soil for 100-200 years (Thompson 1987) while seed of some Acacia spp. have remained viable for at least 50 years (Mott & Groves 1981). Species with a viable long-term seed bank are
very important in restoration of grasslands (Thompson 1992), while in temperate woodlands few perennials occur in the seedbank and those that do are usually short-lived early colonisers. In the jarrah forest of Western Australia, where there is a high proportion of resprouting species in the flora (Bell et al. 1990), only a limited number of species are represented in the seedbank (Vlahos & Bell 1986). Overstorey species are usually not present in any number in the seedbank as there is usually ample opportunity over time for regeneration of long-lived perennials. In contrast, the seed of annual herbs and grasses provide the only opportunity for regeneration, and dormancy ensures germination only under favourable conditions (Schneider & Sharitz 1986; Thompson 1987). In lentic wetlands the seedbank is very important in determining the vegetation community (Thompson 1992), and determination of the composition of the soil seedbank is used to predict the outcome of succession after a disturbance (van der Valk 1981). The role of the seedbank in riparian vegetation is unclear and little work has been done on this, however Malanson (1993) suggests that the highly disturbed nature of the riparian zone and the frequent movement of the soil sediments would indicate that the role would be minimal.

Generally, most of the seed of eucalypts that is released is collected by seed-harvesting ants. Heavy predation of eucalypt seed has been observed in eucalypt woodland in Queensland (Drake 1981) and in mallee scrub in northern Victoria (Wellington & Noble 1985a), where up to 100% of eucalypt seed was removed in a short period of time when seed was placed in feeding stations. It has also been observed in salmon gum woodlands in the wheatbelt of Western Australia (Yates et al. 1995). In these circumstances a build-up of eucalypt seed in the soil occurs only after a disturbance (such as fire) causes massive seed release from the canopy and results in predator satiation (Ashton 1979; O'Dowd & Gill 1984; Wellington & Noble 1985a). However, even where seed predation levels are very high, the limiting factor in recruitment of seedlings may in fact be the number of safe sites for germination (Andersen 1989; Crawley 1992; Stoneman & Dell 1994). Many plants maintain a seedbank for several years on the plant itself, usually in woody fruits. A large proportion of species in the Myrtaceae family which have woody fruits retain large stores of seed in the fruit for several seasons, releasing only after desiccation, through fire or death of a limb (Beardsell et al. 1993). For many temperate eucalypts, seed maturation can take several
months and seeds are retained in the capsules with a continuous low level of seed release occurring, which is accelerated by dry conditions (Cunningham 1957; Wellington & Noble 1985a; Davies & Myerscough 1991). Eucalypt seed is rarely held in the canopy for more than three or four years (Ashton 1975). A canopy-borne seed store is relatively common in families such as Myrtaceae and Proteaceae in Australia (Bellairs & Bell 1990).

Seeds germinate in response to several different stimuli including light, temperature and moisture, and the germination of seed of a particular species can be related to life history traits and response to fire or seed storage (Bell et al. 1993). In many species, seeds germinate soon after they are shed, regardless of conditions. In other species, seeds germinate only under favourable conditions (enforced dormancy) and can remain for long periods in the soil seedbank with intermittent germination from the population (Murdoch & Ellis 1992). Seed dormancy may be innate where germination does not take place even though suitable conditions prevail. This may be due to under-development of the embryo and innate dormancy occurs in many annual species which form long-lived seedbanks (Murdoch & Ellis 1992). Forced dormancy occurs where prevailing conditions are unsuitable for germination and, for example, in many Acacia spp. which have a hard, impermeable seedcoat. Germination is stimulated when the seedcoat is cracked or inhibitors are denatured by heat, usually from a fire (Bell et al. 1993). In experiments on jarrah forest species, greatest germination was recorded at temperatures typical of winter when moisture conditions would be suitable for survival of germinants. Most species also germinated best in continuous dark which simulates seed burial (Bell 1994). Light requirements of germinating seed are also important in terms of the level of shade tolerance of particular species and whether they will successfully establish under shade or within canopy gaps (van der Valk 1992; Bell 1994). In lentic wetlands, because of the unpredictable nature of water levels, temperature provided the best cue for germination of seed from the soil seedbank (Britton & Brock 1994).

Once seed has germinated, it is critical that adequate moisture is available, at least until the seedlings have developed a substantial root system (Wellington & Noble 1985b; Stoneman et al.
Therefore, the coincidence of seedling establishment and adequate rainfall is critical, particularly in Mediterranean-type climates during summer drought. In riparian areas, flooding provides a means of restoring soil water which is critical for seedling establishment (Roberts 1993). For seedlings to establish in the riparian zone, fast growth rates may be necessary (White 1979) and/or some sort of protective barrier (Hancock et al. 1996) so that they can withstand floodwaters the following season. For seedlings establishing on riparian floodplains suitable microsites may also be critical, with some elevation to reduce the effects of waterlogging, but also within a slight depression so that moisture can gather during the dry summer months (Titus 1990; Bren 1992). Degree of shading can be very important for the establishment of many shade-intolerant species, with seedlings only establishing in tree-fall gaps where there are high light levels (Ellison et al. 1993). In a riparian habitat, seedlings growing in heavy shade were two and a half times smaller than seedlings growing in the open (Jones & Sharitz 1989). High levels of leaf litter can also have a large impact on seedling establishment, principally through forming a physical barrier to root penetration in the mineral soil. Flooding can exert a considerable influence on riverbank vegetation as a result of litter displacement, allowing seeds and seedlings access to the mineral soil (Nilsson & Grelsson 1990). Study of the seedling flora of a vegetation community can give important insights into the relative importance of the different seedling strategies within that community and therefore be useful in predicting community dynamics after disturbance (Grime & Hillier 1992).

Vegetative regeneration

In many types of vegetation, the majority of perennial species possess the ability to reproduce vegetatively by a variety of mechanisms such as rhizome, stolon or lignotuber. Vegetative resprouting is particularly common in communities which receive frequent periodic disturbance (James 1984) such as in many wetlands and rivers (van der Valk 1992). For many vegetatively propagating species, such as rushes and sedges, the ability to colonise a new area depends on how far new ramets can establish from the parent plant (van der Valk 1992). For example, many species have a clumped growth form with new ramets produced very close to the parent plant. These species will colonise an area very slowly, if at all, whereas species which can send out
runners and produce independent ramets at some distance from the parent plant can colonise an area more rapidly (van der Valk 1992). The common bracken fern (*Pteridium esculentum*) is an example of a plant that can rapidly colonise areas by producing new ramets from long rhizomes. However, for the majority of species that are able to propagate vegetatively, rapid colonisation of a new area would require establishment from seed. The major role of vegetative propagation for plants is therefore, in most cases, to allow them to persist at a site, particularly following a disturbance.

Many woody plants have the ability to resprout from underground storage organs after defoliation. This has been extensively studied in relation to recovery of vegetation after fire (Gill 1981; Bell *et al.* 1982; Keeley 1986). Resprouting shrubs and trees usually possess one of a number of structures such as a lignotuber or root crown in which carbohydrate reserves and dormant buds are located. The dormant buds are released from inhibition and begin to sprout after the defoliation of the plant. Resprouting species have a greater dependence on the survival of the individual after defoliation whereas non-resprouting species (obligate seeders) rely on the availability of seed to continue the local existence of a species after a disturbance such as fire (Carpenter & Recher 1979). Consequently, obligate seeders tend to put more resources into reproductive effort. Resprouters usually take longer to reach reproductive maturity, produce less flowers less often and have a lower rate of seed production per plant (Hansen *et al.* 1991; Bell *et al.* 1993). Seedlings of resprouter species tend to be slower growing as energy is directed towards building up reserves of carbohydrates for resprouting. As a result they have a much smaller shoot to root ratio and a greater proportion of starch reserves in the roots than obligate seeder species (Pate *et al.* 1990). However, the rapid recovery of established resprouters gives them a competitive advantage over seedlings so that resprouting species may dominate the post-disturbance habitat (Malanson & O'Leary 1982). Replenishment of starch reserves is an important factor in the ability of reprouters to continually resprout after disturbance and very short disturbance intervals increase the chance of mortality as starch reserves may not fully recover until shoot biomass has reached pre-disturbance levels, possibly taking several seasons (Bowen & Pate 1993).
In highly disturbed riparian habitats, the ability to resprout as well as to produce large quantities of seed would be highly advantageous. Many species that occur in riparian habitats in North America, such as *Salix* spp. and *Populus* spp., possess the ability to resprout and produce large quantities of seed (Johnson 1994). This is also the case in some of the dominant riparian trees in Australia, such as *Eucalyptus camaldulensis* and *E. rudis*. Seedlings that establish on new substrates must be able to withstand high water flows in the following or subsequent seasons which could damage and defoliate plants. The time it takes for a species to build up sufficient carbohydrate stores, and therefore the ability to resprout, as well as the interval between floods, are likely to be critical in determining survival during subsequent flood events. An ability to resprout would also enable mature plants to survive physical damage caused by flooding.

**Regeneration of riparian zones**

The processes that affect regeneration of vegetation in riparian zones, such as dispersal, establishment and growth, are ultimately dependent on the landscape structure and function as well as on landscape scale disturbance regimes. Spatial changes among species are affected by temporal changes in the distribution of physical structures and functions and also by the interaction between species (Malanson 1993). In riparian zones, species reproductive strategies may be adapted to the particular high frequency disturbance regime that occurs. These traits may include regular annual seed crops, light seeds which are dispersed by wind and/or water, fast growth rates, ability to resprout and high flood tolerance (White 1979). Floodplain ecosystems tend to be disturbance dependent with a high sub-system instability but a broader system stability (Ward & Stanford 1995).

Recruitment, establishment and survival of riparian trees has been thought to be closely tied to the hydrological regime. There has been evidence of this in North America where cottonwood recruitment on point bars correlated with years of maximum daily flow greater than second year
flood return and these coincided with seed release approximately once in every five years (Bradley & Smith 1986). For *Populus* spp. and *Salix* spp. on the Platte River, summer flooding reduced seedling recruitment and initial survival as it coincided with the normal period for seed germination, whereas low spring flows exposed more river bed and therefore more substrate for seed germination and survival (Johnson 1994). Late summer survival of seedlings depended on river stage, elevation of seedlings and rainfall. On a river island in Wisconsin, successful establishment of vegetation occurred on bare mineral soil when weather conditions were favourable and when there was no prolonged or extensive flooding until the seedlings had become established (Barnes 1985). Regulation of a central U.S. river brought about the loss of significant water level fluctuations resulting in an absence of areas of bare moist substrate and lead to a lack of regeneration of riparian tree species (Friedman et al. 1995). In south-west Colorado, stands of *Populus angustifolia* originated in discrete cohorts in years with both high spring and autumn peak discharges (Baker 1990). On this river, key environmental determinants of riparian vegetation development were cohort age, surface sediment type and soil development, with cohort age correlated with past flooding. Therefore the vegetation mosaic is determined by the periodic disturbance of floods (Baker & Walford 1995).

The effects of fluvial disturbance can be widespread in the river valley, with numerous patches of early successional vegetation close to the river channel (Gregory et al. 1991), while on the floodplain, further from the influence of the active channel and low level flooding, older plant communities are more common (Hawke & Zobel 1974). The vegetation structure can therefore be strongly influenced by the timing and character of recent large scale disturbances (i.e. floods) and the age of stands is related to height above the channel (Baker 1988). Failure of the vegetation to reach later successional stages due to high frequency flooding disturbance has been documented for New Zealand podocarp forest (Duncan 1993). This importance of hydrology was also observed for rivers in southern France, with flood frequency and duration being important in determining species composition. For the rivers of this region, a strong correlation existed between species composition and hydrology, while other significant factors included soil type and geomorphology (Pautou & Decamps 1985; Tabacchi 1995). For a mediterranean riparian
shrub species, seed release of wind- and water-dispersed seeds coincided with peak river flows. Once seeds had dispersed and germinated the principal cause of seedling mortality was somewhat evenly divided between drought (46%) and flooding (41%) (Herrera 1991).

Other factors have been reported as being important in determining establishment success for riparian species. For example, the critical importance of microsites for establishment of various species has been demonstrated in a floodplain wetland (Titus 1990) and for river red gum on the Murray River floodplain in eastern Australia (Bren 1992). In these examples, microsites are important to elevate seedlings from excessive waterlogging but also to provide a site to trap moisture, thus reducing desiccation in the dry period of the year. In a floodplain forest in Texas, U.S.A., effects on seedling mortality included flooding, drought, light and herbivory, with some factors being more important in different years (Streng et al. 1989). For a river in Sweden, the effects of shade and leaf litter were found to be critical in successful establishment (Skoglund & Verwijst 1989). A strong effect of shading on seedling growth has been shown for floodplain forest species in eastern North America (Jones & Sharitz 1989). Litter can have either positive or negative effects on the germination and establishment of riparian vegetation (Xiong & Nilsson 1997). Litter can improve water availability under dry conditions, protect seed from predation or reduce competition but can have negative effects through shading, obstructing emerging seedlings or reducing temperature. Floating litter debris can enhance dispersal of plant diaspores (Xiong & Nilsson 1998), however seeds may not germinate in deposited litter as it may be too loose to retain moisture for germination (Nilsson et al. 1993).

Species diversity of vegetation in the riparian zone can be influenced by many factors including level of disturbance, tolerance to waterlogging (which is influenced by topography), soils and geomorphology, life history traits and climate. On a floodplain, adaptation of species to flooding can result in the development of different communities, with those in flood-prone areas consisting mainly of flood-resistant stress-tolerators while at higher elevations species with competitive traits tend to dominate (Blom et al. 1990). Ability to establish in the riparian zone can be related to some extent to physiological tolerance to flooding, in both adults and seedlings.
Pezeshki & Anderson 1997). This can be through etiolation of the stem above water levels or through the development of adventitious roots and arechyma tissue in the roots (Kozlowski 1984). Riparian vegetation communities can be described in relation to topographic position, from the river flat to various levels of river terrace, with the youngest communities on the river flat (Fonda 1974). In a gradient analysis of floodplain forest in Illinois, species diversity and richness increased with decreasing flooding stress (Bell & del Moral 1977). Seasonal variation in climate, particularly rainfall, can also be important in determining species composition in riparian habitats. In dry years disturbed sites are most likely to be invaded by dryland species whereas in wet years invasion tends to be by species dispersed by water (Decamps et al. 1995).

Life history traits are also very important and riverine species of *Salix* and *Populus* are ideally suited to this habitat, producing large seasonal seed crops which are effectively dispersed by wind and water, having rapid germination and growth as well as an ability to reproduce vegetatively (Johnson 1994). In a riverine wetland, peat thickness and water level were the abiotic variables most strongly correlated with plant community composition. However, only half the species were accounted for in multivariate analysis of the environment variables, with historical factors such as change in water regime and fire frequency also explaining a large proportion of the variation (Jean & Bouchard 1993).

In Australia, recruitment of river red gum (*Eucalyptus camaldulensis*) seedlings on the floodplain of the Murray River is limited by poor establishment of seedlings rather than lack of seed germination. As well as seeds requiring safe sites, flooding of the surrounding forest is necessary every two years to replenish soil moisture (Dexter 1978). Flooding should occur in late winter and recede by late spring to coincide with seed fall in areas of receding floodwaters. Lack of recruitment in these forests has been attributed to increased flooding in summer due to river regulation (Bren & Gibbs 1986). On the Murray River, establishment of the plant community in the littoral zone of the river bank is dependent on falling water levels exposing new substrate for seed germination. Establishment is also affected by water currents, wave action and herbivore grazing so that in many cases regeneration can only take place through vegetative reproduction.
(Roberts & Ludwig 1991). On an ephemeral creek in the semi-arid region of eastern Australia, analysis of size-class structure of *Eucalyptus coolabah* trees indicated that recruitment was episodic and related to past large rainfall events where flooding was considered important to replenish soil moisture, allowing seedlings to survive the dry season (Roberts 1993). Flooding tolerance of establishing seedlings of *Tristaniopsis laurina* and *Acema smithii* could also influence the distribution of these two species in a riparian rainforest in Victoria. Seedlings of *T. laurina* survived waterlogging for a much longer period and therefore were found on the wetter sites along the river (Melick 1990).

**Conclusions**

From this review there are clearly many attributes of riparian vegetation that are important in terms of possible regeneration and rehabilitation. These include concepts of vegetation dynamics and how these relate to the unique physical environment of the riparian zone. Added to this are the effects of disturbance, particularly flooding and livestock grazing, on the processes of regeneration. By describing species composition and life history attributes and how these vary across the elevational gradient of the river, mechanisms that are significant for regeneration of riparian vegetation may be shown. The review has shown that particular life history traits can be important in different plant communities depending on the disturbance regime, management inputs and the physical environment. Although this has been documented for many different types of plant communities, little work has been done specifically on riparian vegetation and particularly not in Australia. The life history traits of both native and exotic plants in the riparian zone will be examined here and can be used to predict the outcome of disturbance.

The literature emphasises the importance of disturbance in the dynamics of vegetation communities, particularly in the riparian zone. In many riparian communities, populations are established by mass recruitment events after some large disturbance, principally flooding, and the population may be maintained between large disturbance events by occasional recruitment.
after some small disturbance (patch dynamics). The role of disturbance is certainly crucial and methods used in the current study focus on determining the relative importance of large scale disturbance (i.e. episodic events) and patch dynamics (i.e. opportunistic recruitment) in recruitment of riparian species. Regeneration in the riparian zone is also clearly tied to the hydrological regime so that an understanding of the regime of the particular river system studied is very important. The regeneration strategies that will predominate in riparian communities will be adapted to regular high frequency disturbance by flooding. These strategies include high annual seed production, wind- or water-dispersed seeds, fast growth rates and the ability to resprout vegetatively. The combinations of these strategies which occur in the riparian zone are not well documented and this will be undertaken as part of this study. Overseas studies, particularly many in North America, have shown the importance of hydrological events on various aspects of seed ecology and phenology, including timing of seed release, dispersal of seed, exposure of moist sediment, the germination and survival of seedlings and the population dynamics of particular species (Bradley & Smith 1986; Johnson 1994; Naiman et al. 1998). These aspects will be explored, in an Australian context, for the two rivers described in this study.
CHAPTER 3

STUDY SITE DESCRIPTIONS

Introduction

The study sites for this project were located on two rivers, the Blackwood River in the south-west and the Ord River in the Kimberley region of north-west Western Australia (Figure 3.1 & 3.2). The Blackwood River was chosen as being representative of river systems in the south-west of Western Australia, with a Mediterranean-type climate and predictable seasonal patterns of rainfall and river flow. In contrast the Ord River is a sub-tropical northern Australian river with river flows that are greatly affected by monsoon rains, resulting in large wet season flows and virtually no flow in the dry season (Table 3.1). The riparian zone on each of these rivers has, at least in some sections, become degraded by livestock grazing and as a consequence of agricultural clearing.

Table 3.1: Catchment statistics for the Ord and Blackwood Rivers.

<table>
<thead>
<tr>
<th>River</th>
<th>Catchment Area (km²)</th>
<th>Rainfall Range (mm yr⁻¹)</th>
<th>Mean Annual Flow (x 10⁶ m³)</th>
<th>Max. Recorded Discharge (m³ sec⁻¹)</th>
<th>Water Quality</th>
<th>Disturbance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ord River</td>
<td>46,100</td>
<td>400 - 700</td>
<td>4,320</td>
<td>31,000</td>
<td>Fresh</td>
<td>Cattle grazing, river regulated in lower reaches</td>
</tr>
<tr>
<td>Blackwood River</td>
<td>28,000</td>
<td>350-1000</td>
<td>659</td>
<td>1,190</td>
<td>Brackish</td>
<td>85% cleared farmland, sheep &amp; cattle grazing</td>
</tr>
</tbody>
</table>
Location

Ord River

The Ord River stretches from its source, in the Durack Ranges, north-west of Halls Creek, to empty into Cambridge Gulf north-west of Kununurra (Figure 3.1). Vegetation in the catchment is predominantly open grassy woodland (Beard 1979) which is grazed by cattle. On the Ord River plains in the upper catchment, degradation of the vegetation through a long history of overgrazing has resulted in severe erosion and extremely high sediment loads in the river. Over large areas, such as at Ord River Station, rehabilitation through fencing and de-stocking has taken place (Fitzgerald 1967). The river has also been dammed in two places, resulting in three discreet sections. Upstream from the Ord River Dam and Lake Argyle, the river flow is essentially natural, with flows influenced by a climate of wet season monsoon rainfall and a long dry season when the river dries up to a series of pools. The middle section of the river, between the Ord River Dam and the diversion dam at Kununurra, has been flooded and water is permanent with levels fluctuating little throughout the year. Downstream of the diversion dam flows are artificially regulated to provide water for irrigation. Water levels are therefore higher in the dry season than under natural conditions and lower levels are experienced in the wet season. Study sites were located in a longitudinal sequence from downstream to upstream, with Site O1 being located downstream of the diversion dam near Carlton Hill Station. Site O2 was located in the middle section of the river, between the Ord River Dam and the diversion dam on Lake Kununurra. Monitoring sites upstream of Lake Argyle were located on the Behn River (Site O3) near the Duncan Road crossing, on the Negri River (Site O4) near the Duncan Road crossing and at the Old Ord River Station (Site O5) adjacent to a Water and Rivers Commission gauging site (Figure 3.1).
Figure 3.1: Location of the study sites within the Ord River catchment.
Figure 3.2: Location of the study sites within the Blackwood River catchment
Blackwood River

The Blackwood River rises in the low rainfall area of inland south-western Western Australia and flows westward to enter the sea at the south-west tip of the continent (Figure 3.2). The river is around 300km long and carries the largest flow of any river in the south-west. Rainfall in the catchment ranges from around 400 mm yr⁻¹ in the east to 1200 mm yr⁻¹ near the coast. The upper and middle reaches are influenced by the large predominance of cleared agricultural land, with many areas having been cleared for 100 years and livestock grazing taking place right up to the river’s edge (Olsen & Skitmore 1991). Clearing in areas of naturally highly saline soils of the upper catchment has resulted in rising salinity levels of the river and in the waters of the upper Blackwood tributaries (Arthur & Beaufort Rivers) becoming saline to brackish (Schofield et al. 1988). Water in the middle to lower sections, which are drained by mainly forested areas, is marginal to fresh before becoming influenced by the salt wedge as the river nears the coast. As the riparian zone on the Blackwood River is heavily influenced by intensive livestock grazing, study sites were set up in pairs at each location, with one site that was heavily grazed and, in close proximity, a site that has had little impact of stock grazing. The main study sites on the Blackwood River included two sites near Nannup (downstream section), one of which had been heavily grazed by livestock so that the composition of the understorey was highly modified (Site B1b), and the other in a forested area which has had no disturbance from livestock (Site B1a). A grazed site and an ungrazed site were also located near the Condinup Bridge near Boyup Brook (middle section) (Site B2a &b). There were another two sites on the Beaufort River (upstream section), an ungrazed site (B3a) and a grazed site (B3b) (Figure 3.2). Two additional sites were also surveyed on the Blackwood River for the effects of relief from grazing and fire on riparian vegetation (Chapter 6). These sites were located in the middle catchment on a tributary of the Blackwood River (Site B4) and on the Blackwood River 5km west of the town of Boyup Brook (Site B5) (Figure 3.2).
Climate

Ord River

The climatic region of the Ord River catchment (between latitudes 14° and 19° S) is described as tropical with a short rainy season (Gentilli 1972). Climatic data for this East Kimberley region was collected from Kununurra Research Station in the north (records from 1944 - 1996) and from Halls Creek Post Office in the south (records from 1890 - 1996) (Bureau of Meteorology). This region has a warm dry monsoonal climate characterised by a rainy season from November to April and a period of virtual drought for the remainder of the year. Gentilli (1972) identified five periods in the seasonal cycle: the cool dry season (May to mid-August); the warm dusty season (mid-August and September); the hot dry-wet transition (October to November); the wet season (December to March); and the hot wet-dry transition (April). There is a marked trend in climate from the coastal region in the north to the inland area in the south. In the northern portion there is generally higher total rainfall, less extremes of temperature and greater humidity than in the south. Mean annual rainfall ranges from 784 mm at Kununurra to 491 mm at Halls Creek, with a rapid onset of rain in the wet season from November and a rapid decline in rainfall after March (Figure 3.3a&b). Rainfall intensity and reliability also decreases to the south. The period of effective rainfall or 'growing season' (i.e. when rainfall exceeds evaporation rates) is around eight months for Kununurra and substantially less for Halls Creek. Highest monthly median rainfall is for January and February (170 mm for both months in Kununurra and 113 mm and 88 mm respectively in Halls Creek) with 0 mm median rainfall for June to September for both sites. Wet season rainfall forms by far the greatest proportion of the annual total with 80-82% of rainfall occurring in the months of December through to March. There are an average of 65 and 51 rain days per year for Kununurra and Halls Creek respectively, with the months of January and February having the highest number of days of rain (14 for both months in Kununurra and 11 and 10 in Halls Creek). For the months of May to September, there is, on average, less than one rain day per month for both Kununurra and Halls Creek. Average rainfall per rain day for the period December to March is 17.5 mm at Kununurra and 9.6 mm at Halls Creek. Annual rainfall variability is moderate but increases as rainfall decreases, with
deviation from the mean being 21% in Kununurra and 31% in Halls Creek (Slatyer 1970). Due to the proximity to the coast, temperature extremes and diurnal variations in temperature are ameliorated in Kununurra compared with Halls Creek. The hottest month for both sites is November, with an average temperature of 38°C and with, on average, 10 days above 40°C. The onset of the wet season has the effect of slightly reducing maximum temperatures (Figure 3.3a&b). July is the coolest month, with average maximum temperatures of 30.3°C and 26.8°C for Kununurra and Halls Creek respectively. Average minimum temperatures range from 24.7°C in November to 14.4°C in July in Kununurra and 24.2°C to 8.9°C in Halls Creek. Humidity is lower in Halls Creek (53% in February to 21% in July, annual mean 40%) than in Kununurra (70% in February to 32% in August, annual mean 47%), due mainly to geographic location and lower rainfall. Humidity levels are in general lower than would be expected for the humid tropics (Slatyer 1970). Annual evaporation rates are similar at both sites at around 2600 mm, with highest evaporation rates occurring in the pre-wet season period between September and November.

Blackwood River

The regime of prevailing winds exerts a strong influence on the climate of the Blackwood River region, with the sub-tropical belt of high pressure (as anticyclones) extending across the region during summer bringing easterly prevailing winds. In autumn, these gradually move northwards and incursions of cyclonic low pressure zones bring most of the winter rains (Gentilli 1972). Frequency of moisture laden unstable squalls, which characterise winter storms, reduces with distance in an easterly direction from the coast. The strongest climatic features of the southwest region are abundant winter rains and intense summer droughts, which are characteristic of the ‘Mediterranean’ climate (Gentilli 1972). Climatic data for this region was collected from Bridgetown Post Office (records from 1887 - 1996) in the central region and Wagin Post Office (records from 1891 - 1996) at the eastern headwaters of the Blackwood River (Bureau of Meteorology) (see Figure 3.2). There is a marked trend in climate from the coastal region in the west to the inland area in the east. In the west there is higher annual rainfall, less extremes of temperature and greater humidity than in the east. The period of effective rainfall or growing
season' (i.e. when rainfall exceeds evaporation rates) is around six months in the east and eight months closer to the coast (Gentilli 1972). Mean annual rainfall ranges from 836 mm in Bridgetown to 440 mm in Wagin. Mean monthly rainfall together with maximum and minimum temperature data are summarised for these sites in Figure 3.3c&d. Highest monthly median rainfall is for July (144 mm in Bridgetown and 66 mm in Wagin), with lowest values of 6.4 mm and 2.8 mm for January at Bridgetown and Wagin respectively. Winter is the period of greatest rainfall, with 45% of the annual total falling from May to August at Bridgetown and 59% at Wagin. There are an average of 140 rain days per year in Bridgetown and 93 per year in Wagin, with July having the most number of days of rain (22 in Bridgetown and 14 in Wagin). For January there are on average 3.3 rain days in Bridgetown and 2.3 rain days in Wagin. Average rainfall per rain day for the period May to August is 7 mm in Bridgetown and 5 mm in Wagin and for December to March is 4 mm and 4.5 mm respectively. Annual rainfall variability is moderate, with deviation from the mean of 14% in Bridgetown and 15% in Wagin. The hottest month for both sites is January, with an average temperature of 29.7°C in Bridgetown and 31°C in Wagin. July is the coolest month, with average maximum temperatures of 15.7°C and 15.2°C for Bridgetown and Wagin respectively. Average minimum temperatures range from 12°C in January to 4.4°C in July for Bridgetown and 14.6°C in February to 5.5°C in August for Wagin. Humidity is lower in Wagin (80% in June and July to 54% in December and January, annual mean 70%) than in Bridgetown (91% in June and July to 60% in December and January, annual mean 75%), due mainly to geographic location and lower rainfall. Annual evaporation rates at Wagin and Bridgetown are between 1600 and 1800 mm yr⁻¹ with highest evaporation rates occurring in summer between December and March.

Comparison of climates

The difference in the climate of the two regions that most affects fluvial processes is rainfall intensity. The principal causes of rain in the Ord River region are instability thunderstorms, monsoonal incursions and tropical thunderstorms (Gentilli 1972). These give rise to a large proportion of high intensity rainfall events in the wet season. For the Blackwood River region, winter rains arise from the advection of moist air in the westerly air streams in the form of rain-
bearing depressions in cyclonic low pressure systems. Rainfall throughout the year tends to be less intense and to occur over a longer period. For example, at Kununurra there is an average of 64 raindays per year (i.e. 11.9 mm rain per rain day), with 14 rain days in the wettest month of January (i.e. 13.6 mm rain per rain day). This compares with an average of 140 rain days for Bridgetown (i.e. 5.9 mm rain per rain day), with 22 rain days in July (i.e. 6.9 mm rain per rain day). Kununurra receives, on average, 80% of its rainfall in the four wettest months, from December to March, whereas Bridgetown receives only 45% of its rainfall from May to August. Similar trends are seen for the drier areas of each region. When mean monthly rainfall is regressed against mean number of rain days per month, the pattern of greater intensity of rainfall events on the Ord River is clearly evident (Figure 3.4). The slope of the regression lines indicate that rainfall intensity is less in the high rainfall months in the Blackwood region, whereas intensity is fairly even throughout the year, if not slightly more in the high rainfall months, for the Ord. This large difference in rainfall intensity of the two regions has obvious implications for river flows and fluvial processes with, for example, high intensity rainfall resulting in greater runoff into drainage channels. Other aspects of climate that are contrasting in the two regions, such as temperature, humidity and evaporation rates would also contribute to shaping the nature of the riparian vegetation on these two rivers.
Figure 3.3: Mean monthly rainfall and maximum and minimum daily temperatures recorded at weather stations on the Ord River (a) & (b) and the Blackwood River (c) & (d).
Figure 3.4: Relationship between rainfall and number of raindays for (a) higher rainfall sites on the Ord River (Kununurra, 784 mm/yr) and the Blackwood River (Bridgetown, 835 mm/yr) and (b) low rainfall sites on the Ord River (Halls Creek, 490 mm/yr) and the Blackwood River (Wagin, 440 mm/yr).
Hydrology

The Ord River rises in the sandstone country of the Durack Range at an altitude of around 400 metres above sea level, gradually sloping down to around 150 metres in the middle catchment at Spring Creek and to about 50 metres at Carlton Gorge and onto the floodplain downstream (see Figure 3.1). The Ord is considered a degraded river (Williams et al. 1996), with cattle grazing in the upper reaches causing extensive erosion and two dams on the lower section resulting in an altered flow regime downstream. Hydrological statistics quoted below are for the unregulated section upstream of Lake Argyle.

Many westward draining rivers in south western Australia, such as the Blackwood River, have an unusual drainage pattern. The Blackwood River rises in terrain of little relief (~250 m asl at Wagin) and with low annual rainfall (<500 mm yr\(^{-1}\)), is ‘rejuvenated’ in the middle reaches as it flows through an area of greater relief down an escarpment and slows again as it meanders across the coastal plain to the sea. The upper catchment is affected by an area of north-south oriented paleo-drainage which is marked by a system of saline lakes. Extensive agricultural clearing in this area has resulted in rising saline water tables and therefore secondary salinisation (Malcolm 1983). These two factors contribute to high salt loads, particularly in the upper reaches of the river. The Blackwood River appears to have a reverse salinity profile, with high salinity in the headwaters, especially in early winter, and fresher middle reaches which drain higher rainfall forested areas (Morrissy 1974).

Monthly river discharge records over an 18 year period from 1975-93 for the Ord and Blackwood Rivers show the much greater discharge for the Ord River (Figure 3.5). The variable nature of flows in terms of magnitude are clearly seen over this period, particularly for the Ord River. On the Ord River, flows are generally restricted to the wet season (December - March), with significant flows being recorded outside this period only once. During the period of records there have been three flows of greater than 10,000 m\(^3\) sec\(^{-1}\) and two years with very little flow.
recorded. Blackwood River discharge is much lower, with the highest levels in winter (May-August) and with some flow continuing for most of the year. Greatest discharge on the Blackwood River for the period of records (1187 m³ sec⁻¹) was in summer 1982 when a cyclonic low pressure system drifted down from the north dropping a large amount of rain and resulting in flash flooding.

The degree of variability of flows of the Ord and Blackwood Rivers is given in Table 3.2 along with a comparison of flows with other rivers throughout the world in different climatic zones. Compared with these other rivers, the Ord River is highly variable in terms of monthly discharge, with only the arid zone rivers of Australia having a higher coefficient of variation (CV), skew and spread. The Blackwood River is also quite variable, with values similar to the Murray and Darling Rivers in eastern Australia.

### Table 3.2: Summary statistics of Australian and world rivers from different climate zones showing mean monthly discharges (m³ s⁻¹) over periods of 15 - 25 years (modified from Walker et al. 1995).

<table>
<thead>
<tr>
<th>River</th>
<th>Country</th>
<th>Climate</th>
<th>Min.</th>
<th>Max.</th>
<th>Mean</th>
<th>CV²</th>
<th>Skew</th>
<th>Median</th>
<th>Spread²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ord</td>
<td>Australia</td>
<td>Trop, D</td>
<td>1285</td>
<td>53</td>
<td>2.86</td>
<td>5.16</td>
<td>1.42</td>
<td>8.87</td>
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<tr>
<td>Blackwood</td>
<td>Australia</td>
<td>W/Temp, SA</td>
<td>0.1</td>
<td>286</td>
<td>18</td>
<td>1.47</td>
<td>3.15</td>
<td>2.73</td>
<td>3.24</td>
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<tr>
<td>Cooper Ck.</td>
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<td>W/Temp, A</td>
<td>0</td>
<td>7593</td>
<td>142</td>
<td>4.54</td>
<td>8.51</td>
<td>6</td>
<td>4.3</td>
</tr>
<tr>
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<td>W/Temp, A</td>
<td>0</td>
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<td>4.66</td>
<td>9.04</td>
<td>1</td>
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<tr>
<td>Darling</td>
<td>Australia</td>
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<td>0</td>
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<td>2.13</td>
<td>47</td>
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</tr>
<tr>
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<td>Australia</td>
<td>W/Temp, SA</td>
<td>6</td>
<td>5710</td>
<td>975</td>
<td>1.06</td>
<td>2.06</td>
<td>646</td>
<td>1.48</td>
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<tr>
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<td>30582</td>
<td>8394</td>
<td>0.94</td>
<td>0.99</td>
<td>4390</td>
<td>2.87</td>
</tr>
<tr>
<td>Niger</td>
<td>Mali</td>
<td>Trop, D</td>
<td>30</td>
<td>2658</td>
<td>1161</td>
<td>0.71</td>
<td>0.06</td>
<td>1156</td>
<td>1.4</td>
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<tr>
<td>Danube</td>
<td>Romania</td>
<td>W/T, C</td>
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<td>13300</td>
<td>5121</td>
<td>0.4</td>
<td>0.74</td>
<td>4920</td>
<td>0.6</td>
</tr>
</tbody>
</table>

Trop=tropical; D=dry; W=warm; Temp=temperate; SA=semi-arid; A=arid

CV² = coefficient of variation.

²Spread = ratio of interquartile range to the median.

Comparison of the hydrographs for 1993/94 for the Ord and Blackwood Rivers highlights the differences in volume and shape (Figure 3.6). The much greater discharge for the Ord River is related to a combination of factors including rainfall intensity, topography/slope and geology and soils, with rainfall intensity being the greatest influence as discussed above. Figure 3.6 also
Figure 3.5: Monthly river discharge data over a 18 year period for (a) the Ord River and (b) the Blackwood River.
Figure 3.6: Daily total river discharge for the Ord River (left hand axis) and the Blackwood River (right hand axis) for 1993/94 highlighting the differences between volume and the shape of the hydrographs.
highlights the influence of groundwater flow on river base flows. There is negligible groundwater influence and therefore base flow on the Ord River, with large steep sloped peaks in flow. In contrast, there is a large base flow on the Blackwood River, with a much gentler slope on both the rising and falling limb of the hydrograph, so that groundwater inflows become the greatest influence on discharge. Discharge figures for the Ord River were taken from above Lake Argyle at Old Ord River Station and cover a catchment area similar to the area of the Blackwood catchment from just below the town of Nannup (Darradup). These results highlight the large 'flashy' nature of flows on the Ord River, with large flows occurring in quick response to rainfall events but quickly returning to very low flows. Flows on the Blackwood River are usually maintained throughout the rainy season and into the drier late spring/early summer period. These features of the hydrology have implications for the adaptation of the riparian vegetation.

Geology

Ord River

The geology of the East Kimberley region is represented by rocks from almost all geologic periods, the oldest including the granite country of the Bow River Hills that were formed in the pre-Cambrian period, some 1900 million years ago (Department of Mines 1972). The geologic formations that are associated with the Ord River basin include the area of low hills of metamorphic rocks to the west of the Ord River from which the Bow River, a major tributary of the Ord River, rises. To the west of this area are the Durack Ranges of mainly sandstone sedimentary rugged ridges and escarpment which formed in the Tertiary Period where the Ord River and another major tributary, the Dunham River, have their headwaters. This area also forms the divide between the Ord and Fitzroy Rivers. To the east and south of Lake Argyle, in the area around Ord River Station, is the Ord River plain. This extensive dissected plateau consists of basalt lava flows 550 million years old which were subsequently covered by shallow seas resulting in sedimentary deposits of limestone, sandstone and mudstone. This plateau
country was uplifted some 20 million years ago and has been extensively incised by creeks and rivers. The Halls Creek fault is a major fracture which extends from the south of the Ord basin to the north into the Northern Territory and has caused horizontal and vertical movements of the landscape. The escarpment along the fault line is characterised by cliffs or higher hills of more resistant rock on one side of the fault or by resistant quartz veins (Stewart et al. 1970). The flat country of the lower Ord River as it flows into Cambridge Gulf is made up of Quaternary alluvial sediment plains.

Blackwood River

Of the south-west province of Western Australia, around 95% is composed of granite-migmatite terrain of Archean age known as the Yilgarn Block (Department of Mines 1972). Small, irregular, patchy areas of metamorphic gneiss rocks, with indistinct boundaries, are scattered throughout the province. The regional tectonic trend is mainly north-westerly and an active seismic zone with a north-west trend across the province is the Meckering line (Mulcahy & Bettenay 1972). This fault line marks the boundary between the westerly limit of wide alluviated valleys of ancient drainage containing salt lake systems and rejuvenated incised river valleys characteristic of the western areas. Archean rocks are poorly exposed east of the Meckering line and are commonly deeply weathered and covered by thick sandy superficial deposits. To the west, fresh rock has been exposed along the sides and floors of the incised drainage systems. The Archean rocks are intruded by mafic dykes of altered quartz dolerite which also trend north-westerly and increase in frequency to the west near the Darling Scarp (Department of Mines 1972). There are small areas of shallow, unconsolidated sediments throughout the area, usually in the upper part of the landscape. The lower catchment on the coastal plain, below the Darling escarpment, is formed of depositional materials of either fluvial or aeolian activity. This includes the Blackwood Plateau of flat-lying Mesozoic sandstones overlain with lateritic remnants. To the west is the Leeuwin Block of Pre-Cambrian gneiss and granulites with overlying sedimentary deposits of limestone and Pleistocene and Holocene aeolian sands (Department of Mines 1972).
Geomorphology and Soils

Ord River

The Ord River area lies in a relatively small range of altitude, with most of the area less than 300 metres above sea level and with only small ridges in the western part more than 600 metres above sea level. A significant proportion of the area consists of rugged rock outcrops with shallow stony soils. The remaining area is undulating to flat with gently undulating plateau surfaces, erosional plains with moderately deep soils formed from weathering of the underlying rock and alluvial plains along the major stream valleys (Stewart et al. 1970). The gently undulating erosional plains in the upper catchment are formed on Cambrian shale and limestone. The area has a clearly defined dendritic drainage pattern and is interspersed with occasional volcanic mesas and buttes of eroded basalt material. The soils consist of brown powdery calcareous loams over deep clay loams on the slopes, with brown cracking clays in depressions and along drainage lines (de Salis 1993). There are also smaller areas of gently undulating country with deep yellow sands over sandstone. This sandstone parent material is particularly resistant to erosion and is strongly jointed which has a significant effect on drainage.

To the north, towards Lake Argyle, is more hilly country of basalt rock outcrops derived from Cambrian volcanics and with pockets of red clayey soils. There are also areas of volcanic structural benches and erosional plains on moderate slopes, with brown loams merging to red clays and brown skeletal soils around the basalt hills and structural benches. Large areas consist of gently undulating erosional plains of calcareous, dolomitic and shale sediments, with soils of brown and grey cracking clays (black soil plains) (Stewart et al. 1970). The Carr-Boyd Ranges between Lake Argyle and the Dunham River form rugged hilly country up to 600 m high of Proterozoic sandstone, siltstone and shales. The soils are shallow and stony with sands and loams on the ridges and duplex soils on the slopes. Most of the drainage is superimposed but is modified to an irregular drainage pattern by the underlying bedrock. To the west of the Ord River plain and forming part of the Halls Creek fault system is the area of the Bow River Hills, consisting of pre-Cambrian granite boulder-strewn hills and granite ridges with open textured
dendritic drainage patterns. Soils are mainly shallow stony sand with much rock outcrop on ridges and upper slopes and with duplex soils on lower slopes and in the valleys. The lower Ord River, below Lake Argyle, is predominantly gently sloping fine textured (black soil) fluvial plains on Quaternary alluvia. This is the floodplain of the Ord River and it is interspersed with broadly meandering channels with broad levees associated with brown sand or sandy loam soils over permeable reddish brown subsoil. Minor areas of sandy country consisting of deep red or yellow sand over Permian sandstone are scattered throughout this area, together with some areas of rock outcrop and skeletal soils of sandstone and shales.

Blackwood River

By the end of the Tertiary Period the Archean shield of the great plateau in the south-west drainage division of Western Australia was mantled by a lateritic soil which developed when climatic conditions were wetter and warmer than the present day climate (McArthur 1991). The laterite consists of a sandy surface and gravelly clay sub-soil underlain by weathered mottled and pallid zone materials and saprolite above basement rock. The original lateritic profile has had a strong influence on the make-up of the present day soils. Today the lateritic profile is rarely found intact (Bettenay et al. 1980) and only remains as remnants, with stripping of the lateritic mantle being more extensive with distance to the east. The soils reflect varying degrees of erosion, colluviation, sorting and leaching, depending on factors such as slope, aspect and landscape position. Erosion has exposed the mottled and pallid zones and in some cases has led to the deposition of erosional material in the valley bottoms. The original sandy surface soils can also be replaced by gravelly sand or sandy loam so that the resultant soil can have a colluvial surface layer and underlying soils of a quite different origin.

The Blackwood River basin can be divided into the upper, middle and lower catchments on the basis of landform, topography, vegetation and land use (Grein 1995). The upper catchment is a zone of ancient drainage of gently undulating plateaux, between 280 m and 400 m above sea level. It is marked by a series of saline lakes and only flows (and therefore only contributes to the Blackwood River discharge) in years of high rainfall. The broad valleys have very low grades,
with local relief of less than 50 m, and contain deep grey to yellow sandplain soils with some laterite remnants on the divides and with loose grey gravelly soils. Shallow duplex soils of the stripped laterite profile and grey to red-brown loams formed on fresh rock can also occur. The zone of rejuvenated drainage west of the Meckering fault line contains clearly defined drainage lines that carry water each year. Most of the landscape is formed of the mottled and pallid zones of remnants of the laterite profile and contains undulating hills, with sandy duplex soils on the slopes and in the broad valley floors, where the duplex soils are underlain with sodic, alkaline clay sub-soils (Northcote et al. 1967). There are also numerous areas of exposed basement rock and laterite breakaways on the ridges with sandy gravel soils. The middle catchment consists of undulating dissected terrain between 260 m and 360 m above sea level, with large remnants of the lateritic plateau consisting of yellow-brown and grey sandy gravel soils. There are also broad flat upland areas of Eocene sedimentary deposits separated by valleys dissected into the underlying bedrock. Valley soils include yellow-brown loamy and sandy gravels and yellow-red loamy duplex soils grading into clays. Further west from Bridgetown, where the Darling Scarp rises from the coastal plain, is a broad undulating laterite plateau where sandy and loamy gravel soils are dominant. The Blackwood River is deeply incised into the plateau, forming a deep-sided valley and exposing fresh rock. Red-brown and yellow-brown loams grading into clays have formed on the fresh rock. Along valley floors river flats contain soils of deep loose brown loams and deep red loams. West of the Darling Scarp is level, slightly undulating terrain formed on Cretaceous and Jurassic Perth Basin sedimentary rocks with elevations of 20 m to 180 m above sea level. This is dissected by the river to form shallow valleys with grey-brown sands and loams. These merge to the west with the low-lying coastal plain of deep loose white sands on Quaternary sediments (Tille & Lantzke 1990).
Vegetation

Ord River

The vegetation of most of the Ord River basin is open woodland or savanna with a grass understorey. In much of the area the composition, density and structure of the understorey has been greatly altered by over 100 years of cattle grazing, the introduction of exotic species and the effects of soil erosion. In severely degraded areas, such as the calcareous soils of the Ord River plains, a rehabilitation project has taken place to control soil erosion and to reduce sediment loads into the river (Fitzgerald 1967). This has seen the de-stocking of large areas and re-vegetation with exotic species such as Cenchrus ciliaris (buffel grass), C. setiger (birdwood grass) and Aerva javanica (kapok bush). The vegetation described here is in the undegraded condition (Beard 1979) and species names have been updated where appropriate from Wheeler et al. (1992) and the State Herbarium records.

In the upper catchment on the Ord River plain, just south of Lake Argyle, the vegetation is a low tree savanna of Eucalyptus opaca and E. argillacea with an understorey of 'Tippera' tall-grass association and dominant grasses including Themeda triandra, Sehima nervosum, Sorghum plumosum, Chrysopogon fallax, Aristida pruinosa and Heteropogon contortus. In the southern portion trees become more sparse and restricted to lower slopes and flats and include Lysiphyllum cunninghamii, Terminalia oblongata and T. arostrata. T. platyphylla and other Terminalia spp form a fringing woodland along drainage lines. The ground layer changes to a short-grass (<30 cm tall) association of Enneapogon spp. and Aristida contorta. On the rocky hills Eucalyptus brevifolia and some E. opaca and Terminalia spp. with a ground layer of Triodia spp. (spinifex) can be found. Large areas of the plain are treeless, with Astrebla spp. (Mitchell grasses) dominant on the areas of black soil and short grasses such as Enneapogon spp. most abundant on the calcareous soils. On the levee frontages of the major streams E. gymnoteles and Lysiphyllum cunninghamii form sparse woodlands, while on the river banks themselves fringing forests of Eucalyptus camaldulensis, E. gymnoteles, Melaleuca leucadendra and Ficus sp. can be found (Perry 1970).
On the lower Ord River where sandy soils overlay sandstone, the vegetation comprises a high-grass savanna woodland of annual sorghum (*Sorghum* spp.) and *Plectrachne pungens* with an overstorey of *Eucalyptus tetrodonta* and *E. miniata*. On the rocky limestone areas the overstorey changes to open woodland of *Terminalia* spp., *Adansonia gregorii*, *Lysiphyllum cunninghamii* and *Ficus* spp. with a similar understorey. The alluvial plains, other than black soil areas, support a savanna of *Eucalyptus tectifera* and *E. byrnesii* with some areas of *Melaleuca viridiflora* and *M. nervosa* and an understorey of tall grasses such as *Sorghum* spp. The black soil plains are sparsely wooded with *Eucalyptus microtheca*, *Terminalia* spp. and *Lysiphyllum cunninghamii*, common shrubs *Acacia farnesiana* and *Carissa lanceolata* and a ground layer of blue-grass and tall-grass community including *Dichanthium* spp. and *Sorghum plumosum*. Frontage woodlands on the levees of the major stream channels consist of *Eucalyptus houseana*, *E. polycarpa*, *E. patellaris*, and *Adansonia gregorii* with a tall-grass understorey of *Sorghum stipoideum*, *Chrysopogon latifolius* and *Panicum* spp.. Fringing forests on the river banks consist of mixed forest with dominants including *Eucalyptus camaldulensis*, *Melaleuca leucadendra*, *M. argentea*, *Pandanus spiralis* *Terminalia platypylha*, *Lophostemon grandiflorus*, *Nauclea orientalis*, *Barringtonia acutangula* and *Ficus* spp..

**Blackwood River**

Most of the south-west of Western Australia, including the Blackwood catchment, is within the South-West Botanical Province which contains the Roe, Avon (upper catchment) and Darling (middle and lower catchment) Botanical Districts (Beard 1981). Species names have been updated from State Herbarium records where appropriate. The majority of the catchment is composed of eucalypt woodlands or forest with a mixed shrub understorey and with the most common families being *Myrtaceae*, *Proteaceae* and *Papilionaceae*. The vegetation composition and density is strongly influenced by landforms, soils and climate. The eastern extent of the catchment is a mosaic of shrub-heath on sandplains, mallee on the slopes and woodland in the valley floors. The dominant mallee species are *Eucalyptus eremophila*, *E. angustissima* and *E. transcontinentalis* with a shrub understorey dominated by *Melaleuca* spp.. Low woodlands are
chiefly composed of *E. gardneri* and *E. falcata* with *E. celastroides* on laterite ridges and a sparse mixed shrub understorey including *Melaleuca* spp. and *Acacia* spp.. There can also be a mid-storey of *Acacia ecuminata*, *A. microbotyra*, *Allocasuarina heugeliana* and *Hakea preissii*. On plateau areas with heavy soils which may be subject to waterlogging there is an association of *E. wandoow* and *E. gardneri*. Further west of this area there is heath vegetation (dominated by *Dryandra* spp) on laterite residuals, while in undulating country there are woodlands of *E. wandoow* on the upper slopes, *E. loxophleba* on the mid-slopes and *E. salmonophloia* and *E. longicornis* on the heavier soil flats. Along the major creeks *E. rudis* is the dominant tree with *Callistemon phoeniceus* forming a major part of the understorey. Where creeks are salty *Casuarina obesa* and *Melaleuca hamulosa* are common with a shrubby understorey of salt tolerant species including *Halosarcia lepidosperma* and *Sarcocornia blackiana*. In the middle catchment the principal elements include woodlands of *Eucalyptus wandoow* on laterite residuals, with *E. wandoow* and *E. loxophleba* on undulating country and *E. loxophleba* and *E. occidentalis* on sandy patches. *E. astringens* and *E. marginata* are found on laterite breakaways, with *E. rudis* and *Melaleuca rhaphiophylla* occurring along creek lines. Further west and south, open forest of *E. marginata* occurs on the laterite hill tops, with *E. wandoow* woodlands on the lower slopes and scattered *Corymbia calophylla* in both areas. On the poorer drained soils *E. occidentalis* occurs with *E. rudis* on the drainage lines. In the lower catchment, particularly along the Darling scarp, are large areas of *E. marginata* and *C. calophylla* forest where laterite or ironstone gravels are present. Along riverbanks *E. rudis*, with *M. rhaphiophylla* as a mid-storey, forms a fringing forest. On sandier soils closer to the coast are areas of *E. marginata* and *Banksia* spp. woodlands, with low woodlands of *Banksia* spp. and *Melaleuca preissiana* where drainage is poor.

**Land Use**

**Ord River**

The East Kimberley region and the area around the Ord River were settled in the 1880's when cattlemen brought stock from Queensland, with some of the earliest leases taken up around the
Ord River plains at Argyle Downs and Ord River Station (Stewart 1970). Cattle numbers expanded rapidly after introduction because of the abundant water and productive pasture, with cattle becoming concentrated on the river frontage where water was readily available. The grasslands, which had evolved through selective grazing by marsupials, could not withstand the greatly increased grazing pressure associated with open range production of hard-hoofed cattle (Fitzgerald 1967). By the 1930’s large areas of land were severely degraded and eroded by overgrazing and this was exacerbated by the effects of drought, fire and feral animals (Fitzgerald 1967). Bare soil surfaces were exposed to the effects of wind and water erosion, particularly the friable calcareous soils, contributing enormous sediment loads to the Ord River. With the contemplation of the building of a dam on the river for irrigation, concerns were raised about the effect of high sediment loads on the storage capacity of the reservoir and a rehabilitation programme on the Ord River plains was instigated in the early 1960’s (Fitzgerald 1967). Land was resumed by the government, stock removed and a revegetation plan implemented. This regeneration programme has seen the establishment in many areas of the introduced grasses *Cenchrus ciliaris* and *C. setiger* and the shrub *Aerva javanica*, but many areas are still without vegetation cover (de Salis 1993). At present cattle grazing for beef production continues throughout the Ord River catchment, except in the area of Purnululu National Park in the south-west.

The Ord river is also affected by the construction of two dams along its length. The diversion dam was constructed in the early 1960s near the town of Kununurra as a pilot dam to test the viability of an irrigated agricultural industry on the lower Ord floodplain. This flooded the section of river above the dam to Carlton Gorge some 45 km upstream, turning it into a reservoir and drowning large areas of riparian vegetation. The river below the dam now runs year round at a fairly constant level, with some input of floodwaters from the Dunham River in the wet season. This area contains the Ord River irrigation scheme, where 15,000 hectares of land on the Ivanhoe plains are irrigated for agriculture including sugar cane, fruit and vegetable production. In 1972, a large dam was constructed at Carlton Gorge to allow the envisaged expansion of the
irrigation scheme. This resulted in the flooding of the lower, northern section of the Ord plains to form Lake Argyle (Water & Rivers Commission 1997).

Blackwood River

The eastern area of the Blackwood catchment in the Narrogin and Wagin districts was sparsely settled in the late 1890's with the main activity being livestock grazing on the native vegetation. Greater settlement and land clearing for agriculture occurred after 1890 with the building of the railway (McArthur 1991). With further settlement, the expansion of sheep production and the use of fertilisers to improve nutrient deficient soils to allow cereal cropping, the area was gradually extensively cleared of native vegetation so that in many areas <10% of the native vegetation remains. The area has extensive, highly saline soils so that secondary salinity, particularly in the lower part of the landscape, is a major problem. Many parts of the middle catchment were settled in the 1880's where the first commercial enterprise was native sandalwood (Santalum spicatum) harvesting. The eastern part of the middle catchment around Boyup Brook has been extensively cleared for improved pasture, mainly for sheep production and with some cropping for fodder. Recently, there has been an increase in plantation forestry on cleared farmland, with Eucalyptus globulus for paper pulp and Pinus pinaster for timber. Much of the land consists of nutrient poor soils which require fertilising to maintain productivity. This region is also susceptible to waterlogging and secondary salinisation, through rising groundwater, in the lower sections of the landscape. To the west, the main activity is timber harvesting in the native E. marginata (Jarrah) forest. Native vegetation on the fertile soils of the Blackwood valley has been extensively cleared for plantations of Pinus radiata (for timber production) as well as for livestock grazing and small areas of orchards. The coastal plain of the lower catchment was settled in the 1830's around Augusta at the mouth of the Blackwood River. Large scale clearing for agriculture took place in the 1920's and was stepped up in the 1950's. This was mainly for improved pasture for dairy and beef cattle with soils regularly treated with fertilisers to correct nutrient deficiencies. There was some timber harvesting in earlier years of karri (E. diversicolor) around Karridale and some planting of Pinus spp. plantations.
CHAPTER 4

DESCRIPTION OF RIPARIAN VEGETATION WITH REGARD TO FLORISTICS AND LIFE FORM

Introduction

Plant communities in the riparian zone are highly productive and can be more species rich than adjacent upland sites (Gregory et al. 1991). Indeed, riparian vegetation is rarely homogenous and usually reflects the effects of disturbance that has created longitudinal and transverse environmental gradients which have led to the formation of complex vegetation communities and high species diversity (Gregory et al. 1991). The riparian zone has also been considered an ecotone where different plant communities overlap, combining elements of both communities to produce an area of higher species richness (Bretschko 1995). In the riparian zone edaphic and lotic processes can both influence community structure and composition. Vegetation patterns, and therefore species richness and diversity, in the high disturbance riparian zone are strongly influenced by species colonising ability (White 1979). In addition, plant colonisation results from the interactions between existing vegetation, spatial patterns in the environment and morphology and physiology of propagules (Glenn-Lewin & van der Maarel 1992). Therefore, to understand recruitment patterns on the rivers assessed in this study, knowledge of the floristics and structure of the specific vegetation communities that occur is required. There have been no specific studies of the vegetation communities on the Blackwood or Ord rivers, only broad scale assessments which describe the vegetation in a very general sense (Beard 1979; Beard 1981). This Chapter provides a description of the vegetation in the riparian zone at the study sites on the Blackwood and Ord rivers in terms of floristics and the major life forms.
Describing the range of different plant life forms that occur is a convenient way of identifying the important functional groups in the riparian zone of these rivers. These groups may be important for the ecological functioning of the system (Hobbs 1992). For example, overstorey trees and emergent macrophytes may have a critical role as a functional group through soil stabilisation and nutrient cycling. Functional groups that have been suggested for terrestrial plants have been based on phenology, life form or life history (Armstrong 1993). In Australian grasslands, life form was the most useful characteristic for gauging community response to disturbance (McIntyre et al. 1995). In the specific environments of the riparian zone particular life forms may be more successful. For example, in highly disturbed environments annual species are favoured due to their fast growth rates and early and prolific seed set (Grime 1979). In contrast, high stress environments (as a result of drought or low nutrients for example) tend to have more perennial species which are generally slow growing, take a long time to reach reproductive maturity and are frugal with resources. Flooding impacts on plants can be described by both disturbance and/or stress depending on intensity of flow or duration of inundation. Therefore the abundance of the different life forms on each river can provide an insight into whether disturbance or stress is the most important ‘driver’ of vegetation community dynamics. Species life history traits, functional groups or vital attributes have been widely used for modelling succession and species composition after disturbance (Brown 1992). Functional grouping of species can also be useful in identifying species tolerance to one or more forms of disturbance, such as flooding and grazing as occurs on some of the Blackwood River sites and all of the Ord River sites. The three main categories of vital attributes used by Noble and Slatyer (1980) included; method of persistence and arrival after disturbance, ability to establish and grow in a developing community and time taken for species to reach critical life stages.

This chapter provides an introduction to the floristics of the vegetation found in the riparian zone on the Blackwood and Ord rivers and investigates the environmental factors that affect the floristics between and within sites. It places species in functional groups based on life form in order to develop an insight into which aspects of the vegetation community are important in the
establishment of riparian vegetation on these rivers. This enables identification of particular features of the vegetation and the riparian environment that influence regeneration. These features include the effects of disturbance and stress, the fate of propagules and the population dynamics of important species, all of which will be explored in greater detail in the following chapters.

Methods

Vegetation surveys were completed in July and August 1997 on the Ord River and in October and November 1997 on the Blackwood River. Descriptions of the surveyed sites on both rivers is given in Chapter 3 and location of each site is shown in Figures 3.1 & 3.2. At each site two transects perpendicular to the river were established, transect length varying for each site depending on the width of the riparian zone. Along each transect, five 10 metre x 10 metre plots were established at variable distances located to coincide with the bands of vegetation, giving a total of 10 plots at each site. All plants rooted within each plot were identified and an estimate of percentage cover was made, where cover is the vertical crown or shoot projection per species.

Species richness and diversity were measured for each plot. Diversity is derived from species richness (number of species within a plot) and evenness (relative abundance). The index of diversity used here was the Shannon-Weiner Index (H'):

\[ H' = \sum p_i \log p_i \]

where \( p \) = the proportion of cover or abundance of a species and \( \log \) is the natural logarithm (Kent & Coker 1992). The Shannon-Weiner index makes the assumption that individuals are sampled from an infinite population. It is based on predicting the likelihood of a particular species being sampled, the higher the value indicating the less certainty of predicting a randomly selected sample and therefore higher diversity. Species evenness (J) can also be calculated from diversity and is an expression of the observed diversity as a proportion of the
maximum possible diversity. An evenness of 1 equates with maximum evenness, with all species having the same abundance or cover.

A description of the soil profile to a depth of 0.5 m was made for each quadrat and soil samples were taken over a depth of 0 - 10 cm for analysis of particle size using the hydrometer method (Page et al. 1986). As there is a gradient of increasing salinity with distance upstream on the Blackwood River, soil electrical conductivity was also measured in each quadrat using a 1:5 soil to de-ionised water solution (Page et al. 1986). Salinity levels on the Ord River are low, and soil salinity was not measured as it was not considered an important environmental attribute that may affect vegetation community composition. A species importance value (IV) was allocated for all species occurring in plots along the transects. This was calculated for each site as IV = relative frequency + relative occurrence + relative cover. Nomenclature used for plant species names followed Green (1985) and Marchant et al. (1987) for the Blackwood River species and Wheeler et al. (1992) for the Ord River species. Species identification and nomenclature were verified with Western Australian Herbarium records.

To identify the functional groups that are important in the riparian zone of these rivers, all plant species were categorised according to life form (i.e. trees, shrubs, perennial herbs, perennial grasses, annual grasses, annual herbs or lianas). Life form groups can, in turn, be categorised by the system proposed by Raunkaier (1934) (see Mueller-Dombois & Ellenberg 1974), based on the height above ground of the perennating organ and on the assumption that species morphology is related to climate (Kent & Coker 1992). Life form groups used here relate to Raunkaier categories thus: trees and shrubs = phanerophytes; perennial herbs = chamaephytes, hemicryptophytes and geophytes; perennial grasses = hemicryptophytes; annual herbs and grasses = therophytes; and lianas = lianas.

Multivariate analysis of the floristic and environmental data from the plots using Detrended Correspondence Analysis (DCA), detrending by segments (ter Braak 1987), was performed to provide a summary of plant species composition and abundance. This enabled a quantitative
comparison of plots so that floristic differences could be identified. DCA axes are scaled in units of average standard deviation (SD) of species turnover where a 50% change in quadrat composition occurs at around 1 SD (Kent & Coker 1992). DCA is an indirect ordination technique designed to overcome the problems of other types of ordination, namely the arch effect and compression of points at the ends of the first axis (Hill & Gauch 1980). DCA has been criticised as being inelegant and arbitrary and performing poorly with skewed species distributions (van Groenewoud 1992; Palmer 1993). Despite these criticisms, it is considered an effective, powerful and robust indirect ordination technique suitable for ecological data (Peet et al. 1988; Kent & Coker 1992). The ordination resulting from DCA is a product of the variability in species data between plots. The floristic differences between sites can be represented by the relative position of plots on the four floristic axes examined. Sites with similar floristics will be positioned close together. The eigenvalues given for each axis in the DCA analysis provide an estimate of the proportion of the variation in the data explained by each axis so that an axis with a low eigen value is unlikely to be readily interpretable or ecologically meaningful. In this Chapter, only those axes that explain the greatest proportion of the variation in the data are presented in the results and related to the floristics as well as to environmental and life form variables. Environmental variables, floristics and lifeform variables were correlated with the values for the important DCA axes after ordination analysis. This gives an indication which of these attributes are influencing the position of each plot along that particular DCA axis. Vegetation plot variables that were correlated with the DCA axes values included species richness, percentage of exotic species and percentage of each of the different life form groups. Environmental variables correlated with DCA axes values included mean annual rainfall, soil type, height (elevation in metres) above base flow water level and distance (in metres) from low water level.
Results

Floristic structure
Total species richness for the six Blackwood River sites was 156 species, with a mean of 41.2±8.7 (SE) per site and ranging from 65 species at Site B2a to 15 species at Site B2b (Table 4.1a). There was a total of 41 families represented across the sites, the most abundant family being Poaceae with 27 species from 21 genera (19 exotic species). Other well represented families included Asteraceae with 12 species in 12 genera (eight exotic species), Cyperaceae with 12 species in seven genera and Myrtaceae with 13 species in six genera. Species richness, diversity and evenness was greatest at the sites undisturbed by grazing. The mean species diversity (H) overall for the Blackwood River sites was 2.2±0.5 and species richness was 40.7±8 but for the ungrazed sites alone species diversity and richness was 2.9 and 56 respectively. Species richness increased with increasing distance from the river for both grazed and ungrazed sites, with a sharp decline in species richness in plots closest to the water’s edge (Figure 4.1a). Exotic species were common, particularly at the sites subject to sheep grazing, making up 67% of species and 82% of cover, while at the sites not affected by grazing exotic species contributed 33% of species and 36% of cover. The majority of the exotic species were annual herbs and grasses from the families Poaceae and Asteraceae. A full list of species found on both rivers is given in Appendix I. The general structure of the riparian vegetation on the Blackwood River is of an overstorey of almost exclusively Eucalyptus rudis throughout the profile and at all sites. Other eucalypts such as E. wandoo, E. marginata and Corymbia calophylla occurred in areas which are rarely flooded, usually some distance from the river. Casuarina obesa tended to replace E. rudis in the upper reaches, in areas affected by secondary salinisation such as at Sites B3a&b. There is a mid-storey of Melaleuca rhaphiophylla fringing the area nearest the water’s edge, with other mid-storey species occurring further along the profile at higher elevations including Banksia seminuda, Kunzea ericifolia, Jacksonia sternbergiana and Dodonea viscosa. The understorey consists of various
Table 4.1a: Summary of floristic data and species origin for the Blackwood River sites. Data are from ten 10m x 10m quadrats on two transects at each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species Richness</th>
<th>Species Diversity (H)</th>
<th>Species Eveness (J)</th>
<th>Origin</th>
<th>No. spp</th>
<th>Cover (%)</th>
<th>No. spp</th>
<th>Cover (%)</th>
<th>No. spp</th>
<th>Cover (%)</th>
<th>No. spp</th>
<th>Cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>B1a</td>
<td>65</td>
<td>3.1</td>
<td>0.74</td>
<td>Native</td>
<td>53</td>
<td>82.3</td>
<td>8</td>
<td>5.0</td>
<td>41</td>
<td>46.0</td>
<td>4</td>
<td>0.7</td>
</tr>
<tr>
<td>B1b (grazed)</td>
<td>38</td>
<td>2.57</td>
<td>0.71</td>
<td>Native</td>
<td>12</td>
<td>21.3</td>
<td>30</td>
<td>68.0</td>
<td>27</td>
<td>43.0</td>
<td>11</td>
<td>43.3</td>
</tr>
<tr>
<td>B2a</td>
<td>68</td>
<td>3.13</td>
<td>0.74</td>
<td>Native</td>
<td>8</td>
<td>5.0</td>
<td>41</td>
<td>46.0</td>
<td>4</td>
<td>0.7</td>
<td>20</td>
<td>63.0</td>
</tr>
<tr>
<td>B2b (grazed)</td>
<td>15</td>
<td>1.16</td>
<td>0.43</td>
<td>Native</td>
<td>13</td>
<td>37.1</td>
<td>15</td>
<td>44.0</td>
<td>13</td>
<td>47.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B3a</td>
<td>35</td>
<td>2.38</td>
<td>0.67</td>
<td>Exotic</td>
<td>13</td>
<td>37.1</td>
<td>15</td>
<td>44.0</td>
<td>13</td>
<td>47.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>B3b (grazed)</td>
<td>26</td>
<td>0.83</td>
<td>0.26</td>
<td>Exotic</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

Table 4.1b: Summary of floristic data and species origin for the Ord River sites. Data are from ten 10m x 10m quadrats on two transects at each site.

<table>
<thead>
<tr>
<th>Site</th>
<th>Species Richness</th>
<th>Species Diversity (H)</th>
<th>Species Eveness (J)</th>
<th>Origin</th>
<th>No. spp</th>
<th>Cover (%)</th>
<th>No. spp</th>
<th>Cover (%)</th>
<th>No. spp</th>
<th>Cover (%)</th>
<th>No. spp</th>
<th>Cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>O1</td>
<td>40</td>
<td>1.3</td>
<td>0.57</td>
<td>Native</td>
<td>31</td>
<td>52.0</td>
<td>19</td>
<td>61.6</td>
<td>20</td>
<td>34.16</td>
<td>17</td>
<td>16.9</td>
</tr>
<tr>
<td>O2</td>
<td>22</td>
<td>0.63</td>
<td>0.37</td>
<td>Native</td>
<td>9</td>
<td>46.0</td>
<td>3</td>
<td>0.4</td>
<td>8</td>
<td>18.9</td>
<td>14</td>
<td>52.1</td>
</tr>
<tr>
<td>O3</td>
<td>25</td>
<td>1.9</td>
<td>0.59</td>
<td>Native</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O4</td>
<td>25</td>
<td>1.96</td>
<td>0.61</td>
<td>Exotic</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>O5</td>
<td>30</td>
<td>2.01</td>
<td>0.59</td>
<td>Exotic</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
</tbody>
</table>
Figure 4.1: Change in mean (±SEM) species richness in 10m x 10m plots with distance from the river for combined sites on a) Blackwood River and b) Ord River. Note change of vertical scale for a & b. n = the number of plots at each distance.
Figure 4.2: Schematic diagrams showing the distribution of species at a) Site 2a on the Blackwood River and b) Site 05 on the Ord River.
shrub species in less frequently flooded areas such as *Melaleuca incana*, *Hypocalymma angustifolium* and *Acacia saligna*, as well as perennial herbs such as *Chorizandra enodis*, *Carex appressa*, *Lepidosperma drummondii*, *Conostylis aculeata* and *Patersonia occidentalis*. Near the water's edge sedges such as *Juncus* spp. and *Lepidosperma* spp. were common as well as exotic species such as the annual herb *Atriplex prostrata* (in the more saline reaches at Sites B2 and B3) and the perennial grass *Cynodon dactylon*. In areas subject to livestock grazing, the understorey tends to become dominated by exotic grasses such as *Ehrharta* spp. and *Lolium rigidum*. A schematic diagram showing the distribution of species along a profile at Site B2a is shown in Figure 4.2a.

At the five Ord River sites a total of 98 species were recorded. There were a total of 36 families represented across the sites. The most common families were Poaceae, with 16 species in 12 genera, Cyperaceae with nine species in six genera and Papilionaceae with seven species in 4 genera. A summary of floristic data and species origin for the Ord River sites is given in Table 4.1b. Across all sites, mean species richness was 27.8±3.4 and species diversity was 1.9±0.05. Compared with the Blackwood sites these values are relatively low and indicate the tendency of particular species to dominate. As occurred at the Blackwood River sites, species richness increased with increased distance from the river, with a large decline in species in plots closest to the water (Figure 4.1b). Exotic species comprised a mean of 28% of species and 34% of cover with Site O2 (Lake Kununurra) and Site O3 (Behm River) having the lowest proportion of exotic species. Structure of the riparian vegetation at the Ord River sites consisted of a much greater diversity in the overstorey, with common species including *Melaleuca leucadendra*, *Cathormion umbellatum*, *Barringtonia acutangula* and *Nauclea orientalis* occurring nearest the water's edge and *Eucalyptus camaldulensis*, *Lophostemon grandisflorus* and *Terminalia platyphylla* usually occurring further from the low water mark. Higher up the bank, in areas which are infrequently flooded, *Eucalyptus gymnoteles* was found and at the fringes of the riparian zone *Eucalyptus houseana* occurred with *Lysiphyllum cunninghamii*. Common mid-storey species included *Ficus coronulata*, *Flueggea virosa* and the exotic *Parkinsonia aculeata* in areas close to the water and *Acacia holosericea* higher up the bank. The understorey tended to be dominated by perennial
grasses at all sites. In particular, the exotic *Cenchrus* spp. were dominant at the upstream sites (Sites 03, 04 & 05) mainly higher up the bank, and the perennial grass *Cynodon dactylon* was dominant in the more frequently flooded areas close to the water. The perennial herb *Achyranthes aspera* was a common understorey species at all sites, with the shrub *Crotalaria* spp. found at higher elevations. A schematic diagram showing the distribution of species along a profile at Site O5 is presented in Figure 4.2b.

**Floristic patterns**

Site ordination (DCA) of floristic data for the vegetation quadrats on the Blackwood River sites showed a separation of quadrats along the first floristic axis and, to a lesser extent, the second floristic axis with 88% of the variance in these first two axes (Figure 4.3a). The length of the axes are around seven and six standard deviations, indicating large floristic differences between quadrats at the extremes of the axes. Along the first axis a geographic gradient from downstream to upstream sites (Site B1 to B3) can be seen. This can be represented by rainfall changes across the sites with a strong negative correlation between mean annual rainfall and DCA axis 1 \( (r = 0.72, p<0.001) \) and with mean annual rainfall decreasing along this axis. Soil salinity was also strongly correlated with DCA axis 1 \( (r = 0.792, p<0.001) \), indicating the change to more salt tolerant species, especially in quadrats at Site B3. This also reflects the trend of increasing salinity from downstream to upstream which is documented for the Blackwood River (Morrissy 1974). The separation of quadrats along the second DCA axis appears to be between grazed and ungrazed sites. There was a positive correlation between species richness of quadrats and DCA axis 2 \( (r = 0.623, p<0.001) \) and the proportion of native perennial herbs and DCA axis 2 \( (r = 0.524, p<0.001) \), with species richness and proportion of native perennial herbs increasing along this axis. There was a negative correlation \( (r = -0.542, p<0.001) \) with proportion of exotic species decreasing along DCA axis 2. For ungrazed sites there was a positive correlation between DCA axis 2 and distance from the water’s edge \( (r = 0.439, p = 0.01) \), showing a change in floristics with distance from the river. It indicates the zonation of the
Figure 4.3: Detrended Correspondence Analysis (DCA) showing scatter of plots along the first two floristic axes for a) Blackwood River with numbers corresponding to the various sites along the river with Site 1 the most downstream site and Site 3 the most upstream site with a = ungrazed sites and b = grazed sites and b) Ord River with Site 1 the most downstream site and Site 5 the most upstream site.
vegetation, with fewer species and increased proportion of annuals and exotic species closer to the water's edge and the occurrence of flood tolerant species such as sedges.

Ordination by DCA for the Ord River sites also showed a separation of sites along the first DCA axis according to the geographical distribution of sites from downstream (Site 01) to upstream (Site 05) (Figure 4.3b). This can be represented by decreasing rainfall across the sites, with a negative correlation between mean annual rainfall and DCA axis 1 \((r= -0.47, p = 0.051)\). For the Ord River quadrats 78% of the variance could be attributed to the first two axes and the length of the axes are around 6 and 5 standard deviations indicating large floristic differences between quadrats at the extremes of these axes. There was also a positive correlation between DCA axis 1 and distance from the water’s edge \((r = 0.437, p = 0.05)\), with distance increasing along DCA axis 1. In addition, distance was positively correlated with elevation \((r = 0.609, p<0.001)\), species richness \((r = 0.332, p<0.001)\) and percentage of perennial herbs \((r = 0.766, p<0.001)\) and negatively correlated with soil clay content \((r = -0.565, p<0.001)\). Proportion of annual species in plots was positively correlated with DCA axis 2 \((r = 0.357, p = 0.054)\). None of the floristic or environmental attributes tested for each quadrat were correlated with DCA axis 3 or 4.

**Life form groups**

Life form groups for the Blackwood River sites are averaged for number of species and cover in Figures 4.4a&b. Annual and perennial herbaceous species were most abundant in terms of number of species, whereas annual grasses had the greatest cover, with cover of shrubs and annual herbs also being prominent. For individual sites, shrubs gave the highest values of both number of species and cover and tree species were highest for cover at the ungrazed sites. Annual grasses were dominant in terms of cover at grazed sites. This included pasture weeds such as *Lolium rigidum* at all sites and *Hordeum leporinum* in the upstream (more saline) sites (Sites B2 & B3) (Table 4.2a). The overstorey was dominated by only a few species on the Blackwood River, with cover of these generally high across all sites. The dominant tree species were *Eucalyptus rudis* and *Melaleuca rhaphiophylla* with *Casuarina obesa* dominant at the saline upstream site (Site B3).
Ord River sites showed a spread of life form types in terms of numbers of species, with trees and shrubs being the most common, but in terms of cover sites were dominated by trees and perennial grasses (Figure 4.4c&d). This trend was common across all sites except for Site O2 (Lake Kununurra) where perennial herb species (in particular the emergent macrophyte *Typha domingensis*) replaced perennial grasses as the second most prominent life form (Table 4.2b). There was a greater richness of overstorey species at the Ord River sites, with the families Myrtaceae (*Eucalyptus* spp., *Melaleuca* spp. and *Lophostemon grandiflorus*), Moraceae (*Ficus* spp.) and Combretaceae (*Terminalia* spp.) being represented by more than one species. The understorey was much less diverse in comparison with the understorey on the Blackwood River sites.

The five top scoring species on the Blackwood River in terms of importance value were all exotic species (Table 4.3a). These were common pasture weeds and included species which are widespread in south-western Australia such as the annual grass *Lolium rigidum* (rye grass) and the annual herb *Romulea rosea* (guildford grass). The exotic perennial grass *Cynodon dactylon* (common couch) is a cosmopolitan weed that occurs throughout Australia. The perenniating organ is a rhizome and couch is a common invader of bare, disturbed sites and is particularly common in the riparian zone. The annual grass *Hordeum leporinum* (barley grass) is somewhat salt tolerant and becomes more dominant in the middle to upper sections of the river (Sites B2 & B3). As for the native species, *Casuarina obesa* dominates in the saline conditions of Site B3 and only occurs at this site. The tree species *Eucalyptus rudis* occurs at all sites and *Melaleuca rhaphiophylla* occurs at all except the saline site B3. These two species are the most common overstorey species in the riparian zone on the Blackwood River. The other two most important native species are sedges in the Cyperaceae family and many of these are common in damp to waterlogged conditions.
Figure 4.4: Number of species and % cover of the major life form types on the Blackwood River (a & b) and Ord River (c & d). Values are means (±SEM) for six sites on the Blackwood River and five sites on the Ord River.
Table 4.2a: Summary of life form groups at the Blackwood River sites.

<table>
<thead>
<tr>
<th>Life Form</th>
<th>Site B1a (grazed)</th>
<th>Site B1b (grazed)</th>
<th>Site B2a (grazed)</th>
<th>Site B3a (grazed)</th>
<th>Site B3b (grazed)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. spp</td>
<td>Cover (%)</td>
<td>No. spp</td>
<td>Cover (%)</td>
<td>No. spp</td>
</tr>
<tr>
<td>Tree</td>
<td>2</td>
<td>20.9</td>
<td>1</td>
<td>10.1</td>
<td>3</td>
</tr>
<tr>
<td>Shrub</td>
<td>20</td>
<td>37.7</td>
<td>2</td>
<td>4.4</td>
<td>13</td>
</tr>
<tr>
<td>Annual herb</td>
<td>20</td>
<td>11.9</td>
<td>16</td>
<td>25.4</td>
<td>22</td>
</tr>
<tr>
<td>Perennial herb</td>
<td>16</td>
<td>14.5</td>
<td>7</td>
<td>7.2</td>
<td>15</td>
</tr>
<tr>
<td>Annual grass</td>
<td>4</td>
<td>16</td>
<td>8</td>
<td>12.3</td>
<td>9</td>
</tr>
<tr>
<td>Perennial grass</td>
<td>3</td>
<td>2.6</td>
<td>3</td>
<td>22.1</td>
<td>6</td>
</tr>
<tr>
<td>Lianas</td>
<td>0</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 4.2b: Summary of life form groups at the Ord River sites.

<table>
<thead>
<tr>
<th>Life Form</th>
<th>Site O1</th>
<th>Site O2</th>
<th>Site O3</th>
<th>Site O4</th>
<th>Site O5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. spp</td>
<td>Cover (%)</td>
<td>No. spp</td>
<td>Cover (%)</td>
<td>No. spp</td>
</tr>
<tr>
<td>Tree</td>
<td>8</td>
<td>55</td>
<td>4</td>
<td>48</td>
<td>9</td>
</tr>
<tr>
<td>Shrub</td>
<td>5</td>
<td>4</td>
<td>4</td>
<td>13</td>
<td>7</td>
</tr>
<tr>
<td>Annual herb</td>
<td>7</td>
<td>0.7</td>
<td>3</td>
<td>9</td>
<td>1</td>
</tr>
<tr>
<td>Perennial herb</td>
<td>11</td>
<td>9</td>
<td>8</td>
<td>30.1</td>
<td>3</td>
</tr>
<tr>
<td>Annual grass</td>
<td>0</td>
<td>-</td>
<td>0</td>
<td>-</td>
<td>0</td>
</tr>
<tr>
<td>Perennial grass</td>
<td>5</td>
<td>29</td>
<td>0</td>
<td>-</td>
<td>4</td>
</tr>
<tr>
<td>Lianas</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>
Couch (C. dactylon) was also the second highest species in terms of importance value for the Ord River sites (Table 4.3b). The two most common overstorey species in the riparian zone of the Ord River, Eucalyptus camaldulensis and Melaleuca leucadendra, were the highest scoring native species and were found at all sites. The exotic perennial buffel grasses Cenchrus ciliaris and C. setiger were introduced as part of the rehabilitation programme on the upper Ord at Old Ord River Station. These species tended to occupy the outermost section of the riparian zone and the frontage lands beyond. The exotic tree legume Parkinsonia aculeata is a common woody weed throughout warmer parts of Australia and is particularly common along watercourses (Wheeler et al. 1992).

Table 4.3a: Highest scoring native and exotic species according to their importance value for the Blackwood River sites. Importance value = relative frequency + relative cover + relative occurrence.

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency (%)</th>
<th>Cover (%)</th>
<th>Importance value</th>
<th>Life form(^1)</th>
<th>Dispersal mode(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lolium rigidum(^*)</td>
<td>67</td>
<td>9.2</td>
<td>18.42</td>
<td>ag</td>
<td>w</td>
</tr>
<tr>
<td>Cynodon dactylon(^*)</td>
<td>29</td>
<td>6.1</td>
<td>11.42</td>
<td>pg</td>
<td>w</td>
</tr>
<tr>
<td>Romulea rosea(^*)</td>
<td>46</td>
<td>3.4</td>
<td>9.76</td>
<td>ah</td>
<td>un</td>
</tr>
<tr>
<td>Briza maxima(^*)</td>
<td>32</td>
<td>3.7</td>
<td>9.21</td>
<td>ag</td>
<td>w</td>
</tr>
<tr>
<td>Hordeum leporinum(^*)</td>
<td>21</td>
<td>4.8</td>
<td>8.44</td>
<td>ag</td>
<td>ve</td>
</tr>
<tr>
<td>Casuarina obesa</td>
<td>24</td>
<td>4.7</td>
<td>8.42</td>
<td>t</td>
<td>w</td>
</tr>
<tr>
<td>Melaleuca rhaphiophylla</td>
<td>21</td>
<td>2.5</td>
<td>6.97</td>
<td>t</td>
<td>w</td>
</tr>
<tr>
<td>Eucalyptus rudis</td>
<td>51</td>
<td>1.1</td>
<td>6.71</td>
<td>t</td>
<td>w</td>
</tr>
<tr>
<td>Juncus pallidus</td>
<td>32</td>
<td>1.6</td>
<td>5.14</td>
<td>ph</td>
<td>un</td>
</tr>
<tr>
<td>Isolepis cernua</td>
<td>32</td>
<td>0.3</td>
<td>4.0</td>
<td>ah</td>
<td>w</td>
</tr>
</tbody>
</table>

\(^*\) Exotic species

\(^1\) Life forms are ag = annual grass; pg = perennial grass; ah = annual herb; ph = perennial herb; sh = shrub; t = tree.

\(^2\) Dispersal modes are w = wind; un = unknown; wa = water; ve = vertebrate external; vi = vertebrate internal.

Table 4.3b: Highest scoring native and exotic species according to their importance value for the Ord River sites. Importance value = relative frequency + relative cover + relative occurrence.

<table>
<thead>
<tr>
<th>Species</th>
<th>Frequency (%)</th>
<th>Cover (%)</th>
<th>Importance value</th>
<th>Life form(^1)</th>
<th>Dispersal mode(^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Melaleuca leucadendra</td>
<td>65</td>
<td>15.2</td>
<td>42.2</td>
<td>t</td>
<td>w</td>
</tr>
<tr>
<td>Cynodon dactylon(^*)</td>
<td>42</td>
<td>11.2</td>
<td>30.4</td>
<td>pg</td>
<td>w</td>
</tr>
<tr>
<td>Eucalyptus camaldulensis</td>
<td>67</td>
<td>7.2</td>
<td>28.6</td>
<td>t</td>
<td>w</td>
</tr>
<tr>
<td>Cenchrus ciliaris(^*)</td>
<td>21</td>
<td>4.5</td>
<td>14.1</td>
<td>pg</td>
<td>w</td>
</tr>
<tr>
<td>Cenchrus setiger(^*)</td>
<td>17</td>
<td>5.5</td>
<td>13.4</td>
<td>pg</td>
<td>w</td>
</tr>
<tr>
<td>Flueggea virosa</td>
<td>13</td>
<td>2.7</td>
<td>8.8</td>
<td>sh</td>
<td>vi</td>
</tr>
<tr>
<td>Lophostemon grandiflorus</td>
<td>23</td>
<td>1.7</td>
<td>8.7</td>
<td>t</td>
<td>w</td>
</tr>
<tr>
<td>Parkinsonia aculeata(^*)</td>
<td>21</td>
<td>0.5</td>
<td>8.3</td>
<td>t</td>
<td>un</td>
</tr>
<tr>
<td>Achyranthes aspera</td>
<td>15</td>
<td>1.5</td>
<td>8.1</td>
<td>ph</td>
<td>ve</td>
</tr>
</tbody>
</table>
Discussion

Floristic structure

For the ungrazed sites on the Blackwood River and all sites on the Ord River, species richness and species diversity were fairly low, indicating the dominance of species which are well adapted to the particular conditions that prevail in the riparian zone. These adaptations include tolerance to high disturbance by flooding, scouring and high stress through waterlogging and periodic dry conditions (Szaro 1990). Variations in species diversity in riparian communities have been considered to be the result of the rate of disturbance (Ward & Stanford 1983) and along disturbance gradients in general, species richness has been reported to be highest at intermediate levels of disturbance (Grime 1979; Huston 1979). However, species diversity may also be influenced by other factors such as productivity (Tilman 1986). In a riparian wetland, species richness has been best described in terms of gradients of disturbance, productivity and spatial heterogeneity (Pollock et al. 1998). For both rivers, species richness tended to increase with distance from the river and therefore probably with reduced frequency of flooding. In particular, a sharp decline in species richness was seen in plots near the water's edge in the littoral zone, which was subject to the greatest flooding disturbance and greatest stress from inundation and waterlogging. The results indicate that for these Western Australian rivers, the riparian zone is not an area of high species richness or diversity and does not follow the generally accepted idea of the riparian zone being an ecotone and of higher species richness as the river collects propagules of species throughout the watershed (Nilsson et al. 1994; Bretschko 1995). Greater species richness in upland sites adjacent to the riparian zone has been found for other rivers in south-western Australia (Hancock et al. 1996).

Life forms

Structure of the vegetation was contrasting on the two rivers with the greatest diversity on the Ord River occurring in the number of overstorey species and the understorey tending to be dominated by only a few species. Species diversity on the Blackwood River was most influenced by the understorey which, particularly on the ungrazed sites, included a high diversity of shrub
species. The overstorey was composed almost exclusively of *Eucalyptus rudis* which is taxonomically similar to *E. camaldulensis* and occupies a similar niche in wetlands and rivers in south-western Australia (Boland *et al.* 1989). The prevalence of the different life forms also differed sharply between the two rivers, with a more diverse structure on the Blackwood River and a number of shrubs, perennial and annual herbs and annual grasses. This differed between grazed and ungrazed sites, with shrubs more dominant at the ungrazed sites and annuals more common in the grazed sites. This is related to the increased disturbance on the grazed sites favouring ruderal species, whereas at the ungrazed sites the prevalence of stress tolerators such as shrubs indicate that stresses brought about by periods of inundation or drought are likely to be an important influence on vegetation structure. On the Ord River, vegetation structure was dominated by trees and perennial grasses, while annual herbs and grasses were only a very small component of the riparian vegetation. The perennial grasses are usually hemicryptophytes which behave like annual species, with the above ground parts dying back to a rhizome or stolon in the dry season and growing rapidly and producing large quantities of seed when conditions are favourable. They are therefore disturbance adapted species. On the Ord River shrub species are more common further from the river at higher elevations where disturbance is less but stress from drought may be greater. Lianas were also common on the Ord River sites but absent from the Blackwood River sites. Soil stability will also affect vegetation physiognomy (Friedel *et al.* 1993) and favour ruderal species and will affect the ability of riparian species to form a soil seedbank. This will be explored further in Chapter 7. At a landscape scale, differences between the rivers are primarily driven by differences in climatic history, present climate, geology and soils (Barlow 1994). The natural disturbance regime and the level of stress caused by flooding on the two rivers are also likely to influence the factors affecting recruitment of the vegetation.

Both rivers had a high level of exotic species, both in terms of number of species and cover, particularly at sites grazed by livestock. The addition of disturbance from livestock grazing in this naturally high disturbance environment makes the riparian zone highly vulnerable to invasion by exotic species which tend to be ruderal species (Grime 1979). Further, the river is an area of high productivity and a natural conduit for dispersal of propagules of exotic species
which can be rapidly transported over long distances. Examples of this include *Atriplex prostrata* and *Rumex* spp. on the Blackwood River and the exotic lianas *Passiflora foetida* and *Cardiospermum halicacabum* on the Ord River. The riparian zone may also provide a reservoir of exotic species within the landscape.

On the Blackwood River there was a clear separation of sites where livestock grazing has resulted in the invasion of exotic species and a decrease in native species richness and diversity. This is typical of other environments that have not had a long history of intensive livestock grazing and where the vegetation is therefore not adapted (McIntyre & Lavorel 1994; Pettit *et al.* 1995). On the Ord River no sites that have not been subject to cattle grazing could be found. All sites have been grazed by cattle for at least the past 50 years (Perry 1970). Therefore, no effects of grazing could be discerned for these sites. The dominance of grasses and lack of shrubs in the understorey is most likely related to climate and natural disturbance regimes and this vegetation, described as woodland with a grassy understorey, is typical of the low latitude summer rainfall areas across northern Australia (Perry 1970). The exotic perennial buffel grasses *Cenchrus ciliaris* and *C. setiger* dominant at Site 05 were introduced as part of the rehabilitation programme on the upper Ord at Old Ord River Station (de Salis 1993). For environments with a long evolutionary history of grazing, species richness tends to be higher with some grazing pressure (McNaughton 1985; Milchunas & Lauenroth 1993). The effects of livestock grazing will be more fully explored in Chapter 6.

**Floristic patterns**

Ordination of the sites showed the longitudinal and transverse trends in the floristics of the plots, with the longitudinal gradient of climate (such as decreasing rainfall) influencing a change in floristics. Other influences along this gradient may be changes in geology and soils. For example, on the Blackwood River there is increasing laterisation of the landscape westward (downstream), and on the Ord River there is a change from a basalt plateau overlain by sedimentary deposits of limestone, sandstone and mudstone on the Ord River plains (at the upstream sites) to the more recent alluvial sediment of the Carlton Plain downstream. On the
Blackwood River floristics of the riparian vegetation is also influenced by increasing river salinity upstream, and is reflected in a change to species which have greater salt tolerance, such as species in the Chenopodaceae family.

On the Blackwood River sites the transverse gradient for plots (identified by the second axis of the DCA ordination) indicated a greater proportion of annual species and reduced species richness closer to the river with increasing proportion of woody perennial species further from the river. Exotic species, which were nearly all annuals, were also more prevalent near the water. This may reflect the increased frequency of disturbance near the water, favouring ruderal species (Abogov 1982). Transportation of seed by the river and the continual exposure of fresh sediments and high soil moisture levels, as well as the reduced competition (which disadvantages competitive dominants (Pickett et al. 1989)), favour these ruderal species which in the south-west are predominantly exotic species. The only perennial species that usually occurred near the river are hydrophytes, such as from the Cyperaceae family, and the trees Eucalyptus rudis and Melaleuca rhaphiophylla which have some waterlogging or inundation tolerance. These generally establish above the summer low water mark with M. rhaphiophylla restricted to the area close to the river channel. The establishment of these species will be investigated further in subsequent chapters.

A transverse gradient was also observed on the Ord River sites, with lower species richness and a greater proportion of annual species nearer the water's edge. This is possibly due to the increased frequency of disturbance and stress. Floristics of the plots are affected by the occurrence at the water's edge of semi-aquatic, emergent macrophyte species such as Typha domingensis. The greater clay content closer to the river, from alluvial deposits, will also affect floristics along the river profile. On many sites, the understorey close to the river was dominated by the perennial grass Cynodon dactylon occurring on the freshly deposited sediments. Away from the river, other perennial grasses became dominant, such as the buffel grasses Cenchrus spp. at the upstream sites. The overstorey species on the Ord River are more diverse than on the Blackwood River but the most common species which occurred at all sites were Eucalyptus camaldulensis and
Melaleuca leucadendra with *M. leucadendra* tending to be restricted to areas close to the water channel. The gradient of change in floristics along the transverse profile away from the river is correlated with elevation and probably reflects a moisture gradient and/or a gradient of flooding disturbance. These factors will be explored further in later chapters.

Disturbance and stress have important roles in shaping the vegetation communities in the riparian zone. Stress, which can include extended periods of inundation and waterlogging or drought, affects the ability of plants to grow and persist in the riparian zone. Disturbance from strong river flows can create gaps for recruitment of plants and the transport of propagules, removal and renewal of soil and replenishment of soil water. The degree to which disturbance and stress affect riparian vegetation will depend on river flow regime, distance from the river, elevation and topographical position within the riparian zone.

This Chapter has provided an overview of the riparian vegetation on the study rivers and provides a basis for further examination of factors that influence establishment. Aspects raised in this Chapter such as the influence of fluvial processes, effects of livestock grazing, the soil seedbank and the fate of seed and seedlings and will be explored in greater detail in the following chapters.
CHAPTER 5

IDENTIFYING THE NATURAL FLOW REGIME AND THE RELATIONSHIP WITH RIPARIAN VEGETATION.

Introduction

The previous Chapter and evidence from the literature indicated the link between riparian vegetation and hydrology, including water flow and fluctuating water levels (Malanson 1993; Naiman & Bilby 1998). This Chapter describes the natural flow regime and the variability of flows into the riparian zone and how this can be related to the vegetation at sites on the Blackwood and Ord rivers. This chapter provides a detailed investigation of the variability in the flow regime of the study rivers over time, of the influence on the floristics of the riparian community identified in Chapter 4 and the establishment of seedlings and size class structure of common overstorey species. This knowledge of historical flows can be used to understand the distribution of riparian species and life forms in the riparian zone on these rivers. An understanding of the variability of historical flows can also be used to predict changes in the vegetation with changes to river flows in regulated systems or with climatic changes.

The fluvial regime and river geomorphology are major influences on the spatial and temporal structure of riparian vegetation (Johnson 1994; Barnes 1997; Johnson 1997). In particular, water flow and fluctuating water levels are important determinants of the structure of riparian vegetation (Gregory et al. 1991; Malanson 1993; Nilsson et al. 1993). The importance of the flow regime on the ecology of aquatic fauna has been discussed for an Australian arid zone river (Puckridge 1999). Puckridge (1999) identified six measures of variability that are important to fish and macro-invertebrate biology including: duration of flow; water depth; shape of the flood
pulse; frequency of the flood pulse; connectivity of water bodies; and permanence. Assessment of the range of flows needed to maintain riparian species should consider more than just the aquatic species (Richter 1997) and should therefore include species of the riparian zone. Measures of temporal variability of flow are useful in describing the range of conditions that the riparian vegetation (as well as other biota) experience.

The flow regime of a river describes the distribution of water through time, and can be used to determine periods of inundation of the riparian environment. Flow essentially “drives” sediment transport and, in fluvially dominated systems, shapes the river channel and consequently the structure of riparian landscapes (Young 1999). This can result in multiple successional stages (e.g. Malanson 1993). Timing, frequency and level of flooding disturbance are also important determinants of vegetation dynamics in the riparian zone. How natural flow disturbance shapes community structure can depend on the frequency, magnitude and predictability of the disturbance (Sousa 1984). Several critical aspects of river flow regimes are recognised as being more ecologically “significant” (Richter et al. 1996). These key aspects include flow magnitude; flow variability; rates of flow change; magnitude and frequency of extreme flow condition; and predictability of flows (Young 1999).

The timing of river flows is important for the dispersal of vegetation propagules and in triggering germination and subsequent establishment of seedlings. This has been extensively reported in the literature (e.g. Barnes 1985; Bradley & Smith 1986; Bren & Gibbs 1986; Johnson 1994). For example, seasonal timing of flows in the Murray River is an important trigger for recruitment of *Eucalyptus camaldulensis* (Bren & Gibbs 1986). Flows are also indirectly important for the maintenance of riparian vegetation in recharging soil water (to reduce water stress), increasing vegetative growth rates (Bacon et al. 1993) and enhancing survival of seedlings (Roberts 1993). On the Murray River in south-eastern Australia, the abundance and composition of plant species was strongly correlated with the degree of water level fluctuation (Walker et al. 1994). In wetlands, changes in frequency and duration of flooding can alter plant species richness.
(Denton & Ganf 1994) and prolonged flooding can affect growth and reproduction of emergent macrophytes (Froend & McComb 1994).

To provide a framework for assessing the relationship between the natural flow regime and the structure of riparian vegetation (including life form groups discussed in the previous chapter), fundamental procedures outlined in the "holistic method" of in-stream flow management (Arthington 1998) have been adopted. This approach emphasises ecosystem level and flow-dependent processes and aims to provide an assessment of environmental water requirements by using information on the relationship between flow and the various ecologically-important attributes of rivers. It assumes that the natural flow regime, or in regulated systems, the historic flow regime, is of fundamental ecological importance in maintaining channel morphology, in-stream biota and riparian vegetation as well as associated floodplain and wetland environments. In regulated rivers, the holistic methodology leads to the development of a modified flow regime based on critical flows to achieve particular ecological, geomorphological and/or water quality objectives. It uses a range of flow-related parameters to determine significant environmental flows and then to develop a suitable (artificial) environmental flow strategy.

This Chapter adapts this method for assessing seasonality and variability of natural flows in the Ord and Blackwood rivers and describes the frequency and variability of flows that would influence riparian vegetation. It provides examples of the influences of riparian flows on various aspects of the riparian zone vegetation including floristics, life form structure and population structure. These can be used to compare similarities and differences in the response of the different vegetation components to the different fluvial regimes. This Chapter provides an example of how this technique can be applied in the management of riparian zones and in planning rehabilitation programs of riparian vegetation. The technique is also useful in improving the ecological knowledge base for assessing environmental flows in regulated systems. Clearly, this is useful in the planning and management of riparian zone vegetation restoration.
Methods

Using the historical daily stream flow record, average monthly flows were assessed to determine the variability of natural flows on the Ord and Blackwood rivers. Stream channel morphology and estimates of Manning’s n (Newbury & Glaboury 1993) was measured at a site on each river to calculate flows that would influence riparian vegetation and flows that would inundate the riparian zone. The historic seasonality and variability of these flows was then assessed. Vegetation plots set up along transects perpendicular to the river (i.e. along an elevational gradient), and described in Chapter 4, were used to assess the effects of particular riparian flows on riparian vegetation floristics, the presence of seedlings and the population structure of overstorey species.

Natural flow regime

Historical flow records (as daily discharge figures in m$^3$s$^{-1}$) were obtained from Water and Rivers Commission (Western Australia) gauging sites. On the Ord River the chosen site was upstream of the Ord River Dam and Lake Argyle in the unregulated section of the river at Old Ord River Station (Station No. 809316) (Site O5, see Figure 3.1). On the Blackwood River the site was located at Darradup (Station No. 609025) (Site B1a, see Figure 3.2). Data were analysed from records covering the period October 1970 to November 1995 (25 years). Although a longer period of continuous record was available for the Blackwood River (from 1958), the 25 year period was used to enable a valid comparison between the two rivers. To determine yearly and seasonal flow patterns and flow variability for the two rivers, mean flows for each month were calculated from daily records along with percentile flows. As a measure of the distributional spread of the daily flows over the period of record, the coefficient of variation (CV) was calculated from daily flows for each month (Zar 1984). However, for skewed data, the mean, and therefore CV, may not accurately represent the central tendency of the data (Zar 1984) so an additional measure of variability ($S_80$ or spread) was also calculated. This measure is derived from the difference between the 90th percentile and the 10th percentile divided by the median (50th percentile).
(Walker et al. 1995; Young 1999). The greater the flow variability, the higher the SSO value. Overall seasonal patterns were described by indices of time-series analysis (Colwell 1974) of predictability (P), constancy (C) and contingency (M). Values of P range from 0 (unpredictable) to 1 (totally predictable). A value of 1 would occur only if flows in every month were the same for every year of record. Constancy (C) would be 1 if flows were totally predictable and identical across all months while contingency would be 1 if flows were totally predictable but different every month. The degree of seasonality can also be indicated by M/P. These Colwell indices together with monthly distribution of flows are a useful first step in defining patterns in the natural flow regime (Davies et al. 1998). Colwell’s Index was calculated using log₂ scale intervals of the median (Q) monthly flows (i.e. 0.5Q, Q, 2Q, 4Q, 8Q, 16Q, 32Q, 64Q) (Gordon et al. 1992) for 25 years of record for each river system. Return period of floods was also calculated for each river based on recorded annual flow peaks plotted against cumulative frequency (p) where p = (rank/n+1) x 100%. This provides an estimate of annual return period of particular flows or the probability of particular flows being equalled or exceeded (Petts 1983). However, because of the short period of record, extreme flow return periods must be regarded with caution.

Riparian flows

Water discharge rates to achieve different stage heights at a particular reach of the river can be calculated using "Manning’s Equation" (Newbury & Gaboury 1993):

\[
v = \frac{(R^{2/3} \times s^{1/2})}{n} \text{ and } R = \frac{A}{p}
\]

where \( v \) = mean velocity (m s⁻¹); \( R \) = hydraulic radius of flow (m);
\( s \) = average reach slope; \( n \) = Manning’s roughness factor;
\( A \) = cross-sectional area of flow (m²); \( p \) = wetted perimeter of flow (m).

Discharge (Q) (m³ s⁻¹) is then calculated as \( Q = v \times A \).

Channel resistance to flow, or Manning’s roughness factor (n), was estimated for different transects from examples of calculated n values for different channel types (i.e. Newbury & Gaboury 1993). Resistance to flow varies greatly depending on the size of the bed material (including rocks and boulders), the vegetation and depth of flow. Calculation of Manning’s Equation allowed the estimation of river discharges, at different stage levels within the river.
channel, that would be important for riparian vegetation (i.e. inundation). Calculation of discharge values were averaged from three transects. Analysing the historical flow record allowed the timing, frequency and duration of these discharges to be quantified and consequently correlated with the associated vegetation data.

To adequately determine river channel morphology at the study sites on the Blackwood and Ord rivers, three cross-sectional transects (including vegetation transects) were measured for distance (m), elevation and slope with a surveyor's automatic level and staff at 10 metre intervals. Channel slope was measured by taking levels 100 metres up and downstream of the transect. Bed materials along the transect (including the presence of gravel, rocks and boulders, large woody debris and vegetation) were recorded to assess channel roughness and hence the Manning's n value (Newbury & Gaboury 1993). An average channel morphology was then determined for a particular reach of the river and river discharge was estimated using Manning's Equation.

Critical flows for riparian vegetation for each river were calculated as:
1. Low flows - below active channel levels, which would expose wet sediments and therefore provide sites for the germination of seed and the establishment of seedlings.
2. Riparian zone flows - where water flows into the riparian vegetation zone, facilitating dispersal of seed, providing soil water recharge and redistribution of sediments.
3. Floodplain flows - where water flows out of the river channel and onto the floodplain where slope levels out and the vegetation consists of mainly terrestrial species.

The occurrence, frequency and duration of these flows were then calculated for each month from historical flow records.

Vegetation plots
At each site on each river, two vegetation transects perpendicular to the river were established, the length of each varying for each site depending on the width of the riparian zone. Along each transect, five 10 metre x 10 metre quadrats were established (see Chapter 4). For each plot, all
plants rooted within the plot were identified and an estimate of percentage cover was made, where cover was determined as the vertical crown or shoot projection per species. In each plot, the stem diameter at breast height (1.5 m) (DBH) was measured for all individuals of the two most common tree species, *Eucalyptus camaldulensis* and *Melaleuca leucadendra* on the Ord River and *E. rudis* and *M. rhaphiophylla* on the Blackwood River. For these species, the number of tree seedlings in each plot was also recorded. For greater precision of determinations of tree DBH and number of seedlings, an additional two transects were established at each site. Multivariate analysis of the floristic and environmental data from the plots was conducted using Detrended Correspondence Analysis (DCA), detrending by segments (ter Braak 1987), which provided a summary of plant species composition and abundance (see Chapter 4). Species were categorised into different life form groups to compare the dominance of the various life forms on each river and the effect of the flow regime.

**Flow regime and vegetation relationships**

The relationship between flow regime and floristics, plant functional types and population structure of the selected species at these sites on the two rivers was considered important for understanding the dynamics of regeneration of plants in the riparian zone. For the period of record, river discharge that would inundate each of the vegetation plots along the vegetation transects at these sites was calculated along with mean duration of inundation and number of events per year (Table 5.1). These were correlated with floristic data for each plot, including the DCA scores calculated in Chapter 4. Data from tree seedling plots and tree diameter plots were correlated with mean period of inundation and number of events per year. The relationship between floristic data from the vegetation plots and mean duration of flooding and mean number of flooding events per year into these plots was assessed using stepwise multiple regression (Zar 1984). In this analysis, vegetation plot data were the dependent variables and mean duration of flooding and mean number of flooding events per year were independent variables.
Table 5.1: River discharges that would inundate vegetation plots (calculated from Manning's equation) and the mean duration and mean number of these events per year.

<table>
<thead>
<tr>
<th>Blackwood River</th>
<th>Ord River</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plot No.</td>
<td>1 Depth (m) @ 275 m³s⁻¹</td>
</tr>
<tr>
<td>1</td>
<td>7.0</td>
</tr>
<tr>
<td>2</td>
<td>6.9</td>
</tr>
<tr>
<td>3</td>
<td>3.4</td>
</tr>
<tr>
<td>4</td>
<td>3.2</td>
</tr>
<tr>
<td>5</td>
<td>2.9</td>
</tr>
<tr>
<td>6</td>
<td>2.5</td>
</tr>
<tr>
<td>7</td>
<td>0.1</td>
</tr>
<tr>
<td>8</td>
<td>0.9</td>
</tr>
<tr>
<td>9</td>
<td>1.1</td>
</tr>
<tr>
<td>10</td>
<td>0.5</td>
</tr>
</tbody>
</table>

1. Mean depth of water (m) in the vegetation plot at a discharge of 275 m³s⁻¹ or 2424 m³s⁻¹
2. Minimum discharge that would inundate each vegetation plot.
3. Mean duration of inundation at each plot over the 25 years of record.
4. Mean number of flow events per year into the plot over the 25 years of record.

Results

Natural flow regime

Historic mean monthly river discharge for the Blackwood River showed a strong seasonality, with 80% of discharge occurring in late winter/early spring of July, August and September (Table 5.2). In contrast, summer and some autumn flows (January to May) made up only 3% of the annual flow. The coefficient of variation (CV) of flows was very high during summer, however values for January and February were distorted by an extreme flow event in late January/early February 1982 caused by a cyclonic depression. If this flow event is excluded, the CV for January and February reduces to 48% and 129% respectively.
Table 5.2: Historic mean monthly flows in gigalitres (GL) and measures of variability for each month from daily flow records for the Blackwood River near the Darradup gauging site for records covering the period 1970 to 1995.

<table>
<thead>
<tr>
<th>Month</th>
<th>Mean</th>
<th>Median</th>
<th>Std. Dev.</th>
<th>Std. Err.</th>
<th>CV %</th>
<th>S80</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>14.75</td>
<td>1.16</td>
<td>67.26</td>
<td>13.45</td>
<td>455</td>
<td>1.25</td>
<td>24</td>
</tr>
<tr>
<td>February</td>
<td>2.86</td>
<td>0.7</td>
<td>8.44</td>
<td>1.69</td>
<td>294</td>
<td>1.52</td>
<td>24</td>
</tr>
<tr>
<td>March</td>
<td>2.35</td>
<td>0.77</td>
<td>6.25</td>
<td>1.25</td>
<td>265.6</td>
<td>2.3</td>
<td>25</td>
</tr>
<tr>
<td>April</td>
<td>2.70</td>
<td>1.61</td>
<td>3.43</td>
<td>0.69</td>
<td>127</td>
<td>2.9</td>
<td>25</td>
</tr>
<tr>
<td>May</td>
<td>5.78</td>
<td>4.68</td>
<td>3.30</td>
<td>0.66</td>
<td>57.2</td>
<td>2.9</td>
<td>25</td>
</tr>
<tr>
<td>June</td>
<td>32.18</td>
<td>19.13</td>
<td>36.04</td>
<td>7.21</td>
<td>112.2</td>
<td>3.8</td>
<td>25</td>
</tr>
<tr>
<td>July</td>
<td>119.88</td>
<td>93.16</td>
<td>90.35</td>
<td>18.07</td>
<td>75.4</td>
<td>3.4</td>
<td>25</td>
</tr>
<tr>
<td>August</td>
<td>163.20</td>
<td>117.18</td>
<td>128.18</td>
<td>25.64</td>
<td>78.5</td>
<td>2.3</td>
<td>25</td>
</tr>
<tr>
<td>September</td>
<td>95.57</td>
<td>73.27</td>
<td>89.08</td>
<td>17.82</td>
<td>93.2</td>
<td>2.3</td>
<td>25</td>
</tr>
<tr>
<td>October</td>
<td>41.02</td>
<td>32.65</td>
<td>31.66</td>
<td>6.33</td>
<td>77.2</td>
<td>2.7</td>
<td>25</td>
</tr>
<tr>
<td>November</td>
<td>12.02</td>
<td>11.33</td>
<td>6.76</td>
<td>1.38</td>
<td>56.2</td>
<td>2.2</td>
<td>24</td>
</tr>
<tr>
<td>December</td>
<td>3.99</td>
<td>3.15</td>
<td>3.89</td>
<td>0.79</td>
<td>97.4</td>
<td>1.8</td>
<td>24</td>
</tr>
</tbody>
</table>

Table 5.3: Historic mean monthly flows in gigalitres (GL) and measures of variability for each month from daily flow records for the Ord River at the Old Ord River gauging site (Site 01) for records covering the period 1970 to 1995.

<table>
<thead>
<tr>
<th>Month</th>
<th>Mean</th>
<th>Median</th>
<th>Std. Dev.</th>
<th>Std. Err.</th>
<th>CV %</th>
<th>S80</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>401.35</td>
<td>203.62</td>
<td>491.31</td>
<td>104.75</td>
<td>122</td>
<td>28.3</td>
<td>21</td>
</tr>
<tr>
<td>February</td>
<td>703.34</td>
<td>196.20</td>
<td>943.19</td>
<td>205.82</td>
<td>134</td>
<td>12.9</td>
<td>20</td>
</tr>
<tr>
<td>March</td>
<td>276.88</td>
<td>166.81</td>
<td>326.28</td>
<td>69.56</td>
<td>118</td>
<td>13.2</td>
<td>22</td>
</tr>
<tr>
<td>April</td>
<td>71.77</td>
<td>10.63</td>
<td>162.39</td>
<td>34.62</td>
<td>226</td>
<td>18.5</td>
<td>22</td>
</tr>
<tr>
<td>May</td>
<td>12.47</td>
<td>1.82</td>
<td>30.80</td>
<td>6.72</td>
<td>249</td>
<td>13.4</td>
<td>21</td>
</tr>
<tr>
<td>June</td>
<td>2.30</td>
<td>0.31</td>
<td>3.45</td>
<td>0.77</td>
<td>151</td>
<td>23.1</td>
<td>20</td>
</tr>
<tr>
<td>July</td>
<td>2.70</td>
<td>0</td>
<td>8.91</td>
<td>1.86</td>
<td>330</td>
<td>-</td>
<td>23</td>
</tr>
<tr>
<td>August</td>
<td>0.89</td>
<td>0</td>
<td>2.02</td>
<td>0.42</td>
<td>227</td>
<td>-</td>
<td>23</td>
</tr>
<tr>
<td>September</td>
<td>2.20</td>
<td>0</td>
<td>7.74</td>
<td>1.61</td>
<td>352</td>
<td>-</td>
<td>23</td>
</tr>
<tr>
<td>October</td>
<td>1.83</td>
<td>0</td>
<td>5.25</td>
<td>1.07</td>
<td>287</td>
<td>-</td>
<td>24</td>
</tr>
<tr>
<td>November</td>
<td>34.18</td>
<td>1.61</td>
<td>101.13</td>
<td>21.08</td>
<td>296</td>
<td>236.3</td>
<td>23</td>
</tr>
<tr>
<td>December</td>
<td>110.66</td>
<td>36.54</td>
<td>239.74</td>
<td>51.11</td>
<td>217</td>
<td>29.2</td>
<td>23</td>
</tr>
</tbody>
</table>

Comparing mean and median values indicates the skewed nature of the data, particularly in the low-flow months, suggesting that the median may be a "better" indicator of general flow conditions as the mean is unduly influenced by occasional, but extreme, flow events. Using the median to measure variability (S80) gives quite different results than the CV, with the highest values measured during winter. Calculation of the Colwell Index showed that the Blackwood River had a highly predictable flow regime (P= 0.71). Constancy of 0.32 with low contingency (M) of 0.34 indicates a strong seasonality of the flows, with this seasonality highly predictable between years (i.e. M/P = 48%). Using the peak discharge levels for each year, a flood return
frequency curve was developed from the available years of data (Figure 5.1a). This indicates that a return frequency flood of 100 years would have a discharge of 1160 m³s⁻¹ and that a discharge of 554 m³s⁻¹ would occur for a 10 year return flood. However, because of the small period of record these estimates are only tentative, particularly for the higher values.

Monthly discharge figures for the Ord River showed a very strong seasonality of flows with 92% of the mean yearly flow occurring from December through to March (Table 5.3). Periods of no-flow were recorded for July to October, with low median flows (i.e. <2 GL) from May to November. Flow variability was very high (CV of >100% for all months), with highest figures measured during the dry season months. The large difference in mean and median values again indicates skewness. Flow variability, determined using S80, was also very high but greatest in the wet season. However, values for July to October could not be calculated because of no-flow in the 50th percentile range for these months. November showed an extremely high S80 value, reflecting the variability of climatic patterns in the transition of seasons from the dry to the wet. Colwell's Index showed a high predictability of flows (P = 0.67), with this mostly attributed to low, constant dry season flows with constancy (C) of 0.44 and 0.20 for contingency (M). The contribution of seasonality to predictability was low (M/P = 29%). Using the peak discharge levels for each year, a flood return frequency curve was developed from the available years of data (Figure 5.1b). This indicates, at this site on the Ord River, that a return flood frequency of 100 years would have a discharge of 19994 m³s⁻¹ and that a discharge of 9458 m³s⁻¹ would occur for a 10 year return flood.
Figure 5.1: Flood frequency curves for a) Blackwood River and b) the Ord River based on the annual maximum discharge recorded for the period 1970 to 1995.
Riparian zone flows

Critical low flows for riparian vegetation were calculated as $<12 \text{ m}^3\text{s}^{-1}$ for the Blackwood River and $<30 \text{ m}^3\text{s}^{-1}$ for the Ord River. Riparian zone flows were $66 - 275 \text{ m}^3\text{s}^{-1}$ for the Blackwood River and $580 - 2424 \text{ m}^3\text{s}^{-1}$ for the Ord River. Floodplain flows were $>1050 \text{ m}^3\text{s}^{-1}$ for the Blackwood River and $>5200 \text{ m}^3\text{s}^{-1}$ for the Ord River.

On the Blackwood River, flows that would inundate the riparian zone occurred on average 2 to 3 times per year and lasted for approximately seven days. These events occurred most frequently during July and August (Table 5.4). Flooding of riparian zones has occurred only twice between November and May over the flow period. This was after the cyclonic rainfall event in January and February 1982 (Cyclone Alby). Most consecutive days of flows $>66 \text{ m}^3\text{s}^{-1}$ was 60 (26/7/83 to 23/9/83) and there were 10 periods of 20 consecutive days of flows of this volume, between June and September (winter). There were 24 days of flows $>275 \text{ m}^3\text{s}^{-1}$, with 20 recorded from July to September and the other four recorded in January 1982. There was only one day of recorded flow of $>1050 \text{ m}^3\text{s}^{-1}$ (over-bank, floodplain flows), recorded on 31/1/1982. Low channel flow events ($<12 \text{ m}^3\text{s}^{-1}$) occurred on average 11 times per year and lasted around 23 days, so for the months November through to May these events are likely on most days. During August, such flows are unlikely and only occurred in one in three years, while July and September had flows $<12 \text{ m}^3\text{s}^{-1}$ less than once a year. The greatest number of consecutive days of $<12 \text{ m}^3\text{s}^{-1}$ flows was 317 days from 29/8/79 to 10/7/80. There were 21 periods of greater than 200 consecutive days of flows $<12 \text{ m}^3\text{s}^{-1}$, with three periods $>300$ days. For the period of analysis, there were 70 days of flows $>12 \text{ m}^3\text{s}^{-1}$ in the dry season (November to April), with the longest consecutive period being 18 days (25/1/82 to 11/2/82). Criteria for beginning of winter flows was the first 10 consecutive flows of $>12 \text{ m}^3\text{s}^{-1}$ but not followed by $>14$ consecutive days of $<12 \text{ m}^3\text{s}^{-1}$. End of winter flows was considered to be 14 consecutive days $<12 \text{ m}^3\text{s}^{-1}$. Winter flows began in June 13 times, in July 11 times and in May once. The earliest start to the winter flows was 30/5/74 and the latest 27/7/76. The end of winter flows with consequent receding water levels occurred in October 16 times,
September 7 times and twice in November. The earliest cessation of winter flows was 1/9/79 and the latest was 9/11/73.

Table 5.4: Summary of flows into the riparian zone at Darradup on the Blackwood River over a 25 yr period from 1970 to 1995. Flows are between 66 m$^3$s$^{-1}$ (active channel flow) and 275 m$^3$s$^{-1}$ (upper limit of riparian vegetation) calculated from profile transects at the site.

<table>
<thead>
<tr>
<th>Month</th>
<th>n (yrs)</th>
<th>Total Days</th>
<th>No. Events</th>
<th>Days/Month Mean±SE</th>
<th>Events/Month Mean±SE</th>
<th>Duration (days) Mean±SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>24</td>
<td>3</td>
<td>1</td>
<td>0.12</td>
<td>0.04</td>
<td>3</td>
</tr>
<tr>
<td>February</td>
<td>25</td>
<td>2</td>
<td>1</td>
<td>0.08</td>
<td>0.04</td>
<td>2</td>
</tr>
<tr>
<td>March</td>
<td>25</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>April</td>
<td>25</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>May</td>
<td>25</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>June</td>
<td>25</td>
<td>27</td>
<td>3</td>
<td>1.08 ± 0.2</td>
<td>0.12 ± 0.05</td>
<td>9 ± 2</td>
</tr>
<tr>
<td>July</td>
<td>25</td>
<td>151</td>
<td>18</td>
<td>6.04 ± 1.6</td>
<td>0.72 ± 0.16</td>
<td>8.4 ± 1.3</td>
</tr>
<tr>
<td>August</td>
<td>25</td>
<td>247</td>
<td>21</td>
<td>9.9 ± 2</td>
<td>0.84 ± 0.12</td>
<td>11.8 ± 2</td>
</tr>
<tr>
<td>September</td>
<td>25</td>
<td>88</td>
<td>11</td>
<td>3.5 ± 1.2</td>
<td>0.44 ± 0.1</td>
<td>8 ± 1.6</td>
</tr>
<tr>
<td>October</td>
<td>25</td>
<td>21</td>
<td>4</td>
<td>0.84 ± 0.13</td>
<td>0.16 ± 0.07</td>
<td>5.25 ± 1.1</td>
</tr>
<tr>
<td>November</td>
<td>24</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>December</td>
<td>24</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

On the Ord River, discharges that would inundate the riparian zone occurred on average about three times per year and lasted approximately two days. Eighty-five percent of these riparian flows occurred from January to March and none occurred between June and October (Table 5.5). The short duration of riparian zone flows is reflected in the steepness of the flood hydrograph for the Ord River (see Figure 3.6). For low channel flows (of <29 m$^3$s$^{-1}$) an average of 15 events occurred per year, each lasting for about 21 days. From May to November, low flows occurred virtually all month, while in the wet season (December to March) there was an average of six low flow events per year. There were thirteen periods of at least 200 consecutive days of flows <29 m$^3$s$^{-1}$. The greatest number of consecutive days of flows <29 m$^3$s$^{-1}$ was 331 days from 19/2/92. For the period of analysis (11/70 to 10/95) there were 25 days in the dry season (May to October) of flows >29 m$^3$s$^{-1}$, with the longest consecutive period being 11 days (1-11/5/74). There were four days of recorded flows of >5200 m$^3$s$^{-1}$ (over bank, floodplain flows). The highest, 16456 m$^3$s$^{-1}$, was recorded on 14/2/80. Criteria for the commencement of wet season flows was the first 3 consecutive flows of >29 m$^3$s$^{-1}$ but not followed by >14 consecutive days of <29 m$^3$s$^{-1}$ after October. End of wet season flows was considered to be 14 consecutive days <29 m$^3$s$^{-1}$ after February. Wet season flows began in December 8 times, in January 8 times, in November 4 times and in February
once. The earliest start to the wet season was 10/11/71 and the latest 3/2/92. The end of wet season flows and the beginning of dry season flows occurred in March 12 times, April 4 times and once during February and May.

Table 5.5: Summary of flows into the riparian zone at Old Ord River Station over a 25 year period from 1970 to 1995. Flows are between 580 m³s⁻¹ (active channel flow) and 2424 m³s⁻¹ (upper limit of riparian vegetation) calculated from profile transects at the site.

<table>
<thead>
<tr>
<th>Month</th>
<th>n (yrs)</th>
<th>Total Days</th>
<th>No. Events</th>
<th>Days/Month Mean±SE</th>
<th>Events/Month Mean±SE</th>
<th>Duration (days) Mean±SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>January</td>
<td>22</td>
<td>39</td>
<td>10</td>
<td>1.9 ± 0.6</td>
<td>0.90 ±0.25</td>
<td>3.9 ± 0.4</td>
</tr>
<tr>
<td>February</td>
<td>21</td>
<td>64</td>
<td>25</td>
<td>2.8 ± 0.8</td>
<td>1.04 ± 0.3</td>
<td>2.6 ± 0.4</td>
</tr>
<tr>
<td>March</td>
<td>22</td>
<td>29</td>
<td>12</td>
<td>1.3 ± 0.5</td>
<td>0.52 ± 0.2</td>
<td>2.4 ± 0.6</td>
</tr>
<tr>
<td>April</td>
<td>22</td>
<td>7</td>
<td>3</td>
<td>0.3 ± 0.2</td>
<td>0.14 ± 0.07</td>
<td>2.3 ± 0.9</td>
</tr>
<tr>
<td>May</td>
<td>21</td>
<td>1</td>
<td>1</td>
<td>0.05</td>
<td>0.05</td>
<td>1</td>
</tr>
<tr>
<td>June</td>
<td>21</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>July</td>
<td>21</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>August</td>
<td>22</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>September</td>
<td>22</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>October</td>
<td>21</td>
<td>0</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>November</td>
<td>22</td>
<td>3</td>
<td>2</td>
<td>0.15 ± 0.05</td>
<td>0.10</td>
<td>1.5</td>
</tr>
<tr>
<td>December</td>
<td>22</td>
<td>4</td>
<td>3</td>
<td>0.21 ± 0.1</td>
<td>0.16</td>
<td>1.3</td>
</tr>
</tbody>
</table>

Vegetation and flooding regime

Vegetation plots showed the large difference in the floristics between the two rivers. The use of historical flows and discharge levels for each vegetation plot showed the different effects of flooding regime on floristics, life form structure and population dynamics of the riparian vegetation.

On the Blackwood River, the dominant life forms in terms of species and cover were shrubs (30% of species and 36% of cover) and perennial herbs (30% of species and 20% of cover), but this varied along the gradient away from the river. Zonation of the vegetation along a flooding gradient is reflected in the relationship to duration and frequency of flooding in the vegetation plots (Table 5.6). Floristics, as indicated by the DCA, showed a strong correlation of frequency of flooding with the first floristic axis. Species richness declined with increased duration of flooding as did the cover of shrubs (Figure 5.2). Cover of exotic species, which were mainly annual herbs and grasses (with the exception of blackberry (Rubus sp.)) increased with both increasing duration and frequency of flooding (Table 5.6). The cover of both perennial grasses and
herbs showed no significant relationship with either flooding variable (Table 5.6). On the Blackwood River, the population structure of the common tree species was not significantly correlated with the flooding variables for either the number of tree seedlings per plot or tree diameter (Table 5.6).

On the Ord River, the dominant life forms were perennial grasses (22% of species and 52% of cover) and trees (16% of species and 40% of cover). Zonation of the vegetation along the flooding gradient was shown by the significant correlation between the first DCA axis and the duration of flooding (Table 5.6).

In contrast to the Blackwood River, there was no significant effect of flooding on species richness or the number of exotic species, whereas cover of shrubs significantly decreased with increasing frequency of flooding (Table 5.6, Figure 5.3). Perennial grasses were the dominant life form on Site 05 on the Ord River (see Chapter 4), and percentage cover increased with duration of flooding. On the Ord River, seedling numbers of the major trees in the vegetation plots was not significantly correlated with the flooding variables. Tree size showed the opposite trend to that seen on the Blackwood River, with tree diameter significantly decreasing with increased flooding frequency (Table 5.6, Figure 5.3).
Figure 5.2: Significant relationships between duration of flooding (b,c & d) and number of flooding events per year (a & e) with floristic attributes of vegetation plots along transects on the Blackwood River site.
Figure 5.3: Significant relationships between duration of flooding (a & b) and number of flooding events per year (c & d) and floristic attributes of vegetation plots along transects on the Ord River site.
Table 5.6: Results of step-wise multiple regression from vegetation plots of floristic variables with duration of flood events in days (x) and number of events per year (z).

<table>
<thead>
<tr>
<th>Dependent variable (y)</th>
<th>$^1R^2$</th>
<th>p</th>
<th>$^2$Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blackwood River</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DCA axis1</td>
<td>0.816</td>
<td>0.003</td>
<td>$y = -0.79 + 3.935x$</td>
</tr>
<tr>
<td>Species richness</td>
<td>0.494</td>
<td>0.023</td>
<td>$y = -0.189x + 35.4$</td>
</tr>
<tr>
<td>% cover exotic spp</td>
<td>0.774</td>
<td>0.0054</td>
<td>$y = -1.307 + 0.254x + 11.191z$</td>
</tr>
<tr>
<td>% cover annual herbs</td>
<td>0.570</td>
<td>0.0116</td>
<td>$y = 1.512 + 0.162x$</td>
</tr>
<tr>
<td>% cover perennial grasses</td>
<td>0.121</td>
<td>0.251</td>
<td></td>
</tr>
<tr>
<td>% cover perennial herbs</td>
<td>0.152</td>
<td>0.562</td>
<td></td>
</tr>
<tr>
<td>% cover shrubs</td>
<td>0.597</td>
<td>0.0088</td>
<td>$y = -23.801z + 45.619$</td>
</tr>
<tr>
<td>No. seedlings</td>
<td>0.292</td>
<td>0.170</td>
<td></td>
</tr>
<tr>
<td>tree DBH</td>
<td>0.357</td>
<td>0.102</td>
<td>$y = 25.606 + 1.899x$</td>
</tr>
<tr>
<td>Ord River</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DCA axis1</td>
<td>0.697</td>
<td>0.014</td>
<td>$y = -0.462x + 6.043$</td>
</tr>
<tr>
<td>Species richness</td>
<td>0.105</td>
<td>0.677</td>
<td></td>
</tr>
<tr>
<td>% cover exotic spp</td>
<td>0.015</td>
<td>0.949</td>
<td></td>
</tr>
<tr>
<td>% cover annual herbs</td>
<td>0.061</td>
<td>0.802</td>
<td></td>
</tr>
<tr>
<td>% cover perennial grasses</td>
<td>0.564</td>
<td>0.0123</td>
<td>$y = 6.214 + 4.665x$</td>
</tr>
<tr>
<td>% cover perennial herbs</td>
<td>0.150</td>
<td>0.392</td>
<td></td>
</tr>
<tr>
<td>% cover shrubs</td>
<td>0.758</td>
<td>0.001</td>
<td>$y = -13.107z + 82.436$</td>
</tr>
<tr>
<td>No. seedlings</td>
<td>0.106</td>
<td>0.407</td>
<td></td>
</tr>
<tr>
<td>tree DBH</td>
<td>0.758</td>
<td>0.0001</td>
<td>$y = -8.539z + 39.429$</td>
</tr>
</tbody>
</table>

$^1R^2$ value is for the independent variable that gives a significant result.
$^2$Model includes the independent variables that give a significant result.

Discussion

This Chapter highlights the strong relationship between the riparian vegetation and stream hydrology for sites on the contrasting Blackwood and Ord rivers. Given this linkage between hydrology and riparian vegetation characteristics, there appears to be wide applicability of this method for identifying the link between riparian vegetation and the flow regime. Historical flow records for a particular river can be related to patterns of vegetation development, such as reproductive phenology and seedling establishment, as well as plant community patterns in riparian zones. Therefore, analysis of natural flow regimes can be used in conjunction with other abiotic and biotic factors to predict the pattern of vegetation dynamics for the riparian zone. For example, on the Murray River in eastern Australia, reduced duration and depth of winter flows and increased summer flows through the dry season increased survival of *E. camaldulensis* seedlings (Bren 1992). The relationship between stream hydrology and the
vegetation has been recorded elsewhere for littoral plants (Walker et al. 1994) and for the population dynamics of *Eucalyptus camaldulensis* seedlings on the Murray River (Bren 1992).

**Natural flow regime**

The natural flow variability of the Blackwood River indicated that it is similar to the Murray/Darling River which experiences moderate variability, while the Ord River has very high variability, similar to the arid zone rivers of inland Australia such as the Diamantina River and Cooper Creek (Walker et al. 1995), (Chapter 3). The flow regime in semi-arid regions of Australia is characterised by long periods of no flow with intermittent very large flows (Puckridge et al. 1998). The Ord River showed strong predictability of flows, mainly due to low, constant, dry season monthly flows, with substantially greater variability in wet season flows. Seasonality thus contributed relatively little to the overall predictability. A similar flow pattern has been reported for streams in the Australian wet tropics (Arthington et al. 1994; Pusey et al. 1995).

The highly predictable seasonality and low variability of flow on the Blackwood River is similar to the flow regime reported for other south-western Australian streams and rivers (Davies et al. 1998). High variability of flows in summer, due to high intensity short duration storms derived from tropical airflows (Gentilli 1972), can lead to episodic recruitment events as floodwaters disperse seed, provide moist seedbeds and create gaps in the vegetation. An example of such an event occurred in January 1982 when rain from a cyclonic depression caused an extreme flood event which resulted in extensive recruitment, particularly of the dominant overstorey species (*E. rudis* and *M. rhaphiophylla*). These species may display varying degrees of serotiny so that seed is generally always available if conditions are conducive to germination.

Flows in the Ord River are strongly seasonal, as a consequence of climatic patterns which are mainly influenced by monsoonal rainfall in the wet season (December to March) (Gentilli 1972). Flow variability is high for all months. Flows are usually of short duration, even in the wet season, being the result of high intensity rainfall events with limited groundwater storage to
sustain higher base flows (see Figure 3.6). The period of seedfall of *E. camaldulensis* and *M. leucadendra* on the Ord River may be related to the reduced flows occurring in March and April. This will be explored in Chapter 7. The episodic recruitment of these species is also likely to be related to the high variability of the flow regime, with the conditions favourable for survival of seedlings being very variable. In addition, the high energy, strong flows that frequently occur can be destructive for establishing seedlings and saplings. Large floods can also be destructive to existing mature trees (Duncan 1993; Piegay & Bravard 1997). For example, during a large flood on the Mississippi River, many riparian trees were killed, however extensive sediment deposition provided substrate for subsequent seedling recruitment (Spink & Rogers 1996).

**Discharge and vegetation relationship**

There was a strong correlation between floristic data in the vegetation plots and both duration and frequency of flooding. This clearly shows the relationship of these flow variables in determining the characteristics of the riparian vegetation and the zonation of the vegetation along a gradient with distance from the low flow water level for both rivers. However, because of the dominance of different vegetation life forms on the two rivers and the different flow regimes, response to flooding is likely to be quite different. For both rivers there was an increase in disturbance-tolerant ruderal species with increased duration and frequency of flooding. These were annual herbs and annual grasses on the Blackwood River and perennial grasses on the Ord River. On the Ord River, perennial grasses are considered tolerant to flooding and are usually short-lived and are able to quickly colonise new sediments. In contrast, woody shrubs tend to be terrestrial species such as *Acacia* spp. which are not tolerant of waterlogging and, as a consequence, are killed by long duration of flooding or frequent flooding. In addition, these species cannot survive on unstable sediments created by frequent flooding. On both rivers cover of shrubs declined with increased flooding. This life form can be fairly long-lived and they are usually stress tolerators which do not persist under frequent disturbance. On the Blackwood River, species richness was reduced with increased duration of flooding and may reflect a gradient in tolerance to the physiological stress of waterlogging. The cover of exotic species (mainly annual species) was greater with increased duration and frequency in flooding and
suggests that high flooding frequency (and therefore high levels of disturbance) enhances the spread of these species which tend to be ruderal species adapted to high levels of disturbance (Grime 1979). Spread of exotics is further enhanced by other disturbances such as fire and livestock grazing which are common disturbances on the Blackwood River (see Chapter 6).

The number of tree seedlings showed no relationship with inundation, indicating that germination of seeds and early establishment of seedlings may be more influenced by other factors including microsite, soil moisture and soil texture. Size class structure of trees and flooding showed no relationship on the Blackwood River. On the Ord River smaller sized (i.e. younger) trees occurred in areas more frequently flooded and large mature trees generally occurred at higher elevations with low flooding frequency. On the Blackwood River, trees (particularly E. rudis) can establish and mature anywhere throughout the profile, including at low elevations near the water's edge, indicating that newly established trees are not unduly affected by floodwaters. Smaller size classes tended to occur in areas less prone to flooding and perhaps in areas where presumably competition from older trees is less intense. The spatial distribution of tree size classes within the riparian zone will be examined in detail in Chapter 9.

The relationship between natural flow regime and riparian vegetation outlined in this chapter, for these rivers, indicates different models of vegetation dynamics for each river. On the Ord River, the large wet season floods capable of scouring soil and destroying vegetation are highly episodic and in the intervening years smaller floods allow the development of the existing trees and the recruitment of younger age classes. This prevents the establishment of stable states and therefore the ecosystem is characterised by long periods of transition between short-lived stable states. In contrast, lower energy, more predictable seasonal flooding on the Blackwood River allows mature stands of trees to develop throughout the river profile. This disturbance regime results in long periods of stable states with short periods of transition. This aspect will explored in more detail in following chapters.
Aspects of the methodology of the “holistic method” adapted here was useful for identifying the natural flood disturbance regime that occurred at these sites and their impacts on vegetation dynamics of the riparian vegetation. The addition of vegetation data can strengthen the applicability of the holistic method for determining ecologically significant river flows for setting criteria for environmental water requirements in regulated river systems. Previously, this has been determined with reference to riparian vegetation but without quantitative data (i.e. Davies et al. 1998). The techniques described here can be used to compare the response of different vegetation components of the riparian vegetation to different fluvial regimes. This technique can be expanded and applied in the management of riparian zones and in planning rehabilitation programs, such as for deciding the appropriate species to be planted in different landscape positions within the riparian zone. It may also be useful for improving the ecological knowledge base for setting environmental flows in regulated systems. Clearly, this technique is useful in the management of the vegetation in the riparian zone, not only for natural systems but also for regulated systems.
CHAPTER 6

EFFECTS OF LIVESTOCK GRAZING AND FIRE DISTURBANCE ON RIPARIAN VEGETATION

Introduction

One of the most serious impacts on the riparian zone is due to livestock. Livestock, usually cattle or sheep, can have direct impacts such as destruction and trampling of vegetation. They can also cause erosion (by trampling stream banks), compaction of the soil, increased nutrient levels, both in-stream and in the soil, and also increased in-stream turbidity (Fleischner 1994). On most rivers in the agricultural and pastoral zones of Australia, livestock have free access to the riparian zone for summer watering and grazing. In the Kimberley region of north-western Australia, cattle overgrazing of the native vegetation has caused major erosion and siltation problems in many rivers (Williams et al. 1996). With the loss of native species and reduction in cover, an increase in nutrient levels and disturbance of the soil surface, livestock can also promote invasion by weeds (usually annual ruderal species) and bring about changes in vegetation structure (Kauffman et al. 1983; Fleischner 1994). In many semi-arid areas, the riparian zone is highly susceptible to grazing as livestock tend to congregate in this zone which is the most productive and may be the only source of water (Wilson 1990; Armour et al. 1994). Grazing by domestic livestock can dramatically change the structure of the vegetation by preventing recruitment of trees and shrubs, thus transforming woodlands into grasslands (Chesterfield 1986; Gibson & Kirkpatrick 1989; Cheal 1993). In some semi-arid regions of Australia the opposite problem has emerged, with livestock promoting invasion by unpalatable woody shrubs and thus adversely modifying native grasslands (Hodgkinson & Harrington 1985; Williams 1990). In some
pastoral areas of Australia, such as chenopod shrublands, palatable species may become locally extinct under continued grazing pressure from domestic stock (Wilson 1990).

Identification of the proportion of different life form groups among plants within a community can be useful in providing a means of predicting the community response to continued stress and disturbance such as from grazing or fire. Individual plant species response to grazing varies according to growth form and reproductive strategy. For example, annual species are more tolerant of disturbance, due to their fast growth rates and early and prolific seed set, than perennial species which tend to be comparatively slow growing and usually require several years to reach reproductive maturity (Grime 1974). Other groups, such as perennial grasses, avoid heavy grazing pressure by having above-ground growth occurring in winter and spring, and dying back to an underground storage organ over summer or the dry season (Pate & Dixon 1981) when grazing pressures are usually heaviest. This situation may occur in riparian areas that are continuously grazed. These functional strategies of plants have been observed in riverine lentic ecosystems in which competition and stress tolerance were found to be the most important traits rather than disturbance (Hills et al. 1994)

Fencing to exclude stock, or to at least manage grazing, is a fundamental step towards achieving rehabilitation of degraded riparian sites. Whether grazing needs to be excluded completely will depend on the type of community and the level of existing degradation (Armour et al. 1994). In environments that have had a long history of grazing and where the vegetation has adapted to this form of stress, the exclusion of livestock may result in changes to the vegetation structure such as invasion by woody plants and reduction in species diversity (Williams 1990; Milchunas & Lauenroth 1993). Experiments on grazing exclusion in riparian vegetation have shown a reduction in species richness and an increase in plant cover (Kauffman et al. 1983). Predicting which particular species are most affected by livestock grazing and which species are likely to return after stock exclusion is important for managing the rehabilitation of degraded riparian areas.
Altered fire regime is another impact within riparian zones that may have detrimental effects on regeneration and particularly in combination with livestock grazing. Many plants in the riparian zone may require a disturbance such as strong river flows or fire to provide gaps for recruitment (Kellman & Tackaberry 1993) and to stimulate seed release (Lamont et al. 1991) and germination (Shea et al. 1979). In managed areas, prescribed fires for fuel-reduction or to stimulate new growth of edible species may be too frequent, resulting in the loss of many species and the increase in weeds (Busch & Smith 1993), or fire may be too infrequent to create gaps to stimulate recruitment of native riparian species.

A large proportion of the riparian zone of the Blackwood River and virtually all of the Ord River are subjected to uncontrolled livestock grazing and fire. Therefore a study of the recruitment of riparian vegetation of these rivers needs to investigate the effects of these disturbances. Vegetation analysis in Chapter 4 indicated that a major determinant of floristic composition is livestock grazing, particularly for the Blackwood River sites. These differences will be explored in greater detail in this Chapter, along with preliminary results of the recovery of vegetation where grazing has been excluded.

This Chapter will examine aspects of livestock and fire disturbance in the riparian zone. These include surveying what effects livestock grazing has had on the floristics of sites on the Blackwood and Ord Rivers, particularly in relation to species richness and diversity; structural changes in terms of life form; and seedling establishment and continued recruitment of particular species. This chapter will provide a more detailed analysis of the effects of livestock grazing on the riparian vegetation that were described Chapter 4. In addition, using grazing exclusion plots, this Chapter will describe short term changes in the vegetation in the absence of grazing and will present some data on the effects of fire on riparian vegetation on these rivers.
Methods

Sites surveyed for comparison of grazed and ungrazed riparian zones are described in Chapters 3 & 4 and included Sites B1a & b, B2a & b and B3a & b on the Blackwood River and Sites O4 & O5 on the Ord River. Blackwood River Site B1 was located on the lower section of the middle catchment with Site B1a in an area of intact jarrah (*Eucalyptus marginata*) forest upslope of the riparian zone. Site B1b is some 5 kilometres upstream in an area where land upslope of the riparian zone has been cleared for pasture and is grazed by cattle which have free access to the riparian zone. Site B2a was located in a remnant of around 10 hectares of the original jarrah/wandoo woodland surrounded by cleared agricultural land. Site B2b was on the opposite bank of the river, in an area of pasture cleared down to the riparian zone and which is grazed by sheep. Site B3 was in the upper catchment in the area most affected by salinity and consisted of a remnant of native vegetation of around 30 hectares adjacent to the river (Site B3a) and of an area of cleared land 1 kilometre upstream adjacent to the riparian zone which is grazed by sheep (Site B3b). Stocking rates in the grazed sites can vary considerably but usually range from 0.5 - 5 sheep per hectare, with greatest grazing pressure in summer when annual pastures die off and there is a lack of green feed in the surrounding agricultural land. In areas cleared for agriculture, a strip of riparian vegetation along the river was generally left with at least the overstorey intact.

For the Ord River, areas of the riparian zone that are not grazed by cattle are extremely rare and so for this comparison a site within the Ord River regeneration area (Site O5) was selected as a non-grazed site. This site has been free from cattle grazing for the past 30 years, although it was heavily grazed in the past (de Salis 1993). Throughout this Chapter this site will be referred to as ungrazed, although this is not strictly the case. It was compared to Site O4 on the Negri River (a major tributary of the Ord River) around 8 kilometres downstream which is currently being grazed at around 1 animal per 10 hectares, although cattle densities are probably much higher around the river during the dry season (Petheram & Kok 1991).
At each site, transects perpendicular to the river were established, the length of each varying depending on the width of the riparian zone. Along each transect, 10 metre x 10 metre quadrats were established at variable distances located to coincide with the bands of vegetation, giving a total of 10 quadrats at each site. Within each plot, all plants rooted within the plot were identified and an estimate of percentage cover was made, where cover is the vertical crown or shoot projection per species. In addition, along the 10 metre wide belt transects, size class (as diameter at breast height (DBH)) distribution of overstorey species was recorded. Vegetation surveys were completed in July and August 1997 on the Ord River and in October and November 1997 on the Blackwood River. Response to grazing of species common to both grazed and ungrazed sites is compared using a response index (Williams 1969). This is the ratio of cover of a species per unit area in grazed quadrats to the cover of a species per unit area in ungrazed quadrats.

Exclosure plots were established at three grazed riparian sites on the Blackwood River (Site B4, Site B5 and Site B3b, see Figure 3.2). These sites were adjacent to cleared agricultural land and had been subject to livestock grazing for at least the last 25 years. At each site five 10 metre x 10 metre quadrats were pegged out and a sheep-proof ring-lock fence was erected around each plot. Adjacent to each fenced plot an open 10 metre x 10 metre plot was also pegged. While fencing excluded domestic livestock, rabbits and native herbivores could gain access. All plants rooted within each plot were identified and an estimate of percentage cover was made. The initial survey of all exclosure and adjacent open plots was completed in September and October 1996 for Site B4 and Site B3b and October 1997 for Site B5, with subsequent surveys carried out in October 1997 and 1998.

On the Ord River livestock exclosure plots were set up in April 1998 at Site O1 (in the area downstream of the Diversion Dam) and were re-surveyed in April 1999. Three 20 metre x 20 metre plots were fenced with three strands of barbed wire to exclude cattle and adjacent to each of these exclosure plots a 20 metre x 20 metre open plot was also pegged out. Fencing was designed to exclude cattle but allow access to native herbivores.
For each survey at all sites all species within a plot were recorded and their percentage cover within the plot was estimated. Numbers of seedlings of overstorey species was also recorded within each plot. To identify the effects of grazing on plant functional types, species were grouped according to life form. Attributes within each plot were averaged for a site so that grazed and ungrazed sites could be compared. A Mann-Whitney non-parametric U test was performed for species richness and total vegetation cover between means for the exclosure plots and adjacent open plots to test for a significant change after 12 months.

At Site B2a (ungrazed) on the Blackwood River a wildfire occurred in April 1997 and the transects on this site were re-measured in April 1999 (i.e. two years post-fire) to assess the recovery of and effect of this fire on the riparian vegetation. At Site B4 on the Blackwood River a controlled bum was carried out in May 1996 in part of the heavily grazed riparian zone and five 10 metre x 10 metre exclosure and open plots were established in this area to assess the effect of fire on natural regeneration and to compare changes with the plots in the unburnt area. In addition, to assess the effect of fire on the release of seed from the dominant overstorey species at this site, Melaleuca rhaphiophylla, thirty branches from ten trees at each of the burnt and unburnt sites were examined and the proportion of open fruit was recorded.

Results

Comparison of grazed and ungrazed riparian areas

For two of the three paired sites on the Blackwood River, species richness and diversity was significantly higher at the ungrazed sites than at grazed sites (Table 6.1). Percentage of litter within a plot was also significantly greater in ungrazed plots whereas percentage of bare ground and number of tree seedlings was not. In terms of species, native perennial herbs, and particularly
shrubs, showed significantly greater numbers in the ungrazed sites, comprising an average of 26% of species and 31% of cover in the ungrazed sites with no shrubs present in the grazed sites on the Blackwood River (Table 6.2). Cover of perennial herbs was significantly greater at the grazed Site B3b due to the dominance of a single unpalatable sedge species, *Gahnia trifida*. There was significantly greater foliage cover of exotic annual herbs and exotic grasses in the grazed site at Site B1 and of exotic grasses at Site B3. There was generally a high proportion of cover of exotic species in the ungrazed locations at all sites.

Table 6.1: Comparison of floristic attributes, percentage bare ground and percentage litter cover as well as number of tree seedlings between ungrazed and grazed locations at three sites on the Blackwood River. Figures are means of 10 plots at each site. P values are for Mann-Whitney U test for ungrazed and grazed comparisons.

<table>
<thead>
<tr>
<th></th>
<th>Site B1</th>
<th>Site B2</th>
<th>Site B3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>b</td>
<td>p</td>
</tr>
<tr>
<td>Species richness</td>
<td>29.3</td>
<td>12.1</td>
<td>0.004</td>
</tr>
<tr>
<td>Species diversity</td>
<td>2.5</td>
<td>1.3</td>
<td>0.006</td>
</tr>
<tr>
<td>% bare ground</td>
<td>38.7</td>
<td>19.1</td>
<td>0.540</td>
</tr>
<tr>
<td>% litter cover</td>
<td>27.5</td>
<td>4.1</td>
<td>0.005</td>
</tr>
<tr>
<td>tree seedlings</td>
<td>4.3</td>
<td>15.3</td>
<td>0.127</td>
</tr>
</tbody>
</table>

For theOrd River comparison there was no significant difference in any of the floristic attributes or life form groups between the grazed (Site O4) and ungrazed (Site O5) sites (Tables 6.3 & 6.4). An exception was the significantly greater cover of exotic species at the ungrazed site which is most likely due to the deliberate introduction of species such as *Cenchrus ciliaris*, *C. setiger* and *Aerva javanica* to stabilise highly degraded areas at this site (Site O5) (de Salis 1993). There was also a significantly greater proportion of bare ground at the grazed Ord River site (Table 6.3).
Table 6.2: Comparison of plant life form groups between ungrazed and grazed locations at three sites on the Blackwood River by number of species and percentage foliage cover. Figures are means of 10 plots at each site. P values are for Mann-Whitney U test for ungrazed and grazed comparisons.

<table>
<thead>
<tr>
<th>Life Form¹</th>
<th>Site B1</th>
<th></th>
<th>Site B2</th>
<th></th>
<th>Site B3</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>a</td>
<td>a</td>
<td>b</td>
<td>b</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td>ungrazed</td>
<td>grazed</td>
<td>ungrazed</td>
<td>grazed</td>
<td>ungrazed</td>
<td>grazed</td>
</tr>
<tr>
<td></td>
<td>species</td>
<td>species</td>
<td>species</td>
<td>species</td>
<td>species</td>
<td>species</td>
</tr>
<tr>
<td>nah</td>
<td>4.7</td>
<td>2</td>
<td>1</td>
<td>0.3</td>
<td>0.37</td>
<td>3</td>
</tr>
<tr>
<td>eah</td>
<td>4.5</td>
<td>4.7</td>
<td>4.3</td>
<td>2.5</td>
<td>0.10</td>
<td>2.7</td>
</tr>
<tr>
<td>eg</td>
<td>1.8</td>
<td>2.8</td>
<td>3.2</td>
<td>3.2</td>
<td>-</td>
<td>3.2</td>
</tr>
<tr>
<td>nph</td>
<td>6.5</td>
<td>1.3</td>
<td>3.5</td>
<td>0</td>
<td>-</td>
<td>1.0</td>
</tr>
<tr>
<td>rs</td>
<td>10.2</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td>% foliage cover</td>
<td>6.3</td>
<td>4.3</td>
<td>0.6</td>
<td>0.1</td>
<td>0.38</td>
<td>0.5</td>
</tr>
<tr>
<td>nah</td>
<td>5.1</td>
<td>18.1</td>
<td>11.7</td>
<td>2.1</td>
<td>0.15</td>
<td>7.5</td>
</tr>
<tr>
<td>eah</td>
<td>9.4</td>
<td>28.3</td>
<td>19.7</td>
<td>27.3</td>
<td>0.47</td>
<td>18.3</td>
</tr>
<tr>
<td>eg</td>
<td>13.4</td>
<td>5.3</td>
<td>9.4</td>
<td>0</td>
<td>-</td>
<td>6.3</td>
</tr>
<tr>
<td>nph</td>
<td>10.2</td>
<td>0</td>
<td>17.6</td>
<td>0</td>
<td>-</td>
<td>22.5</td>
</tr>
<tr>
<td>% cover</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹Life Forms: nah=native annual herbs; eah=exotic annual herbs; eg=exotic grasses; nph=native perennial herbs; ns=native shrubs.

Grazing response index gives an indication of the response of particular species to grazing. This showed the strong positive response to grazing of many species of exotic annual herbs and grasses at the Blackwood River sites, although some of these species, such as the exotic annual herb common to disturbed areas, *Hypochaeris glabra*, showed a negative response (Table 6.5). Native perennial grasses had a fairly neutral or slightly negative response to grazing, with species benefiting from a reduction in cover of other perennial species at grazed sites but also being susceptible to heavy grazing. At the Ord River sites, species representing a variety of life forms responded positively to grazing (Table 6.5), including the exotic vine *Passiflora foetida*, a widespread weed of rivers and creeks in the Kimberley region (Wheeler *et al.* 1992).
Table 6.3: Comparison of floristic attributes, percentage bare ground and percentage litter cover as well as number of tree seedlings between ungrazed and grazed locations on the Ord River. Figures are means of 10 plots at each site. P values are for Mann-Whitney U test for ungrazed and grazed comparisons.

<table>
<thead>
<tr>
<th></th>
<th>Site O5 ungrazed</th>
<th>Site O4 grazed</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species Richness</td>
<td>7.2</td>
<td>5.7</td>
<td>0.23</td>
</tr>
<tr>
<td>Species Diversity</td>
<td>2.0</td>
<td>2.0</td>
<td>0.46</td>
</tr>
<tr>
<td>% bare ground</td>
<td>19.0</td>
<td>56.5</td>
<td>0.01</td>
</tr>
<tr>
<td>% litter cover</td>
<td>9.7</td>
<td>9.2</td>
<td>0.32</td>
</tr>
<tr>
<td>No. of tree seedlings</td>
<td>49.0</td>
<td>28.0</td>
<td>0.14</td>
</tr>
</tbody>
</table>

Table 6.4: Comparison of plant life form groups between ungrazed and grazed locations on the Ord River by number of species and percentage foliage cover. Figures are means of 10 plots at each site. P values are for Mann-Whitney U test for ungrazed and grazed comparisons.

<table>
<thead>
<tr>
<th>Life form</th>
<th>Site O5 ungrazed</th>
<th>Site O4 grazed</th>
<th>p</th>
<th>Site O5 ungrazed</th>
<th>Site O4 grazed</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>exotic species</td>
<td>3.4</td>
<td>1.9</td>
<td>0.06</td>
<td>48.3</td>
<td>13.5</td>
<td>0.001</td>
</tr>
<tr>
<td>annual herbs</td>
<td>0.3</td>
<td>0.1</td>
<td>0.92</td>
<td>0.53</td>
<td>0.05</td>
<td>0.84</td>
</tr>
<tr>
<td>perennial grasses</td>
<td>2.1</td>
<td>1.8</td>
<td>0.46</td>
<td>46.7</td>
<td>13.6</td>
<td>0.001</td>
</tr>
<tr>
<td>perennial herbs</td>
<td>0.5</td>
<td>0.3</td>
<td>0.52</td>
<td>0.17</td>
<td>0.31</td>
<td>0.21</td>
</tr>
<tr>
<td>shrubs</td>
<td>1.4</td>
<td>1.2</td>
<td>0.78</td>
<td>1.6</td>
<td>0.57</td>
<td>0.24</td>
</tr>
<tr>
<td>trees</td>
<td>2.0</td>
<td>2.1</td>
<td>0.89</td>
<td>28.1</td>
<td>22.0</td>
<td>0.47</td>
</tr>
<tr>
<td>lianas</td>
<td>0.5</td>
<td>0.2</td>
<td>0.75</td>
<td>1.5</td>
<td>2.4</td>
<td>0.12</td>
</tr>
</tbody>
</table>

Comparison of size class distribution of overstorey species for grazed and ungrazed sites on the Blackwood River reveals the absence of trees in the smallest size class (i.e. juveniles and saplings) at the grazed sites (Figure 6.1a). This may indicate that little recruitment into the population has taken place for some time. In contrast, the greatest proportion of trees at the ungrazed sites are in the smallest size class, as would be expected as large numbers of recruits enter the population with numbers reducing over time through natural attrition. On the Ord River, size class distribution was similar for both grazed and ungrazed sites, with the greatest proportion in the smallest size class and numbers reducing with size class (Figure 6.1b).
Figure 6.1: Comparison of size class distribution of overstorey species at grazed and ungrazed sites on the a) Blackwood River and b) Ord River sites.
Table 6.5: Grazing response index (cover in grazed/cover in ungrazed) for species common to grazed and ungrazed sites on the Blackwood and Ord rivers.

<table>
<thead>
<tr>
<th>Blackwood River Species (life form)</th>
<th>Grazing response index</th>
<th>Ord River Species</th>
<th>Grazing response index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Avena fatua (ag)*</td>
<td>23.5</td>
<td>Passiflora foetida (v)*</td>
<td>16</td>
</tr>
<tr>
<td>Aira careophyllea (ag)*</td>
<td>7.1</td>
<td>Eragrostis tenellula (ag)</td>
<td>5.2</td>
</tr>
<tr>
<td>Romulea rosea (ah)*</td>
<td>6.9</td>
<td>Sida fibulifera (s)</td>
<td>5.1</td>
</tr>
<tr>
<td>Cynodon dactylon (pg)*</td>
<td>4.4</td>
<td>Heteropogon contortus (pg)</td>
<td>4.6</td>
</tr>
<tr>
<td>Vulpia myuros (ag)*</td>
<td>4.3</td>
<td>Achyranthes aspera (ph)</td>
<td>2.5</td>
</tr>
<tr>
<td>Arctotheca calendula (ah)*</td>
<td>3.5</td>
<td>Parkinsonia aculeata (s)*</td>
<td>1.6</td>
</tr>
<tr>
<td>Lolium rigidum (ag)*</td>
<td>2.7</td>
<td>Cynodon dactylon (pg)*</td>
<td>1.0</td>
</tr>
<tr>
<td>Gahnia trifida (ph)</td>
<td>2.4</td>
<td>Datura inoxia (ah)*</td>
<td>1.0</td>
</tr>
<tr>
<td>Bromus diandrus (ag)*</td>
<td>2.1</td>
<td>Crotalaria novaehollandiae (s)</td>
<td>0.7</td>
</tr>
<tr>
<td>Ptilotus mangelsii (ph)</td>
<td>1.5</td>
<td>Cypres holoschoenus (ph)</td>
<td>0.6</td>
</tr>
<tr>
<td>Briza minor (ag)*</td>
<td>1.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Danthonia caespitosa (pg)</td>
<td>1.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Helipterum cotula (ah)</td>
<td>1.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anagallis arvensis (ah)*</td>
<td>0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Neurachne alopecuroidea (pg)</td>
<td>0.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Austrostipa elegantissima (pg)</td>
<td>0.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hypochaeris glabra (ah)*</td>
<td>0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Galium murale (ah)*</td>
<td>0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oxalis corniculata (ah)*</td>
<td>0.13</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cotula turbinata (ah)*</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 life forms include: ah = annual herb, ag = annual grass, ph = perennial herb, pg = perennial grass, s = shrub, v = vine.

2 Grazing response index = mean cover at grazed site/mean cover at ungrazed site

Grazing exclusion from grazed riparian land

After three years 'relief' from grazing, vegetation in exclosure plots at the heavily grazed sites on the Blackwood River have shown only small changes. The major difference has been a slight increase in species and cover of exotic species and also some native species (Figure 6.2). Changes have been variable across the sites as the majority of species are annuals and therefore are highly influenced by yearly variations in climatic conditions, particularly timing and amount of rainfall. Only at Site B3b has there been a noticeable increase in cover of native species in exclosure plots relative to open plots due to the growth of the perennial herb Gahnia trifida, with a relative growth rate in exclosure plots of 0.32 m² yr⁻¹ compared to 0.17 m² yr⁻¹ in the open plots. Changes in number of species and cover of the different life form groups in the exclosure
plots relative to changes in adjacent open plots over the study period show similar variability between sites (Figure 6.3). Native perennial grasses and herbs increased in both number of species and cover at all sites. Indicating that they have benefited from relief from grazing. Exotic annual herbs and grasses had generally increased but yearly variability would make discerning any trends difficult at this early stage. At the only site where shrubs were originally present (Site B4) these had also increased in number and cover, including the legume species *Acacia acuminata* and *Jacksonia furcellata*. The abundance of seedlings of overstorey species was similar in exclosure and open plots at two of the sites but numbers were much greater in the exclosure plot at Site B3b (Figure 6.4). New seedlings appeared each year in both exclosure and open plots but older seedlings were rarely seen in the open plots. There was some survival of seedlings into subsequent years in the exclosure plots (Figure 6.4).

Exclosure plots at Site O1 on the Ord River showed no significant increase in the number of species but a significant increase in cover of the vegetation after 12 months. Mean number of species per 400 m² changed from 15.7±0.9 to 18.3±0.7 (p = 0.415) and mean total vegetation cover increased from 110.5±8 to 164±17 (p = 0.003). In contrast, in the adjacent open plots species richness fell slightly, but not statistically significantly, after 12 months, with mean number of species changing from 18.3±3 to 16.6±2 (p = 0.211) but vegetation cover significantly decreased from 133±10.4 to 96.4±3 (p = 0.004). At the initial survey and after 12 months there was no significant difference in the mean number of species between exclosure and open plots (p=0.324) and (p=0.169). While vegetation cover was significantly greater in the open plots initially (p=0.012), after 12 months cover in the exclosure plots was significantly greater (p=0.008). In terms of life form groups, number of species in each group have not changed significantly in either exclosure or open plots (Figure 6.5a). For cover, annual herbs, perennial herbs and lianas had shown the greatest increase in the exclosure plots, while perennial grasses have declined in the open plots (Figure 6.5b).
Figure 6.2: Change in number of species and percentage cover of vegetation in plots where livestock grazing has been excluded, compared with adjacent open plots where grazing has continued, at three riparian sites on the Blackwood River. Values are obtained from the means (±SEM) of five plots at each site.
Figure 6.3: Change in number of species and percentage cover of different life form groups in exclosure plots relative to adjacent grazed plots after 3 years at Site B3b and Site B4 and 2 years at Site B5 on the Blackwood River. Values are obtained from the means of five plots at each site.
Figure 6.4: Occurrence of tree seedlings (*Eucalyptus rudis* & *Melaleuca rhaphiophylla* at Site B4 & B5, *Casuarina obesa* at Site B3b) over a three year period in fenced exclosure plots and adjacent unfenced grazed plots at three riparian zone locations subjected to heavy livestock grazing on the Blackwood River.
Figure 6.5: Change in (a) number of species and (b) percentage cover of different life form groups in fenced and adjacent open plots over 12 months at riparian site (O1) subjected to cattle grazing on the Ord River.
Effects of fire on riparian vegetation

In fenced plots at Site B4 which were burnt in 1996 cover of exotic herbs increased from 37% to 52% (p=0.003) and in unburnt plots decreased from 27% to 24% (p=0.314) after 3 years. Cover of exotic grasses also increased from 17% to 66% in burnt plots (p=0.014) and from 40% to 71% (p=0.023) in unburnt plots. Thus fire had either no effect or a slightly negative effect on reducing the cover of these exotic life forms which were dominant at this site prior to burning. A similar result was seen in the numbers of species of these life forms. For native plants, although not significant, there was a decrease in cover (10.6% to 3.6%, p=0.08) and species richness increased slightly (4 to 5.5, p=0.46). Number of species of native perennial herbs has increased in the burnt plots and cover of perennial grasses has also increased, while there has been a reduction in cover of annual herbs. In unburnt plots, over the same period, cover of perennial herbs and shrubs has also increased (Figure 6.6). Overall, for native perennial species, five species have been gained and one lost in the burnt plots after three years and six species have been gained and two lost in the unburnt plots. The fire at this site appears to have initially stimulated the germination of seedlings of the main overstorey species (*Melaleuca rhaphiophylla* and *Eucalyptus rudis*) (Figure 6.7). However after three years the number of seedlings and young saplings is similar for the burnt and unburnt plots. Inspection of mature seed capsules on branches of *Melaleuca rhaphiophylla* showed no significant difference in the proportion of open capsules between the burnt (47.9% of capsules open) and unburnt plots (48.7% of capsules open) (p = 0.96). This would indicate that fire has not stimulated a greater release of seed.

Twenty four months after a wildfire in an ungrazed riparian site on the Blackwood River (Site B2a) species numbers have changed little from pre-burn levels measured in 1997 (Figure 6.8). Cover of exotic species has increased significantly after the fire, from a plot mean(±SEM) of 31±6% to 72±5% (p<0.0001). The greatest increases were in the exotic grasses, particularly *Ehrharta calycina* and *E. longiflora*. The native annual grass *Austrostipa compressa* was also prominent post-burn (2.5±0.5%), but was not recorded at this site pre-burn. Cover of native perennial herbs and shrubs decreased from 29±5.4% pre-burn to 19.4±3% post-burn (p=0.084).
Figure 6.6: Change in number of species and cover of different native life form groups in burnt and unburnt fenced plots in a heavily grazed riparian site (Site B4) on the Blackwood River.

Figure 6.7: Occurrence of tree seedlings (*Eucalyptus rudis* & *Melaleuca rhaphiophylla*) in fenced, burnt and fenced, unburnt plots over a three year period at Site B4 on the Blackwood River.
a) Mean No. Species  

<table>
<thead>
<tr>
<th>Species</th>
<th>1:ne-burn post-burn</th>
</tr>
</thead>
</table>

b) Mean cover

- 100
- 90
- 80
- 70
- 60
- 50
- 40
- 30
- 20
- 10
- 0

Figure 6.8: Change in (a) mean number of species and (b) mean cover of different life form groups before (pre-burn) and 24 months after (post-burn) a wildfire at Site B2a on the Blackwood River.
Many common species such as Acacia saligna, Hypocalymma angustifolium, Melaleuca rhaphiophylla and M. incana had been completely defoliated by the fire but the majority of individuals had resprouted from underground lignotubers or epicormic buds. In addition, many seedlings of native perennial species were observed, including Eucalyptus rudis (10 seedlings), Melaleuca rhaphiophylla (54), Acacia saligna (122), Jacksonia sternbergiana (21), Hypocalyma angustifolium (10) and Dodonea viscosa (5).

Discussion

Grazing effects on riparian vegetation
One obvious effect of intensive herbivory in a native plant community is a reduction of species diversity through the elimination of palatable species (Whelan 1989). If intense grazing continues over a long period the grazed area will tend towards becoming a grassland because of the competitive advantage in the life cycle of grasses (Miles 1979). This trend has been documented in sub-alpine woodlands in the eastern states of Australia (Bryant 1971; Wimbush & Costin 1979; Gibson & Kirkpatrick 1989).

Disturbances such as grazing and soil disturbance have led to loss of native species, with partial replacement by exotics in temperate Australian grasslands (McIntyre & Lavorel 1994). On the Blackwood River livestock grazing in the riparian zone has resulted in species richness and diversity being reduced as many native perennial species have been lost and replaced by fewer exotic annual species. The exotic species recorded at the study sites are mainly grasses and annual herbs most of which are ruderal species with characteristics which allow them to thrive in highly disturbed environments. These attributes include seed dormancy, short life histories and early flowering (Grime 1979). The invasion by exotic species may also be enhanced by the reduction in cover of perennial species creating gaps which ruderal species are best able to exploit. Native perennial shrubs and herbs have suffered the most significant loss of species. These species are generally slow-growing stress tolerators which are particularly susceptible to
grazing pressure in the late summer and early autumn when annual pasture species have died leaving perennial plants in the riparian zone to provide the only source of green feed for livestock and the river as the only source of water. This loss of perennial species has also resulted in a simplification of the structure of the riparian vegetation, an impact observed in other environments in Australia (Gibson & Kirkpatrick 1989; Cheal 1993). In riparian zones in the USA, livestock grazing has been shown to reduce species richness and to alter vegetation structure by the loss of woody perennial species in particular (Kauffman et al. 1983; Fleischner 1994). In environments with a long history of grazing, species diversity usually exhibits a bell shaped response (Grime 1974), with highest species diversity at intermediate levels of disturbance (such as grazing) and species diversity reduced in the absence of grazing (McNaughton 1985; Williams 1990; Milchunas & Laurenroth 1995). However, environments in south-western Australia, although they are adapted to some grazing by herbivores such as kangaroos, are poorly adapted to heavy grazing by large, hard-hoofed herbivores such as sheep and cattle.

Large numbers of exotic grasses and annual herbs were seen in ungrazed riparian areas. This may be due to the high level of natural disturbance of the riparian zone and the availability of moisture which favours these ruderal species. These conditions suit the ruderals capacity for fast growth rates and ability to rapidly exploit resources while they are available. This and other forms of disturbance, such as edge effects, increased fire frequency and fertiliser drift combine to affect remnants of native vegetation in an agricultural matrix (Saunders et al. 1991). Transportation of seed of ruderal species may also be facilitated by water-borne dispersal along the river. At Site B3 the riparian vegetation is also affected by rising levels of salinity, where many salt tolerant exotics such as *Atriplex prostrata* and *Hordeum leporinum* can colonise.

These results have shown that grazing does not inhibit germination of seed of overstorey species. However, from analysis of size classes and results from the exclosure plots it is clear that these new germinants are generally not surviving beyond the first 12 months. Grazing and competition for light and moisture from weeds and detrimental effects on soil structure, such as compaction,
are likely to be the most important factors in preventing survival of tree seedlings (De Steven 1991; Pettit et al. 1998). This lack of recruitment is a serious threat to the composition and structure of the riparian vegetation because of the important role of trees in the functioning of the riparian zone (Bunn 1993).

On the Ord River there was little difference between grazed and ungrazed sites, which may reflect the long history of grazing of this environment and the dominance of the understorey by Poaceae spp. which are generally well adapted to grazing (Wilson 1990). The grassy understorey predominant in the east Kimberley has evolved as a result of the seasonally dry climate and the frequent burning regime (Beard 1979). Grazing animals other than cattle, including feral horses, donkeys, goats and pigs may also have a considerable impact on the riparian zone vegetation. Significantly reduced cover of perennial grasses and a larger proportion of area of bare ground are the only indicators of greater grazing pressure at the grazed site (Site O4). The fact that the ungrazed site (Site O5) was heavily grazed in the past may contribute to the lack of difference between the grazed and ungrazed sites. High levels of bare ground at the grazed site may indicate that livestock are causing problems by increasing the erosion potential in the riparian zone through destruction and trampling, a common problem of over-grazing (Wilson 1990; Armour et al. 1994). Seedlings of overstorey species were recorded for both grazed and ungrazed Ord River sites and the size class distribution indicates that recruitment into both populations is taking place. Grazing therefore does not appear to affect tree recruitment. This may indicate that abiotic factors such as river hydrology and geomorphology are more influential than livestock grazing on overstorey recruitment on the Ord River sites and mask the effects of grazing on the vegetation (Friedel et al. 1993). The influence of river fluvial processes on recruitment patterns of the vegetation will be explored in later chapters. There may also have not been enough sites sampled to discern any effect of grazing. Further, sampling may also need to be stratified to isolate the grazing effect from the influence of other factors. Other possible explanations for the lack of recruitment of overstorey species on the grazed sites on the Blackwood River while recruitment was adequate on the Ord River, is the greater grazing intensity on the Blackwood River. However, grazing intensity in the
The palatability of the overstory species of *Eucalyptus* and *Melaleuca* are unlikely to be different for the two rivers. The processes by which livestock grazing can prevent the recruitment of riparian overstory species is an important aspect of regeneration in the riparian zone and requires further investigation to clarify these issues.

There is wide variation in individual species response to grazing. On the Blackwood River native shrubs are obviously the most susceptible to grazing as they are almost completely absent from the heavily grazed sites. Common pasture weeds such as the annual grasses *Avena fatua* and *Aira careophyllea* and the exotic annual forb *Romulea rosea* all responded positively to grazing and would be regarded as increaser species (see Hacker 1987). These annuals are ruderal species, well adapted to exploiting disturbed conditions (Grime *et al.* 1986). They complete their life cycle in less than one year and therefore are usually absent in the dry summer months when grazing pressure in the riparian zone is most intense as livestock feed has disappeared from surrounding annual pastures. Other annual exotics such as *Hypochaeris glabra* showed a negative response to grazing. This species has been reported as being highly palatable to stock and therefore is a decreaser species (Williams 1969), however it is well adapted to colonising disturbed sites and under favourable conditions can occur as a short-lived perennial species (Marchant *et al.* 1987), which with relief from heavy grazing, can rapidly colonise and dominate a site. Native perennial grasses such as *Dantlwnia caespitosa* and *Stipa elegantissma* show little response to grazing. They are generally not palatable to stock and the above ground parts of the plants die back in summer thus avoiding the season of highest grazing pressure. In fact, *D. caespitosa* has been reported as an increaser species with livestock grazing in woodlands in western New South Wales (Williams 1969).

Species which showed a positive response to grazing on the Ord River include the increaser perennial grasses *Heteropogon contortus* and *Eragrostis tenellula* which both tend to be
unpalatable to stock when mature (Petheram & Kok 1991). The buffel grasses (*Cenchrus ciliaris* and *C. setiger*) showed a negative response to grazing. These species were planted for rehabilitation of degraded rangeland at Site 05 (de Salis 1993), where they have extensively invaded the riparian zone. They are highly valued for livestock feed and for their ability to establish on degraded rangeland (Petheram & Kok 1991; de Salis 1993). Native perennial species such as the shrub *Crotalaria novae-hollandiae* and the sedge *Cyperus holoschoenus* showed a negative response to grazing. These perennial species, particularly the shrubs, are the most susceptible to livestock grazing, with green foliage available all year round and fairly low stature rendering the whole above-ground part of the plant accessible to livestock, including the perenniating organ which is usually above or at ground level. *C. novae-hollandiae* is reported to be a common species of disturbed sites and not very palatable to stock but will be grazed in the absence of more palatable species (Petheram & Kok 1991).

**Effects of relief from grazing**

The results of exclosure experiments on the Blackwood River showed little improvement after three years, with only minor increases in the occurrence and cover of native species. Increase in these species may be difficult in competition with the greater abundance of exotic grasses and annual herbs which have increased in cover in the absence of grazing. Exclosure experiments in a riparian zone in the United States have shown an increase in competition between plants with rapid vegetative growth of strong competitors (Kauffman et al. 1983). The study sites in the riparian zone in the present study are highly degraded and perhaps do not contain sufficient stores of vegetative and sexual reproductive material of native species, such as underground storage organs or a soil seedbank, to allow natural regeneration. These sites may require intervention in the form of weed removal and reseeding or replanting to re-establish native species. Sources of seed available through the seedbank and through dispersal will be discussed in subsequent chapters.

Ord River exclosure plots showed a marked increase in vegetation cover and therefore biomass over a 12 month period (one growing season). Over the same period, adjacent open plots showed a
decrease in vegetation cover, indicating that these changes in cover are not due to yearly variation in climatic conditions, such as extended wet season or substantial rainfall events in the dry season. However, 12 months is an insufficient period to fully assess the recovery of the vegetation with relief from livestock grazing, and therefore livestock impact. These preliminary results do indicate, however, that there is a grazing effect on the vegetation. In a long term study of cattle grazing in the riparian zone on a stream in north central USA, shrubs and graminoid species showed the greatest increase in cover with relief from cattle grazing in exclosure plots, and cattle were estimated to utilise 65% of annual growth of the vegetation in the grazed plots (Shultz & Leininger 1990). On the Ord River, seedlings of tree and shrub species such as Barringtonia acutangula, Sesbania formosa, Parkinsonia aculeata and Acacia farnesiana were uncommon but some did occur in both exclosure and open plots so that there appears to be no effect of grazing on germination of seedlings. This concurs with observations in the surveys of the grazed and ungrazed sites. Cover of perennial grasses remained the same and cover of perennial herbs increased in the exclosure plots while both reduced in the open plots, suggesting that these life forms are the most affected by livestock grazing. Although cover of these life forms is reduced in the grazed plots this does not necessarily indicate that the area is being degraded or that species are being lost, as species richness between plots showed little difference. Exclosure plots on the Ord River do not show the same initial level of degradation (such as invasion of exotic plants and loss of native species) that were seen on the Blackwood River sites and, as a consequence, recovery with grazing relief may be more rapid. High growth rates experienced in the tropics, due to warm temperatures and adequate moisture, may also speed up the recovery of biomass.

These results are short term and a much longer period is required to look at the vegetation dynamics and successional processes of these sites. Pioneer species such as annuals may eventually be replaced by another suite of species depending on future disturbance and management (Onans & Parsons 1980; Wahren et al. 1994). The riparian zone may need some episodic disturbance such as a flood and/or particular climatic conditions for a successful recruitment event.
Fire

Recovery of the riparian vegetation from fire at an ungrazed site (Site B2a) on the Blackwood River highlights the importance of resprouting in the recovery process for this vegetation. Many of the native woody species at this site are facultative seeder/sprouters which allows them to recover leaf area quickly after fire through resprouting from epicormic buds or from an underground storage organ such as a lignotuber (James 1984) and also to re-establish through germinating seed. Resprouting after defoliation is a common strategy in fire-prone environments in Australia (Gill 1981) and in the jarrah forest of south western Australia (Bell & Koch 1980) and the facultative seeder/sprouter strategy is considered to be the most resilient strategy in environments where predictable low frequency disturbance such as fire is common (Keeley 1986).

Weed species became more prominent in a grazed Blackwood River site (Site B4) after burning. This was also seen in the burnt exclosure plots, with little effect on native species. However, there may be a detrimental effect as fire enhances the invasion of exotic grasses and annual herbs which, because of their high flammability, in turn makes the vegetation more fire prone (Milberg & Lamont 1995). Exotic grass species such as Ehrharta spp., which is common in degraded areas of the riparian zone on the Blackwood River, have been recorded elsewhere as increasing fire frequency (Baird 1977). The combination of increased fire frequency and rising salinity has lead to the replacement of native riparian woody species by an invasive weed, Tamarix ramosissma in the south-western United States (Busch 1995). The combination of disturbances such as flooding and increased fire frequency in the riparian zone can favour ruderal species such as annuals (Grime 1979) which are generally exotic species and strong competitors and which can prevent the re-establishment of native perennial species (Hobbs 1988).

Burning may enhance the germination of seed of overstory species and improve short term survival by creating areas of bare ground suitable for seed germination (Wellington & Noble 1985b) but once the biomass of annual species recover these may quickly reduce survival of seedlings. Counter-intuitively, the fire did not appear to stimulate greater seed release from
Melaleuca rhaphiophylla fruit. However, the trees in the unburnt area were not in good health and were senescent with many dying branches, so that a hot dry late summer/autumn caused the opening of the seed capsules anyway. Unfortunately, as assessment of fire effects was made opportunistically, no observation was made of the pre-burn status of the M. rhaphiophylla capsules in the area that was burnt.

Although no direct examples of the effects of fire on riparian vegetation were measured on the Ord River, data from experimental fires on a wet tropical river at Kakadu in the Northern Territory (Douglas 1999) indicated that time of year was a critical aspect of the effect of fire on the riparian vegetation. Annual late dry season burning resulted in significantly less diverse and abundant riparian communities and recovery was slower than after burning early in the season. Vegetative resprouting from epicormic buds and lignotubers was the principal method of biomass recovery for the perennial vegetation (Douglas 1999). In the dry tropics there is a shift towards greater grass cover following late dry season fires (Bowman et al. 1988) and this probably extends into the riparian zone. In fact, because of the greater abundance of mesic species and rainforest species, the vegetation in the riparian zone is much more susceptible to fire than the surrounding upland vegetation, with greater probability of a loss of species richness. For example, Douglas (1999) recorded no vine species in riparian areas that were burnt annually compared to many species of vine in riparian areas that had not been burnt. The occurrence of vines at all the study sites on the Ord River (see Chapter 4) would indicate that these areas have not been subject to fire recently.

This Chapter has detailed aspects of disturbance from livestock grazing and fire on riparian vegetation, particularly on life form groups and recruitment from seed of overstorey species. It has shown that on the Blackwood River livestock grazing has significantly changed the structure and floristics of the riparian vegetation and is inhibiting the recruitment of the overstorey species (principally Eucalyptus rudis and Melaleuca rhaphiophylla). Enclosure plots indicated that recovery of native perennial species, with grazing relief, may be slow and require a disturbance event to reduce competition from annual exotic species and stimulate recruitment.
On the Ord River, effects of livestock grazing were not as obvious and may be masked by other forms of disturbance or stress. Long term monitoring of exclosure plots will provide more conclusive evidence on livestock grazing effects. This Chapter also implicates the importance of the role of sources of seed in the resilience of riparian vegetation to these disturbances. Factors influencing survival of seedlings and the possible role of fluvial processes in recruitment of the vegetation will be examined in more detail in the following chapters.
CHAPTER 7

SOURCES OF SEED FOR RECRUITMENT OF RIPARIAN COMMUNITIES

Introduction

Mechanisms significant for recruitment are important in contributing to maintenance and the resilience to disturbance of the riparian vegetation. These mechanisms include aspects of the phenology of reproduction and growth, development and release of propagules, dispersal of propagules and the storage of mature seed that will germinate when conditions become suitable. The riparian zone can be a high disturbance environment through flooding, but also, as discussed in the previous Chapter, through livestock grazing and fire. Strategies for regeneration that are successful in this environment will help to shape the vegetation communities it supports. This Chapter assesses the relative importance of these mechanisms by examining the contents of the seedbank in the soil, the storage of seed on trees, mechanisms for propagule dispersal, the importance of dispersal by water and the survival and longevity of seed. This is achieved through a survey of the content of the soil seedbank, the dispersal mechanisms found in the riparian vegetation, the abundance of propagules in flood debris and a focus on the reproductive phenology and fate of seed of the two most common overstorey species identified in Chapter 4. These were, *Eucalyptus camaldulensis* and *Melaleuca leucadendra* on the Ord River and *E. rudis* and *M. rhaphiophylla* on the Blackwood River.

*Eucalyptus camaldulensis* is a dominant riverine species on the Ord River and throughout continental Australia, except for the south-west where it is replaced by *E. rudis* which is a closely related species that is known to hybridise with *E. camaldulensis* (Boland et al. 1989). *E. rudis* is the most common large tree that occurs in the riparian zone of south-west rivers, including the Blackwood River. *Melaleuca leucadendra* on the Ord River and *M. rhaphiophylla* on the Blackwood River have similar ecological traits and are common components in the overstorey or
midstorey, having high tolerance to inundation and waterlogged conditions. By studying these functionally equivalent riparian tree species in two contrasting river systems and climatic zones, the influence of different physical environments on seedling recruitment in the riparian zone can be understood.

For recruitment to take place plant propagules of native species must generally come from nearby undisturbed vegetation in the canopy seed store or from seed stored in the soil seedbank. Regeneration of native vegetation from seed stored in the soil is therefore very important (Onans & Parsons 1980). The seedbank will have a bearing on species composition after a disturbance such as grazing or fire (Roberts 1986), allowing recovery from catastrophic events (such as wildfire), severe grazing or clearing (Grime 1979). In lentic wetlands, the seedbank is also very important in determining the vegetation community (Thompson 1992) and assessment of the composition of the soil seedbank can be used to predict the outcome of succession after a disturbance (van der Valk 1981). The role of the seedbank in the riparian zone is unclear and little work has been done on this, however the highly disturbed nature of the riparian zone and the frequent movement of soil sediments would suggest that the role may be minimal (Malanson 1993). In the riparian zone, the soil seedbank is therefore likely to be important only for annual or ephemeral species that can germinate and complete their life cycle within one season, thereby avoiding seasonal flooding. The seedbank may be more abundant at higher elevations from the river where soil is less likely to be scoured away or in protected wetland areas that act like lotic systems. For seeds to enter the long term seedbank they need some form of dormancy and be able to maintain viability for a long period of time, ensuring that germination only occurs under favourable conditions (Schneider & Sharitz 1986; Thompson 1987). For the Myrtaceaeous overstorey species studied on these rivers survival and longevity of seed may not be sufficient for them to enter the soil seedbank.

Dispersal of propagules is an important mechanism for successful colonisation and establishment of species and is likely to influence the vegetation structure of communities (Brown 1992). Successful colonisation can be dependent upon species' ability to disperse into a particular
environment (Barrat-Segretain 1996). Identifying the array and establishing the relative importance of different plant diaspore dispersal modes in a plant community can help identify the relative advantage of a dispersal type in a particular habitat (Willson 1992). Recolonisation and spatial patterns of succession can also be related to the relative importance of the different modes of dispersal. Plant dispersal unit in combination with life form and reproductive strategy has been used to predict species composition after disturbance (McIntyre et al. 1995). In riparian habitats, longitudinal gradients of dispersal mode have been identified (Weaver et al. 1925), with wind dispersal being more prevalent in the headwaters and dispersal by animals being more important in the lower reaches.

An obvious means of secondary dispersal for riparian plants is via water (Malanson 1993). Species may release seeds into flowing water so that they can be dispersed further downstream away from parent trees and deposited on newly exposed sediment when waters recede (Naiman et al. 1998). For this to occur, seeds need to be able to float and maintain viability (Nilsson et al. 1991b). In addition, reproductive phenology, particularly seed fall, needs to coincide with seasonal changes in river hydrology. Timing of seed production and seed fall is also very important so that seed is released at times of most favourable conditions. This includes, after floodwaters have receded and fresh soil is exposed (White 1979), when soil moisture levels are high (Roberts 1993) and when there is peak abundance of seed vectors (Willson 1992). Seed may be released from the fruit on the tree or remain within the fruit when it dehisces to be released later as the fruit dries out or is broken up by physical or chemical deterioration. During floods, woody plant debris large and small is carried downstream. This debris tends to accumulate around obstacles or at the high flow mark along the river and may contain an important source of propagules for recruitment of riparian plants in the form of fruit and seeds (Naiman et al. 1998).

This Chapter investigates the soil seedbank in the riparian zone at study sites on the Blackwood and Ord rivers and whether diversity and abundance changes with lateral distance from the river. It will also assess seed predation by ants and longevity of seed of *E. camaldulensis* and *M. leucadendra* on the Ord River and *E. rudis* and *M. rhaphiophylla* on the Blackwood River. This
will indicate whether these are likely to be factors in the ability of these species to become part of the soil seedbank and to therefore be available for regeneration when favourable conditions arise. The spectrum and abundance of different dispersal modes encountered in the riparian vegetation on these two rivers will also be documented. Flood debris is examined as an important source of plant propagules and for its role in the dispersal of these propagules, as will the floating ability of particular representative species and therefore their potential to use river flows as a dispersal mechanism. The reproductive phenology of the study species will also be described.

Methods

Soil seedbank

On the Blackwood River at Sites B1a, B2a, and B3a soil samples were collected in November 1997 along the two vegetation transects at distances from the river (low water level) of 0-10 metres, 10-20 metres, 20-30 metres, 30-40 metres and 40-50 metres, giving 10 samples per site and a total of 30 samples. On the Ord River samples were collected in July 1997 at Sites O1, O4 & O5 along the vegetation transects at distances from the river (dry season water level) of 0-10 metres, 10-20 metres, 20-30 metres, 40-50 metres and 70-80 metres, giving 10 samples per site and a total of 30 samples. At each sampling point, ten 5 cm x 5 cm cores of soil were taken to a depth of 10 cm on a radius of 0.5 metre. These samples were then bulked to give a soil sample of 2500 cm$^3$ at each sampling point. Samples were transferred to a glasshouse in Perth where seedling trays of 35 cm x 40 cm x 5 cm were lined with hessian and a layer of vermiculite, over which a soil sample was thinly spread. Soil in each tray was divided in half with one half receiving tap water and the other water infused with smoke from burning of plant material which has been shown to improve germination of some seeds (Brown 1993; Dixon et al. 1995). Trays were watered daily in ambient conditions for both light and temperature. Each sample was given an initial treatment of a broad spectrum fungicide (Benlate 1g L$^{-1}$) and watered with a liquid fertiliser initially and later as required. Germination was recorded weekly over a 16 week period and specimens of some
individuals were transplanted into pots and grown until identification was possible. Soil in the
trays was then turned over, to release any seed that may have been too deeply buried to allow
germination, and monitoring continued until germination in the trays ceased.

**Propagule dispersal mode**

All species of plants identified in vegetation plots surveyed in Chapter 4 were categorised
according to their principal mode of diaspore dispersal (i.e. Willson et al. 1990; Malanson 1993).
This was based mainly on examining the morphology and structure of the seed or fruit and on
field observation (Willson et al. 1990). It should be noted that many species may have an
important secondary mode of diaspore dispersal, such as by water in the riparian zone for those
diaspores with the ability to float (Nilsson et al. 1991b). Dispersal categories are based on
those suggested by Malanson (1993) and include hydrochores (dispersed by water), including
diaspores of aquatic plants with structures which enhance floating ability (cyclochores);
anemochores (dispersed by wind) which can include diaspores with wings (pterochores), very
small hard seeds (sporochores) or diaspores with hair-like or plumose appendages
(pogonochores); and zoochores (dispersed by animals), diaspores of which can be transported
internally for fleshy fruited species (sarcochores) or externally for diaspores with spiny or
glandular appendages (desmochores) and which also include plants with an elaiosome and
which are thus transported by ants (myrmechores) (Berg 1975). Where the principal form of
dispersal was not obvious from the structure of the diaspore or had not been observed, it was
considered unknown.

**Flood debris samples**

At each site on both rivers, five samples of 2500 cm³ were collected of flood debris that had
accumulated, usually at the high water mark from the previous years wet season or winter high
flows or where debris had accumulated around an obstruction. Samples were taken in the
vicinity of the vegetation transects at each site. Samples were air dried in oven at 50° C for 12
hours and then sieved in a 2 mm mesh sieve. The larger material was examined and the presence
of all fruit and seed was, where possible, identified and recorded. The sample portion less than 2
mm in size was mixed with coarse sand, spread onto trays and treated as for the soil seedbank samples to record germination of seed within the debris samples. Differences between sample means of soil and debris samples were analysed using paired t tests (Zar 1984). The Czekanowski Index (Kent & Coker 1992) was used to measure the floristic similarity between soil and debris samples. The coefficient values range between 0 (complete dissimilarity) and 1 (total similarity) and are based on the joint occurrence of a species using abundance data.

Seed floating

Seed and fruit of commonly occurring species were collected from the study sites on the Blackwood and Ord rivers for a seed floating experiment. These species included, from the Blackwood River, the trees *Banksia seminuda*, *Exocarpos spartetus* and *Dodonea viscosa*, the shrub *Acacia saligna*, the exotic herb *Rumex crispus* and the sedges *Lepidosperma gladiatum*, *Juncus pallidus* and *Carex appressa*. On the Ord River, the species included the trees *Ficus coronulata*, *Terminalia platyphylla*, *T. hadleyana*, *Cathormion umbellatum* and *Pandanus spiralis*, the shrub *Abrus precatorius* and the exotic vine *Passiflora foetida*. Five replicates of 20 seeds or fruit of each species were placed into 100 ml beakers of deionised water which were stirred daily. Percentage of seeds floating was recorded for each species over a one month period. For the two major overstorey species on the Blackwood River (*Eucalyptus rudis* and *Melaleuca rhaphiophylla*) and the Ord River (*Eucalyptus camaldulensis* and *Melaleuca leucadendra*), five replicates of 50 seeds each were floated over a one month period and any seeds that germinated during this time were recorded.

Reproductive phenology of target species

Phenology of the two dominant overstorey species on each river was monitored over a two year period. On the Blackwood River, 10 seed traps were placed at Sites B1a & b and B2a & b under the canopy of *Eucalyptus rudis* trees where estimated canopy cover above the traps was greater than 60%. Traps consisted of a cone-shaped calico sack with an opening of 44 cm diameter (area of 0.15 m²) suspended on steel posts one metre from the ground. Contents of traps were examined every two months for the presence of seed and other reproductive material such as opercula and
aborted flowers and fruit. To measure seed fall for *Melaleuca rhaphiophylla*, closed mature fruit on branches of ten trees at each site were tagged and these fruit were examined every two months for open capsules. During each visit, along vegetation transects, percentage of trees flowering and/or fruiting as well as whether this was light, medium or heavy was recorded. The stage of development of fruit or flowers was also recorded as well as the presence of fruit from previous seasons' growth. On the Ord River, reproductive status of all trees along the vegetation transects were recorded during each visit. Seed traps were not used on the Ord River due to the difficulties of access during the wet season. Instead, branches of *E. camaldulensis* and *M. leucadendra* with flower buds and/or new un-open fruit were tagged in July 1996 and the number of open fruit was recorded at subsequent visits in March 1997, December 1997, April 1998 and April 1999. The timing of flowering and seed release of these Ord River species was confirmed with Department of Conservation and Land Management staff in Kununurra and with a local seed collector (C. Dupe, personal communication).

**Seed Longevity**

The longevity in the soil of seed of *E. rudis* and *M. rhaphiophylla* on the Blackwood River was tested by burying nine lots of 50 seeds at a depth of 1 cm at Site Blb. The location of each burial site was clearly marked and after 1, 6 and 12 months, three lots of seed were retrieved by taking a soil core sufficiently large and deep to encompass the burial site. These soil cores were then spread thinly on a bed of filter paper and vermiculite saturated with deionised water and placed in growth cabinets at 20°C. These were watered daily and germination of seed was recorded until no further germination took place. Similar cores nearby were also taken at the same time and treated to promote seed germination to assess the natural occurrence of seed. Control replicates of seed of each species that had not been buried was also germinated at this time and germination results for buried seeds are expressed as a percentage of numbers of control seeds germinating. On the Ord River, this procedure was repeated for seed of *E. camaldulensis* and *M. leucadendra*, except that seed was retrieved after six months and 12 months only.
Seed predation

Rates of seed removal of the four study species by ants was assessed by recording the loss of seed from ant feeding stations (i.e. Yates et al. 1995). Feeding stations consisted of a petri dish with a lid on a plywood board with three access holes cut into the side of the petri dish. Ten seeds were placed in the middle of the petri dishes and removal of seed was monitored every two hours over an eight hour period of daylight for two days. Each feeding station consisted of two petri dishes, one of which ants were prevented from entering by placing a sticky barrier around the entrances. This was done to assess the loss of seed other than from predation, such as by wind. Ten pairs of feeding stations were deployed at one site on each river and the experiment was repeated in November 1997 and March 1998 at Site B1 on the Blackwood River and July 1996 and April 1998 at Site O1 on the Ord River.

Results

Soil seedbank

Number of species and abundance of germinants in soil samples showed no significant difference (t test, p > 0.1) between the two watering treatments (smoke water and tap water) and results presented here are therefore for combined watering treatments. On the Blackwood River a total of 45 species from 23 families germinated from soil samples (Table 7.1), with an average of 1318 ± 535 seeds m².

Species which occurred most often included the exotic annual herbs Hypochaeris glabra, Juncus bufonius and J. capitatus and the exotic annual grasses Briza minor and Lolium rigidum. Species with greatest number of germinants also included the exotic annual herbs Romulea rosea, Rumex acetosella and Galium murale and the exotic annual grass Aira caryophyllea. The greatest proportion of species were annual herbs, making up 76% of species and 78% of germinants, with native perennials including grasses, shrubs and trees making up less than 2% of the germinating seed.
Table 7.1: Species germinating from soil and debris stored seed collected in November 1997 at 3 sites on the Blackwood River. *exotic species

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Soil samples (n=30)</th>
<th>Debris samples (n=15)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>No.</td>
<td>Freq. %</td>
</tr>
<tr>
<td><strong>Exotic annual herbs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Anagallis arvensis</td>
<td>Primulaceae</td>
<td>78</td>
<td>57</td>
</tr>
<tr>
<td>*Arctotheca calendula</td>
<td>Asteraceae</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>*Atriplex prostrata</td>
<td>Chenopodaceae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Cotula turbinate</td>
<td>Asteraceae</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>*Crassula alata</td>
<td>Crassulaceae</td>
<td>82</td>
<td>29</td>
</tr>
<tr>
<td>*Crassula glomerata</td>
<td>Crassulaceae</td>
<td>22</td>
<td>43</td>
</tr>
<tr>
<td>*Epilobium sp.</td>
<td>Onagraceae</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>*Erodium botrys</td>
<td>Geraniaceae</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>*Galium verum</td>
<td>Rubiaceae</td>
<td>20</td>
<td>30</td>
</tr>
<tr>
<td>*Hypochaeris glabra</td>
<td>Asteraceae</td>
<td>44</td>
<td>56</td>
</tr>
<tr>
<td>*Juncus bufonius</td>
<td>Juncaceae</td>
<td>296</td>
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</tr>
<tr>
<td>*Juncus capitatus</td>
<td>Juncaceae</td>
<td>120</td>
<td>100</td>
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<tr>
<td>*Menusa pulegium</td>
<td>Lamiaceae</td>
<td>20</td>
<td>12</td>
</tr>
<tr>
<td>*Monopsis simplex</td>
<td>Lobeliaceae</td>
<td>56</td>
<td>43</td>
</tr>
<tr>
<td>*Oxalis corniculata</td>
<td>Oxalidaceae</td>
<td>6</td>
<td>43</td>
</tr>
<tr>
<td>*Petroselum sativum</td>
<td>Caryophyllaceae</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>*Romulae rosea</td>
<td>Iridaceae</td>
<td>14</td>
<td>30</td>
</tr>
<tr>
<td>*Rumex acetosella</td>
<td>Polygonaceae</td>
<td>10</td>
<td>6</td>
</tr>
<tr>
<td>*Rumex crispus</td>
<td>Polygonaceae</td>
<td>16</td>
<td>30</td>
</tr>
<tr>
<td>*Sagina apetala</td>
<td>Caryophyllaceae</td>
<td>64</td>
<td>6</td>
</tr>
<tr>
<td>*Spergularia rubra</td>
<td>Caryophyllaceae</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>*Trifolium campestre</td>
<td>Fabaceae</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>*Trifolium subterraneum</td>
<td>Fabaceae</td>
<td>34</td>
<td>17</td>
</tr>
<tr>
<td><strong>Native annual herbs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alternathera nodiflora</td>
<td>Amaranthaceae</td>
<td>64</td>
<td>13</td>
</tr>
<tr>
<td>annual herb</td>
<td>Asteraceae</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>Apera brizula</td>
<td>Centrolepidae</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>Helipterum cotula</td>
<td>Asteraceae</td>
<td>29</td>
<td>9</td>
</tr>
<tr>
<td>Helipterum laevum</td>
<td>Asteraceae</td>
<td>50</td>
<td>42</td>
</tr>
<tr>
<td>Isopogon australis</td>
<td>Caryophyllaceae</td>
<td>20</td>
<td>12</td>
</tr>
<tr>
<td>Lobelia alata</td>
<td>Lobeliaceae</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Podolepis lessonii</td>
<td>Asteraceae</td>
<td>6</td>
<td>3</td>
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<tr>
<td>Portulacea microphylla</td>
<td>Euphorbiaceae</td>
<td>8</td>
<td>3</td>
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<tr>
<td>Quinertia urvelia</td>
<td>Asteraceae</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Schoenus annual</td>
<td>Caryophyllaceae</td>
<td>1</td>
<td>3</td>
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<tr>
<td>Waltheriana priesii</td>
<td>Campanulaceae</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td><strong>Exotic grasses</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>*Aira careophylla</td>
<td>Poaceae</td>
<td>78</td>
<td>30</td>
</tr>
<tr>
<td>*Avena fatua</td>
<td>Poaceae</td>
<td>24</td>
<td>9</td>
</tr>
<tr>
<td>*Bromus iconio</td>
<td>Poaceae</td>
<td>98</td>
<td>67</td>
</tr>
<tr>
<td>*Ehrharta longiflora</td>
<td>Poaceae</td>
<td>20</td>
<td>6</td>
</tr>
<tr>
<td>*Lotus rigidum</td>
<td>Poaceae</td>
<td>105</td>
<td>57</td>
</tr>
<tr>
<td>*Holcus lanatus</td>
<td>Poaceae</td>
<td>28</td>
<td>6</td>
</tr>
<tr>
<td><strong>Native perennial herbs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Comesperma virgatum</td>
<td>Polygalaceae</td>
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<td>3</td>
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<tr>
<td>Lepidosperma sp.</td>
<td>Cyperaceae</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td><strong>Native Shrubs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Halocarpus lepidoperma</td>
<td>Chenopodaceae</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td><strong>Native Trees</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eucalyptus rufus</td>
<td>Myrtaceae</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Melaleuca rhaphiophylla</td>
<td>Myrtaceae</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>unidentified</td>
<td></td>
<td>15</td>
<td>5</td>
</tr>
</tbody>
</table>
### Table 7.2: Species germinating from soil and debris stored seed collected in July 1997 at 3 sites on the Ord River. *exotic species*

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Soil samples (n=30)</th>
<th>Debris samples (n=15)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No.</td>
<td>Freq. %</td>
<td>No.</td>
</tr>
<tr>
<td><strong>annual herbs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blumea diffusa</td>
<td>Asteraceae</td>
<td>70</td>
<td>8</td>
</tr>
<tr>
<td>Heliotropium sp.</td>
<td>Asteraceae</td>
<td>10</td>
<td>25</td>
</tr>
<tr>
<td>Asteraceae sp. annual</td>
<td>Asteraceae</td>
<td>4</td>
<td>17</td>
</tr>
<tr>
<td>Asteraceae sp.2</td>
<td>Asteraceae</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Cyperis sp. annual</td>
<td>Cyperaceae</td>
<td>36</td>
<td>42</td>
</tr>
<tr>
<td>Cyperis sp.2</td>
<td>Cyperaceae</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Euphorbia sp.</td>
<td>Euphorbiaceae</td>
<td>81</td>
<td>42</td>
</tr>
<tr>
<td>Indigofera sp.</td>
<td>Papilionaceae</td>
<td>18</td>
<td>25</td>
</tr>
<tr>
<td><em>Hyptis suaveolens</em></td>
<td>Laminaceae</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td><em>Sida acuta</em></td>
<td>Malvaceae</td>
<td>23</td>
<td>19</td>
</tr>
<tr>
<td>Portulaca sp.</td>
<td>Portulacaceae</td>
<td>12</td>
<td>7</td>
</tr>
<tr>
<td>Calandrina quadrivalvis</td>
<td>Solanaceae</td>
<td>2</td>
<td>16</td>
</tr>
<tr>
<td><em>Solanum sp.</em></td>
<td>Solanaceae</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Annual herb</td>
<td></td>
<td>3</td>
<td>17</td>
</tr>
<tr>
<td>Annual herb2</td>
<td></td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td><strong>annual grasses</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eragrostis tenellula</td>
<td>Poaceae</td>
<td>20</td>
<td>25</td>
</tr>
<tr>
<td>Poaceae sp. annual</td>
<td>Poaceae</td>
<td>26</td>
<td>50</td>
</tr>
<tr>
<td>Sporobolus sp.</td>
<td>Poaceae</td>
<td>13</td>
<td>17</td>
</tr>
<tr>
<td>Brachyacne convergens</td>
<td>Poaceae</td>
<td>8</td>
<td>15</td>
</tr>
<tr>
<td><strong>perennial grasses</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paspalidium jubiflorum</td>
<td>Poaceae</td>
<td>54</td>
<td>31</td>
</tr>
<tr>
<td>Cynodon dactylon</td>
<td>Poaceae</td>
<td>75</td>
<td>43</td>
</tr>
<tr>
<td><em>Cenchrus ciliaris</em></td>
<td>Poaceae</td>
<td>110</td>
<td>41</td>
</tr>
<tr>
<td>Heteropogon contortus</td>
<td>Poaceae</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Poaceae sp.1</td>
<td>Poaceae</td>
<td>9</td>
<td>25</td>
</tr>
<tr>
<td>Poaceae sp.2</td>
<td>Poaceae</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Poaceae sp.3</td>
<td>Poaceae</td>
<td>3</td>
<td>8</td>
</tr>
<tr>
<td><strong>perennial herbs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Achyranthes aspera</td>
<td>Amaranthaceae</td>
<td>43</td>
<td>50</td>
</tr>
<tr>
<td>Cyperis sp.</td>
<td>Cyperaceae</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Bilbostylis barbata</td>
<td>Cyperaceae</td>
<td>6</td>
<td>32</td>
</tr>
<tr>
<td>Fimbristylis sp.</td>
<td>Cyperaceae</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td><em>Passiflora foetida</em></td>
<td>Passifloraceae</td>
<td>13</td>
<td>100</td>
</tr>
<tr>
<td><strong>shrubs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acacia sp.</td>
<td>Mimosaceae</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Crotonidaria sp.</td>
<td>Papilionaceae</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td><em>Calotropis procera</em></td>
<td>Asclepiadaceae</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td><strong>trees</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eucalyptus sp.</td>
<td>Myrtaceae</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>Terminalia platyphylla</td>
<td>Combretaceae</td>
<td>11</td>
<td>20</td>
</tr>
<tr>
<td>Terminalia bursaria</td>
<td>Combretaceae</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>Melaleuca leucadendra</td>
<td>Myrtaceae</td>
<td>43</td>
<td>67</td>
</tr>
<tr>
<td>Eucalyptus camaldulensis</td>
<td>Myrtaceae</td>
<td>20</td>
<td>32</td>
</tr>
<tr>
<td><em>Nauclea orientalis</em></td>
<td>Rubiaceae</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td>unidentified</td>
<td></td>
<td>16</td>
<td>4</td>
</tr>
</tbody>
</table>
(Figure 7.1a). There was a high level of variability among soil samples, with the number of germinants ranging from 54 to 330 per sample and number of species ranging from 7 to 20.

Variation in abundance of germinants with distance from the Blackwood River is shown in Figure 7.2 a&b. The relationship between abundance of the soil seedbank and distance from the river is shown in Table 7.3 with no significant correlation with any life form group, although total abundance of viable seed in the soil appears to increase further from the river.

For the Ord River, a total of 32 species from 17 families were recorded in the soil samples, with an average of 652 ± 291 seeds m⁻² (Table 7.2). Common species included the annual herb *Euphorbia* sp., the perennial herb *Achyranthes aspera* and the tree *Melaleuca leucadendra*, with the most abundant species including *Euphorbia* sp and the perennial grasses *Cynodon dactylon*, *Cenchrus* sp. and *Paspalidium* sp. Perennial grasses and annual herbs were the dominant life forms in terms of species and abundance on the Ord River, although there was large variation between samples (Figure 7.2). Woody perennials (trees and shrubs) also made up a more substantial proportion of germinants in terms of species and abundance than was seen in the Blackwood River samples. Variability between samples was also high, with abundance ranging from 10 to 178 per sample and species from 3 to 12. There was no significant relationship between distance from the river and total soil seed bank abundance (Figure 7.2 c&d, Table 7.3). However, numbers of germinants of grasses increased with distance from the river while number of germinants of woody perennials decreased with distance from the river (Table 7.3).
Figure 7.1: Mean percentage (±SD) of each life form by species and number of germinants in soil samples averaged from 30 samples at three sites on (a) the Blackwood River and (b) the Ord River.
Figure 7.2: Mean (±SE) total number of species and total number of germinants in soil seedbank samples with distance from the river channel for the Blackwood River (a) & (b) and the Ord River (c) & (d).
Dispersal mechanisms

The spectra of diaspore dispersal types for the Blackwood River showed the dominance of wind dispersal both in terms of number of species and cover (Figures 7.3 a&b). The number of plant species for which the major form of diaspore dispersal was not known, that is, had no obvious morphological structure for dispersal, was also high. The same trend was seen for individual sites, but with water dispersal significant in terms of cover at Sites B1b, B2a and B3a, where semi-aquatic species, such as emergent macrophytes, occurred. Only one species, the exotic rambling shrub *Rubus discolor* (Blackberry), was thought to be primarily dispersed by birds. This species is also probably effectively dispersed by water as its distribution may indicate. Secondary dispersal by water is also likely for many species and, based on diaspore ability to float, a mean of 63% of species across the sites could also be effectively dispersed by water.

Table 7.3: Relationship between distance from the river of a soil sample and the abundance of germinants in the sample for total species and for the various life form groups from 30 samples on the Blackwood and Ord rivers.

<table>
<thead>
<tr>
<th>Blackwood River</th>
<th>r value</th>
<th>p value</th>
<th>Ord River</th>
<th>r value</th>
<th>p value</th>
</tr>
</thead>
<tbody>
<tr>
<td>total germinants</td>
<td>0.727</td>
<td>0.0643</td>
<td>total germinants</td>
<td>0.052</td>
<td>0.9840</td>
</tr>
<tr>
<td>exotic annual herbs</td>
<td>0.685</td>
<td>0.0890</td>
<td>annual herbs</td>
<td>-0.468</td>
<td>0.1463</td>
</tr>
<tr>
<td>native annual herbs</td>
<td>-0.335</td>
<td>0.4625</td>
<td>grasses</td>
<td>0.685</td>
<td>0.0090</td>
</tr>
<tr>
<td>exotic grasses</td>
<td>0.332</td>
<td>0.4675</td>
<td>woody perennials</td>
<td>-0.651</td>
<td>0.0190</td>
</tr>
<tr>
<td>woody perennials</td>
<td>0.180</td>
<td>0.6991</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 7.3: Number of species and % cover of the major seed dispersal types on the Blackwood River (a & b) and Ord River (c & d). Values are means (±SEM) for six sites on the Blackwood River and five sites on the Ord River.
Wind dispersal was the dominant dispersal mechanism of plants on the Ord River, particularly in terms of cover (Figure 7.3 c&d). Species with an 'unknown' dispersal mechanism were the second most common but there was generally a greater spread of dispersal types among species than measured on the Blackwood River. Species with dispersal by frugivorous animals were the second most common in terms of cover for the Ord sites. These included the fleshy fruited *Ficus* spp. which are well represented at all sites and are fed upon by flying foxes and birds, but similar to many species can also be effectively dispersed by water. The dominance of wind dispersal is apparent for all sites along the river, particularly at the upstream sites (Sites O3, O4, O5). At the downstream sites, water dispersal as a primary mechanism is well represented. This may be because of the greater number of emergent macrophytes on these sites of permanent water. Similar to the Blackwood River sites, many species, based on their ability to float, can also be dispersed by water, with a mean of 69% of species across all of the sites.

**Flood debris samples**

Results of germination tests for flood debris samples on the Blackwood River showed that all but one of the species found in the debris samples were also present in the soil samples (Table 7.1). The exception was the annual herb *Atriplex prostrata*. Due to large differences in the abundance of species, Czekanowski Similarity Index was low (0.45). When soil samples and debris samples were compared for total number of species and abundance there was no significant difference (\( p=0.645 \) and \( p=0.711 \) respectively). For the different life forms, abundance of trees was significantly greater in the debris samples (19±13) (mean±SE) than in the soil samples (1.5±1) (\( p=0.0009 \)). There was no significant difference between debris and soil samples for any other life forms. Visual examination of flood debris samples identified eight species of woody perennials, with *Corymbia calophylla* the only species not generally found in the riparian zone (Table 7.4). The majority of species were identified from their fruit which were mainly woody capsules. The two most common riparian species *Eucalyptus rudis* and *Melaleuca rhapsiphylla*, were numerically dominant in the debris samples, with large numbers of open fruit. Un-open capsules were dried to
release seeds which were counted giving an average of 30.2±10.3 seeds per capsule for *E. rudis* with 61% viability and 20±8.1 seeds per capsule for *M. rhaphiophylla* with 12% viability.

Table 7.4: Fruit and seed of woody perennial species identified in flood debris samples at three sites on the Blackwood River. Results are tabulated from five 2500 cm³ bulked samples taken from each site in December 1997.

<table>
<thead>
<tr>
<th>Site</th>
<th>Habitat</th>
<th>Species</th>
<th>Plant material</th>
</tr>
</thead>
<tbody>
<tr>
<td>B1a</td>
<td>riparian</td>
<td><em>Eucalyptus rudis</em></td>
<td>289 open fruit; 10 seeds</td>
</tr>
<tr>
<td></td>
<td>upland</td>
<td><em>Corymbia calophylla</em></td>
<td>19 closed fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td><em>Melaleuca rhaphiophylla</em></td>
<td>149 open fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td><em>Melaleuca sp</em></td>
<td>30 open fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td><em>Banksia seminuda</em></td>
<td>8 fruiting cone fragments</td>
</tr>
<tr>
<td>B2a</td>
<td>riparian</td>
<td><em>Eucalyptus rudis</em></td>
<td>142 open fruit; 52 unopen fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td><em>Melaleuca rhaphiophylla</em></td>
<td>159 open fruit</td>
</tr>
<tr>
<td>B3a</td>
<td>riparian</td>
<td><em>Eucalyptus rudis</em></td>
<td>16 open fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td><em>Casuarina obesa</em></td>
<td>41 open cones</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td><em>Eucalyptus occidentalis</em></td>
<td>3 open fruit</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td><em>Melaleuca laterifolia</em></td>
<td>21 open fruit</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td><em>Melaleuca uncinata</em></td>
<td>19 open fruit</td>
</tr>
</tbody>
</table>

In flood debris samples on the Ord River, 68% of species that germinated were also recorded in the soil samples (Table 7.2), with a similarity index between the debris and soil of 0.22. Comparison of soil and debris samples showed no significant difference for total germinants or for annual herbs or grasses (p>0.05 in both cases). The exception was for woody perennial species which had a significantly greater number of germinants in the debris samples (37±3) compared with soil samples (10±2.8) (p=0.003). Examination of debris samples showed 16 species, 11 of which were common riparian zone species, the other five species are normally found further out on the floodplain (Table 7.5). Species were identified from a mixture of fruit and seeds, with the most abundant species being the common riparian trees at the study sites, *Eucalyptus camaldulensis* and *Melaleuca leucadendra*. All the woody capsules from these species were open and had therefore already released seed.
Table 7.5: Fruit and seed of woody perennial species identified in flood debris samples at three sites on the Ord River. Results are tabulated from five 2500 cm$^3$ bulked samples taken from each site in April 1997.

<table>
<thead>
<tr>
<th>Site</th>
<th>Habitat</th>
<th>Species</th>
<th>Plant material</th>
</tr>
</thead>
<tbody>
<tr>
<td>O5</td>
<td>riparian</td>
<td>Eucalyptus camaldulensis</td>
<td>173 open fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Melaleuca leucadendra</td>
<td>101 open fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Ficus coronulata</td>
<td>6 fruit</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td>Acacia sp</td>
<td>1 open fruit pod</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Lophostemon grandiflorus</td>
<td>10 unopened fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Nauclea orientalis</td>
<td>3 fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Terminalia platyphylla</td>
<td>47 fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Pandanus spiralis</td>
<td>3 seeds</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td>Eucalyptus sp 'bloodwood'</td>
<td>10 open fruit</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td>Eucalyptus chlorophylla</td>
<td>6 open fruit</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td>Eucalyptus houseana</td>
<td>18 open fruit</td>
</tr>
<tr>
<td>O4</td>
<td>riparian</td>
<td>Eucalyptus camaldulensis</td>
<td>167 open fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Nauclea orientalis</td>
<td>20 fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Ficus coronulata</td>
<td>30 fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Terminalia platyphylla</td>
<td>34 fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Pandanus spiralis</td>
<td>1 seed</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Barringtonia acutangula</td>
<td>6 fruit</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td>Hakea sp</td>
<td>1 fruit</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td>Eucalyptus sp 'bloodwood'</td>
<td>5 open fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Melaleuca leucadendra</td>
<td>84 open fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Lophostemon grandiflorus</td>
<td>24 closed fruit</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td>Eucalyptus gymnotales</td>
<td>122 closed fruits</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td>Eucalyptus argillacea</td>
<td>2 open fruit</td>
</tr>
<tr>
<td>O1</td>
<td>riparian</td>
<td>Melaleuca leucadendra</td>
<td>118 open fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Eucalyptus camaldulensis</td>
<td>177 open fruit; 10 seed</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Terminalia platyphylla</td>
<td>11 fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Lophostemon grandiflorus</td>
<td>5 fruit</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td>Eucalyptus microtheca</td>
<td>6 open fruit</td>
</tr>
<tr>
<td></td>
<td>floodplain</td>
<td>Eucalyptus sp 'bloodwood'</td>
<td>6 open fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Pandanus spiralis</td>
<td>11 seeds</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Barringtonia acutangula</td>
<td>3 fruit</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Nauclea orientalis</td>
<td>2 seeds</td>
</tr>
<tr>
<td></td>
<td>riparian</td>
<td>Ficus coronulata</td>
<td>6 fruit</td>
</tr>
<tr>
<td></td>
<td>hillslopes/floodplain</td>
<td>Adansonia gregorii</td>
<td>1 fruit</td>
</tr>
</tbody>
</table>

Seed floating

The results of seed floating trials of representative species common in the riparian zone of each river indicated that seeds of the majority of species tested had some floating ability (Table 7.6, Figure 7.4). For the Blackwood River, seed of most species floated for at least five days and up to 30 days for Dodonea viscosa, Juncus pallida and Lepidosperma gladiatum, with seed of some species germinating while floating and then sinking. Some species did not float at all, including
*Acacia saligna* and *Exocarpos sparteus*. In the case of *Banksia seminuda*, although seeds did not float at all, the fruiting cone was buoyant. Of the Ord River species, the legume *Abrus precatorius* did not float at all and *Cathormion umbellatum* seeds did not float themselves but seeds were released in intact pods which were buoyant. The pods started to break up after 20 days and the seeds subsequently sank. Only the seeds of *Pandanus spiralis* were all still floating after 30 days.

For the most common overstorey species on each river seed of all species began to germinate within six to nine days, while floating (Figure 7.4). Germinated seed subsequently sank. Average floating times ranged from 5.6 days for *E. rudis* to 10.4 days for *E. camaldulensis*. All seeds remained afloat for at least four days for all species except *E. rudis* which began to lose buoyancy after one day.

**Reproductive phenology**

Seasonal reproductive phenology for *Eucalyptus camaldulensis* and *Melaleuca leucadendra* on the Ord River and *E. rudis* and *M. rhaphiophylla* on the Blackwood River is summarised for a 12 month period and compared with mean monthly river discharge (Figures 7.5 a&b). For both *Eucalyptus* species seedfall appeared to be timed to coincide with that period of the year when river water levels were receding, that is, March/April for *E. camaldulensis* and September to November for *E. rudis*. For *E. camaldulensis* flowering and seed fall occur in a single annual cycle, with fruit maturing and releasing seed and little seed appearing to remain in the canopy. In contrast, *E. rudis* flowers from August to November with fruit and seed developing over summer. Greatest seed release from these matured capsules is not until the following early summer period. Seed is therefore retained on the tree so that some seed may be released throughout the year with a peak in the early summer period (Figure 7.6).

A similar contrast is seen for *Melaleuca* species with *M. leucadendra* on the Ord River releasing all seed from February to April, in the period after flowering and fruit development from the previous August to January. *M. rhaphiophylla* on the Blackwood River flowers in September to November. Fruit development occurred over summer and autumn and the woody fruit and seed are
retained on the plant for several years. Seed release appeared to be opportunistic after the desiccation of the fruit.

Table 7.6: Seed floating ability of representative common species from the Blackwood and Ord rivers. Values are means of five replicates of 20 seeds.

<table>
<thead>
<tr>
<th></th>
<th>Percentage seed floating</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Days 0 5 10 20 30</td>
</tr>
<tr>
<td><strong>Blackwood River</strong></td>
<td></td>
</tr>
<tr>
<td>Juncus pallidus</td>
<td>100 81 75 58 55</td>
</tr>
<tr>
<td>Lepidasperma gladiatum</td>
<td>100 65 22 19 6</td>
</tr>
<tr>
<td>Acacia saligna</td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td>Dodonea viscosa fruit</td>
<td>100 40 0 0 0</td>
</tr>
<tr>
<td>Dodonea viscosa seed</td>
<td>100 58 36 36 17</td>
</tr>
<tr>
<td>Rumex crispus fruit</td>
<td>100 61 35 33 0</td>
</tr>
<tr>
<td>Rumex crispus seed</td>
<td>100 100 83 74 72</td>
</tr>
<tr>
<td>Carex appressa</td>
<td>100 82 73 73 71</td>
</tr>
<tr>
<td>Banksia seminuda</td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td>Exocarpos sparteus</td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td><strong>Ord River</strong></td>
<td></td>
</tr>
<tr>
<td>Ficus coronulata fruit</td>
<td>100 90 80 20 10</td>
</tr>
<tr>
<td>Passiflora foetida fruit</td>
<td>100 43 31 30 6</td>
</tr>
<tr>
<td>Passiflora foetida seed</td>
<td>100 83 25 0 0</td>
</tr>
<tr>
<td>Pandanus spiralis</td>
<td>100 100 100 100 100</td>
</tr>
<tr>
<td>Terminalia platypHYlla</td>
<td>100 31 0 0 0</td>
</tr>
<tr>
<td>Terminalia hadleyana</td>
<td>100 83 66 66 8</td>
</tr>
<tr>
<td>Cathormion umbellatum fruit</td>
<td>100 100 100 41 0</td>
</tr>
<tr>
<td>Cathormion umbellatum seed</td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td>Abrus precatorius</td>
<td>0 0 0 0 0</td>
</tr>
</tbody>
</table>
Figure 7.4: Floating duration of seed of two major overstorey species on the Ord River (a & b) and the Blackwood River (c & d) and the percentage of seed that germinated while floating. Values are the mean percentage of five replicates of 50 seeds. Mean, median, mode and range are for the duration in days that seed remained floating.
Figure 7.5: Relationship between phenology of selected riparian species with monthly river flow levels for the (a) Ord River and the (b) Blackwood River.
Figure 7.6: Mean monthly number of seeds (± SE) of *Eucalyptus rudis* in seedfall traps averaged over 15 traps at three sites.
Fate of seed

On the Blackwood River, after seed burial for one month 75±10% (mean±SE) of buried seeds of E. _rudis_ and 79±9% of _M. rhaphiophylla_ seeds germinated. After six months of burial 19±12% of _E. rudis_ and 0% of _M. rhaphiophylla_ seed germinated and by 12 months no further seed of either species germinated. For Ord River species, after six months of burial 4±1.5% of _E. camaldulensis_ seed and nil _M. leucadendra_ seed germinated. No germination of these species was recorded in the non-seeded soil cores on either river. In ant feeding stations, after eight hours, all seed of _E. rudis_ and _M. rhaphiophylla_ had been removed from 60% of the feeding stations and no seed had been removed from the other 40% of stations. This indicated that seed is efficiently harvested once it has been located. All seed of _E. camaldulensis_ had been removed from 40% of feeding stations after eight hours and from 90% of stations after 24 hours. All seed of _M. leucadendra_ had been removed from 20% of feeding stations after 24 hours.

Discussion

The results show the potential for regeneration from seed of riparian species on the Blackwood and Ord rivers. They indicated that in the riparian zone regeneration of vegetation from soil seedbanks is probably important for annual species of herbs and grasses but of only minor significance for perennial species. For perennial species, particularly overstorey species, direct seedfall from existing vegetation is important and the enhanced dispersal by floating downstream and up-slope with flood debris is a consequential recruitment mechanism. Reproductive phenology of the four species monitored in this study appears to be well adapted to the hydrological regimes on the respective rivers.

Riparian soil seedbank

Recruitment from a soil seedbank is limited for perennial species and is probably only important for ephemeral species. These ephemeral species tend to be ruderals which are adapted to high
levels of disturbance and possess mechanisms such as seed dormancy which allow them to persist in the soil seedbank (Grime et al. 1986; Thompson 1987). Overstorey species of the Ord and Blackwood rivers were not present in any number in the soil seedbank in this study. This was also reported for a riverine swamp in the eastern United States (Schneider & Sharitz 1986). Seed predation and limited longevity of seed may be the main reasons for this, at least for the species looked at in the study. Ants have been reported to harvest large proportions of Eucalyptus seed in forests (Ashton 1979), in woodland (Yates et al. 1995) and in mallee communities (Wellington & Noble 1985a). Ant activity is usually seasonal (Andersen 1989) and the effects of seed predation may have less impact during times of massive seedfall (mast seeding), when predator satiation can occur (Janzen 1971). Seed of E. salmonophloia has been reported to have limited viability in the soil (Yates et al. 1995), as was seen here, and therefore limited ability to enter the soil seedbank. In evolutionary terms, the cause for the dominance of annual species in the soil seedbank may be, whereas there are other opportunities for regeneration of long-lived perennials, the seed of annual herbs and grasses provide the only opportunity for regeneration. Dormancy of seed ensures germination only under favourable conditions (Schneider & Sharitz 1986; Thompson 1987).

The limited number of perennial species represented in the seedbank indicated that regeneration of these species does not come from the seedbank alone, if at all. Numbers of seed found in this study (1318 m² for the Blackwood River sites and 652 m² for the Ord River sites) is within the same range of other studies of a riverine swamp (600 - 3500 m²) (Schneider & Sharitz 1986) and jarrah forest (767 m²) (Vlahos & Bell 1986). The elevated values are mainly due to the high numbers of annual species which are generally exotic weeds on the Blackwood River. This correlates with the high numbers of these species in the vegetation (see Chapter 4) which would enable the build-up of large numbers of seed in the soil. The transient nature of the soil, particularly close to the river, may explain the gradient of increased seed numbers in the soil seedbank away from the river. For the Ord River, the greater numbers of grass seed with distance from the river reflects the dominance of grass in the understorey vegetation as the conditions become more terrestrial and therefore less influenced by the river. The greater number
of tree seeds may indicate the importance of river flow for the dispersal of tree seed. Samples of the soil seedbank were taken at only one time during the year and these results therefore may reflect both the permanent and transient seedbank. To distinguish between the permanent and transient seedbank, samples would need to be taken at various times throughout the year (Gross 1990; Thompson 1992). The time of year that samples in the present study were taken would most likely coincide with the greatest number of seeds in the soil, particularly the overstorey species which have a limited viability. Results showed a high degree of variability of numbers of seeds in samples, highlighting the need to take many small samples to adequately survey the soil seedbank (Brock et al. 1994). The nature of seed dispersal would suggest a clumped distribution of seed stored in the soil (Thompson 1987).

Many species can reproduce vegetatively through rhizomes, lignotubers and stolons, etc (James 1984), which allow them to expand in an area or recover from disturbance. For the overstorey species examined here, although they can recover from defoliation or partial destruction of above-ground biomass through vegetative resprouting, colonisation of a new area usually requires establishment from seed. However, some species (e.g. *Salix* spp.) possess vegetative propagules that can be effectively dispersed downstream in river flows. An important function of vegetative propagation for species is therefore to allow persistence at a site after a disturbance, through rapid expansion and colonisation of new substrate (van der Valk 1992). The rapid recovery of established resprouters gives them a competitive advantage over seedlings and consequently resprouting species may dominate the post-disturbance habitat (Malanson & O'Leary 1982). Many species that occur in riparian habitats in North America, such as *Salix* spp. and *Populus* spp., possess the ability to resprout and produce large quantities of seeds (Johnson 1994), as do some of the dominant riparian trees on the study rivers, such as *Eucalyptus camaldulensis* and *E. rudis*.

**Dispersal mechanisms**

The river is important for dispersal of diaspores, despite wind dispersal being the most common mode of dispersal on both rivers. Wind-dispersed seeds are not only those with obvious
morphological features, such as the winged seeds of *Casuarina obesa* (Blackwood River) and *Lysiphyllum cunninghamii* (Ord River) or pappus of many Asteraceae species, but also small seeds that can be effectively blown reasonable distances (Malanson 1993), such as *Eucalyptus* and *Melaleuca* species. Most species with a primary form of dispersal such as wind or by animals are also capable of secondary dispersal by water (Sauer 1988; Thebaud & Debussche 1991). The distance of dispersal depending on floating capacity, although non-floating seed can be ‘rafted’ on other debris (Nilsson & Grelsson 1990). Water dispersal may be particularly important for rapid movement of seed downstream during floods and over much greater distances than would be achieved by wind dispersal alone. Water dispersal can also move seed up-slope and tend to concentrate seed in pools and depressions where moisture levels will be relatively high. Few species have diaspores with obvious structures for water dispersal, examples include the introduced vine *Cardiospermum halicacabum* on the Ord River and *Atriplex prostrata* on the Blackwood River. In fact, species with particular structures for water dispersal are considered rare (Willson *et al.* 1990). On a riparian meadow site, water dispersal was considered the only source of seeds not already present (Skoglund 1990). Species with fleshy fruit or inflorescence such as *Ficus* spp. on the Ord River or *Rubus discolor* on the Blackwood River are buoyant in water and can be effectively dispersed in this way. Indeed, the inflorescence of *Ficus* spp. have been observed to be eaten by fish and to have their seed dispersed in this manner (Malanson 1993). Many other species can have features that would also aid water dispersal such as hairs (Herrera 1991) or wings, as in *Dodonea viscosa* and *Casuarina obesa*. Many plants simply have light seeds with a large surface area to volume ratio, such as *Eucalyptus* and *Melaleuca* spp.. On the Ord River, there was a greater variation of dispersal types, with many species having diaspores dispersed by animals, both internally and externally with external dispersal by vertebrates being common in riparian zones in disturbed and grazed habitats (Sorensen 1986).

Riparian species rarely rely entirely on the river for the spread of diaspores. However one species that appears to is *Cathormiom umbellatum*, which only occurs fringing the river and has buoyant pods which dehisce, usually into or near the water, with large non-buoyant seed intact and only releasing the seed after decomposition of the pod. *Barringtonia acutangula* is also
restricted to the water's edge and has large buoyant fruit. No examples of species relying on the river for dispersal were obvious on the Blackwood River. Therefore, although water dispersal can be important for the rapid movement of propagules downstream and over long distances (Nilsson et al. 1993), it is not essential for the majority of species. No longitudinal trend in dispersal modes was seen on the study rivers as was observed by Weaver et al. (1925) for a Nebraska river in the USA. This may be due to river morphological processes and species physiological traits also influencing species distribution.

**Dispersal by water in debris and seed floating**

Flood debris is shown here to be an important source of propagules, at least for some of the perennial species on both rivers, with a significant amount of seed in debris samples and significantly more than occurred in the soil samples. Flood debris is seen to have an important ecological role in the colonisation and establishment of riparian vegetation (Naiman et al. 1998) through the accumulation of sediment and the transport and concentration of propagules. The occurrence of seed in debris also indicates the importance of secondary dispersal of seed by water. This has been reported for other riparian habitats (Schneider & Sharitz 1988; Johansson et al. 1996). Although seed floating ability is probably advantageous it does not have to be for very long as debris movement downstream in a flooded river is rapid (Nilsson et al. 1997) and seed may be carried on more buoyant debris (Nilsson & Grelsson 1990) or in buoyant fruits. Visual examination of the flood debris samples showed that the majority of species present are common riparian inhabitants, although several terrestrial species were also present. These species would enter the riparian system through overland flow. Floating seed of the studied overstorey species germinates readily while floating and then lose buoyancy as the hypocotyl develops. This suggests that for successful establishment of seedlings, seeds need to be washed onto near shore sediments or left along debris lines when water is rapidly receding, soon after seed fall.

**Reproductive phenology**

For the four species examined here on the Blackwood and Ord rivers there is a good correlation between reproductive phenology and hydrology. In particular, seed fall appears to coincide
with the end of the rainy season when river water levels start to recede, exposing moist bare sediment ideal for germination of seed. Reproductive phenology of the four species reflects their adaptation to their environment. Maturation of flowers and seed takes place within a couple of months in many tropical eucalypts (Eldridge et al. 1993; Brooker & Kleinig 1994), as opposed to more than two years in some southern eucalypts (Ashton 1975). The period of greatest seedfall for *E. camaldulensis*, *M. leucadendra* and *E. rudis* is timed to coincide with receding floodwaters when moist sediments favourable for seed germination and survival are exposed. This adaptation has been reported for riparian species of *Populus* and *Salix* in the central United States (Bradley & Smith 1986; Johnson 1994) and in the south-eastern United States (Schneider & Sharitz 1988). Indeed, phenological events in many species are thought to be timed to abiotic conditions (Estabrook et al. 1982). The Ord River species release the majority of seed over a short period of time at the end of the wet season which provides their only opportunity for recruitment for the year. Other northern Australian *Eucalyptus* spp. have been reported to display a similar reproductive phenology (Bowman et al. 1991; Fensham 1992; Setterfield & Williams 1996). The small seed of these species do not survive long in the soil and therefore do not become incorporated into the soil seedbank. Therefore post-dispersal conditions may limit recruitment. *E. rudis* on the Blackwood River retains mature seed in the canopy for at least 12 months. Although there is a time of peak seed release, some seed is released all year round so there is potential for germination of seed whenever conditions are favourable, and for continuous recruitment into the stable community. For many temperate eucalypts seed maturation can take several months and mature seeds are retained in the capsules while a continuous low level of seed release occurs, which is accelerated by dry conditions (Cunningham 1957; Wellington & Noble 1985a; Davies & Myerscough 1991). Interestingly, reproductive phenology of *E. camaldulensis* occurring on the Murray River in south-eastern Australia is similar to that documented here for *E. rudis* on the Blackwood River (Dexter et al. 1986). These rivers have similar fluvial regimes and climatic conditions. *M. rhaphiophylla* retains mature fruit on the tree and appears to only release seed with the desiccation of the woody fruit. This can happen after disturbance such as flooding or during strong winds when branches are commonly broken off and carried downstream onto point bars. This may result in the release of seed when conditions are most favourable for
successful germination, such as onto bare sediments when floodwaters are receding and away from competition of a understorey of sedges and dense canopy cover. Large floods will also create gaps in the vegetation. Fire may also result in the release of seed of *Melaleuca* spp. in wetlands (Froend et al. 1993).

These results of reproductive phenology are summarised from over only three years of observation and are therefore tentative. There is generally wide variation in annual fruit and seed production in *Eucalyptus* species caused by such limitations as amount of resources available for flower and fruit development, seasonal weather conditions, predation and fire (Ashton 1975; House 1997). It has been reported that years of heavy seed production are commonly preceded by several years of low seed production (Burrows & Burrows 1992). Therefore, to confirm the results presented here requires long term monitoring.

The overstorey species on the Blackwood River (*E. rudis* and *M. rhaphiophylla*) exhibited some degree of a canopy seedbank (serotiny), particularly *M. rhaphiophylla* which appears to retain seed on the plant for a number of years. For the Ord River species, in contrast, only *E. camaldulensis* showed limited serotiny. A large proportion of species in the Myrtaceae family which have woody fruits retain large stores of seed in the fruit for several seasons, releasing seed only after desiccation through fire or death of a limb (Beardsell *et al.* 1993). *Eucalyptus* spp. in general show a varying degree of serotiny. However eucalypt seed is rarely held in the canopy for more than three or four years (House 1997).

This Chapter has shown the mechanisms which are important for the storage and dispersal of seed in the riparian zone. Using the four common overstorey species, that is *E. rudis* and *M. rhaphiophylla* (Blackwood River) and *E. camaldulensis* and *M. leucaedendra* (Ord River) the following two chapters will explore the conditions which are necessary to allow successful germination of seed, the establishment of seedlings and their subsequent recruitment into the population.
CHAPTER 8

SEEDLING RECRUITMENT OF SELECTED RIPARIAN SPECIES

Introduction

After considering sources of seed (i.e. seedbank, flood debris and dispersal) in the previous Chapter, this Chapter focuses on the factors that influence the establishment of seedlings of riparian species and therefore their regeneration niche (see Grubb 1977). These factors include the effects of temperature on the germination of seed and of microsite scale environmental conditions on young seedlings as well as the resilience and growth of young seedlings under environmental extremes of flood and drought. In addition, because of the influence of rising salinity levels on riparian plants on the Blackwood River, especially in the upper reaches, the effect of salinity on germination of seed and survival of seedlings will also be examined. The two most common overstorey species from each river system (identified in Chapter 4 and described in Chapter 7) have been chosen for this study. That is, *Eucalyptus rudis* and *Melaleuca rhaphiophylla* on the Blackwood River and *E. camaldulensis* and *M. leucadendra* on the Ord River.

Temperature and moisture play a critical role in providing the stimulus for seed germination and this is linked to climatic conditions, with many plants evolving to germinate when conditions are most favourable for survival (Mott & Groves 1981). Seed dormancy has evolved to delay germination until environmental conditions are such that they provide the best chance of survival (Thompson 1992). In many cases germination is cued to temperature and therefore for most species there is an optimal temperature above and below which germination is delayed but not prevented (Bell *et al.* 1993). For eucalypts in southern Australia constant temperature (range
15° - 25° C) gives enhanced germination than alternating temperatures and most species have a germination requirement for light (Boland et al. 1980). Species from northern Australia may have higher temperature requirements for germination (around 30° C). Species from environments where soil moisture is available longer into the dry season, such as the riparian zone or wetlands, may also have higher optimal germination temperatures (Bell & Williams 1997). Species of Eucalyptus and Melaleuca generally have some species-specific tolerance to saline conditions during germination but are generally much more sensitive than halophytes (van der Moezel & Bell 1987). Rising salinity levels in the Blackwood River may inhibit germination of these important species in the riparian zone.

Successful establishment of seedlings following germination can be greatly influenced by position in the landscape (Bell & Williams 1997). Microsites which can retain moisture and maintain high humidity provide the right conditions for successful germination and early establishment of seedlings (Battaglia & Reid 1993; Pollock et al. 1998). The occurrence of elevated microsites which provide such conditions can affect the distribution of seedlings in flooded riparian wetlands (Titus 1990; Bren 1992). Soil type is also important in terms of compaction and bulk density, moisture retention and nutrient availability. Litter, even small amounts, has been shown to reduce seedling survival rates (Fowler 1988) and the interaction of flooding and litter accumulation can affect plant establishment in the riparian zone (Nilsson & Grelsson 1990). Competition, particularly with grasses, has been reported as influencing growth and survival of seedlings (Withers 1978; Noble 1984; Davidson & Reid 1989) and livestock grazing has been suggested to improve E. camaldulensis seedling survival by reducing competition with grasses (Dexter 1978). The previous Chapter showed that timing of seedfall for three of the four study species occurred to coincide with receding river water levels and it was postulated that this was to allow seed to fall onto moist sediments which are conducive to survival of germinating seed. This Chapter will examine the fate of germinating seed and seedlings in this and other areas of the riparian zone.
In the riparian zone of the Ord and Blackwood rivers, high flows occur regularly almost every year. Therefore establishing seedlings will be subjected, depending on their location, elevation and level of flooding, to extended periods of waterlogging, inundation or total submergence. The flooding tolerance of plant species varies widely and is important in determining species composition and distribution (Kramer & Kozlowski 1979). Flooding effects include suppression of transpiration and photosynthesis and a subsequent reduction in growth (Ernst 1990; Blom & Voesnek 1996). Responses to flooding include formation of adventitious roots, stem elongation and formation of aerenchyma cells in the roots of flood tolerant species (Blom & Voesnek 1996). Establishing the degree of flood tolerance of the selected species in this study will indicate their potential distribution on these rivers.

This Chapter examines the ecological factors that influence seed germination and the survival and growth of seedlings in the particular riparian environments of the Ord and Blackwood rivers. It examines what are the optimum temperatures required for the selected species on each river and the rate of germination of these species at various temperatures that may be experienced throughout the year. It investigates conditions that are likely to allow successful early establishment of seedlings and, for the selected species, tolerance to various degrees of flooding. The previous Chapter examined the sources of seed of riparian species which enable their recruitment into the riparian zone and this chapter takes the next step to examine the conditions necessary for the germination of this seed and the establishment and growth of resulting seedlings.

Methods

Seed germination

Seed used in germination trials was supplied by the Department of Conservation and Land Management seed store (Manjimup) for Blackwood River species (*Eucalyptus rudis*, *Melaleuca rhaphiophylla* and *M. cuticularis*) and by a commercial seed supplier (C. Dupe, Kununurra) for
the Ord River species \((Eucalyptus\ \text{camaldulensis}\ \text{ssp. obtusa} \text{ and }\ Melaleuca\ \text{leucadendra})\). For the experiment on the effects of salinity on germination, seed collections of \(E.\ \text{rudis}\) were from two localities, one from an area with freshwater conditions (Narinup) and the other from a saline environment (Narrogin). Seed of \(M.\ \text{cuticularis}\) was also tested as this species tends to replace \(M.\ \text{rhaphiophylla}\) in saline areas. For the temperature effects experiment, seed of \(E.\ \text{rudis}\) was from the Collie River in the catchment adjacent to the Blackwood River catchment where water quality is similar to the Blackwood River in being marginal to brackish.

In the trial on temperature effects on germination, seed from the four target species were tested \((E.\ \text{camaldulensis} \text{ and } M.\ \text{leucadendra} \text{ from the Ord River, } E.\ \text{rudis} \text{ and } M.\ \text{rhaphiophylla} \text{ for the Blackwood River})\). Twenty replicates of 50 seeds of each of the four species were placed in 9 cm petri dishes that contained vermiculite and a Whatman No. 4 filter paper which were wetted up with 25 ml deionised water and given a light spray of fungicide (Benlate 1g L\(^{-1}\)). A replicate of each species on the petri dishes was placed in a moistened plastic bag which was sealed to reduce evaporation and five replicates of each species were placed in growth chambers at 15° C, 20° C, 25° C and 30° C. Chambers were in 12 hours continuous light (2500 lux) and 12 hours dark and were monitored daily over 20 days. A regime of continuous temperature was chosen as studies have shown that for many species alternating temperatures have shown no positive effect and the diurnal temperature range is adequately represented by the mean (Mott & Groves 1981).

Seed was considered to have germinated when the radicle had emerged and as germinants were counted they were removed. Seed that did not germinate was dissected and visually examined and almost all of this material did not contain a developed embryo inside the seed coat. This indicated that germination levels reflect, reasonably well, seed viability for each species.

Total germination after 20 days for each treatment and species was presented and the effect of temperature was tested using a one-way analysis of variance and Fischer’s LSD post hoc test (Zar 1984). Initial germination speed \(\left(1/T_{50}\right)\) for each species and temperature was calculated as the time in days for at least one seed to germinate from any replicate. Median germination speed \(\left(1/T_{50\%}\right)\) was the time for at least 50% of viable seed to germinate (Lush \textit{et al.} 1984).
The germination trial on the effects of salinity on germination was restricted to the Blackwood River species including two ecotypes of *E. rudis*, *M. rhaphiophylla* and *M. cuticularis*. The same procedure was used as for the temperature trial except that growth chambers were set at a constant 25° C and the twenty replicates were watered with one of four levels of salt concentration: 0 mScm$^{-1}$ (i.e. deionised water only), 10 mScm$^{-1}$, 20 mScm$^{-1}$ or 30 mScm$^{-1}$. Saline solutions of the desired concentrations were achieved by adding NaCl into a beaker of deionised water until the desired electrical conductivity was obtained.

**Seedling establishment**

To examine where within the riparian zone seedlings are most likely to establish, seedling plots were set up and environmental parameters that may be important for establishment of seedlings were recorded. At Sites O4 and O5 on the upper Ord River (in the unregulated section) and on the middle section at Sites B1 and B2 on the Blackwood River (see Figures 3.1 & 3.2) six 200 metre line transects were set up perpendicular to the river. One metre square seedling quadrats were laid out adjacent to the transects where seedlings occurred. Within each quadrat heights of all one year old seedlings were recorded. For each quadrat a number of environmental parameters were recorded: surface soil type using field texture analysis (McDonald & Isbell 1984); four categories of microtopography where plots occurred, including depression, flat area, slope and rise; surface soil moisture status with four categories including dry, moist, waterlogged and inundated; elevation above river base flow level measured along the transect with an automatic level and staff; a visual estimate of % bare ground and % litter; distance of seedling plot from river base flow level; and distance to nearest seed tree. Frequency of seedling plots for each environmental parameter was collated. For quantitative parameters (elevation, % litter, distance to water and distance to nearest seed tree) correlation analysis against seedling density was performed. For each categorical parameter (soil type, microtopography and surface soil moisture status) a Krusall-Wallis test (non-parametric ANOVA analogue) was conducted for seedling density to test if there were significant differences between categories for each parameter and seedling density or number of quadrats. A non-parametric ‘Tukey-type’ multiple
comparison test was carried out to separate differences between category means (Zar 1984). As there were unequal numbers of quadrats in the categories for each parameter, the five seedling density scores around the median score were used for the subsequent analysis.

In addition to these plots, to measure the survival and growth of seedlings, transects were set up in areas close to the river where germination had recently taken place. On the Blackwood River, seedling plots were located opportunistically in an area at Site B2a where a large germination event had taken place along the river edge in exposed moist sediment from the receding winter high water levels in November 1996. At this site three belt transects were set up perpendicular to the river from the water level to the top of the bank. The transects were 10 metres long and one metre wide and were divided into 10 contiguous 1 m² plots. In each plot all seedlings of *E. rudis* and *M. rhaphiophylla* were counted and seedling height was measured. Elevation along the transects was measured, using an automatic level and staff, as well as distance from the water. At 0 m, 4 m and 8 m soil samples were taken to measure gravimetric soil moisture percentage and electrical conductivity using a 1:5 soil deionised water solution (Klute 1986). Transects were measured every two months for a period of 48 weeks.

On the Ord River, seedling transects were located on a sediment island and on a depositional area of the river on the inside of a bend. Transects were located at Site 01 and Site 04. Belt transects 10 m long and 1 m wide were divided into 10 contiguous 1 m² plots. In each plot all seedlings of *M. leucadendra* were counted and seedling height was measured. Elevation along the transects was fairly flat and at 0 m, 4 m and 8 m from the water soil samples were taken to measure gravimetric soil moisture content (%). From flood debris marks in the nearby vegetation and from recorded river discharge levels for the measurement period, seedling plots were inundated to a level of at least one metre at both sites for approximately three months during the wet season (December to March). Transects were measured four times, in August 1996, April 1997, December 1997 and April 1998.
Effects of flooding

A flooding experiment was set up to test the effect on survival and growth of various levels of flooding on seedlings of the four target species. One hundred and forty four seedlings of each species were raised in a commercial nursery for six months. They were transferred to 380 cm³ volume pots with a commercial potting mix, sealed at the top with a clay plug and allowed to settle in for three weeks prior to commencement of the experiment. Forty eight seedlings of each species were assigned to one of four treatments: 1) control - pots were free-draining and watered daily; 2) waterlogged - pots were sat in water to ~1 cm below the top of the pot so that soil was permanently waterlogged; 3) flooded - pots were placed in water to a depth of 20 cm so that approximately the lower one third of each seedling was under water; 4) submerged - pots were placed in water to a depth of 55 cm so that seedlings were completely under water. Three plastic tubs (600 mm x 500 mm x 600 mm) were used for each treatment giving three replicates of 12 seedlings of each species per treatment. Tubs were arranged on three levels so that water circulated through all the tubs and was then pumped back up to the top tub. Tubs were also orientated so that the duration of sunlight and shade in all tubs was similar. At the commencement of the experiment, and after 4, 8 and 12 weeks, one seedling of each species was removed from each tub. Plant moisture status was assessed by measuring shoot xylem pressure potential using a Scholander pressure bomb (Scholander et al. 1964) as an indication of the physiological effects of flooding. Seedlings were oven dried at 50° C for 24 hours and roots and shoot was weighed to give a measurement of dry weight total biomass and also root:shoot ratio. Top height of all seedlings was also measured, every two weeks, from soil surface to the top of the plant and the occurrence of any adventitious roots was recorded. Relative growth rates were calculated over the 12 week period as:

\[ RGR = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1} \]

where \( W_1 \) and \( W_2 \) are the total dry weights at the beginning and end of the sampling period and \( t_1 \) and \( t_2 \) are the dates of sampling (Kramer & Kozlowski 1979). This was done for each species in each treatment to allow for the variable growth patterns of the different species (Bidwell 1974). Differences between treatment means were tested using a Kruskal-Wallis non-parametric
ANOVA analogue and the 'Tukey type' non-parametric multiple comparison (Zar 1984). Water temperatures in the tubs ranged from 14° C in the morning to 22° C by mid-afternoon at the beginning of the experiment (4th September 1997) to 17° C to 26° C at the end of 12 weeks. Day time dissolved oxygen levels in the tubs were measured weekly with a portable dissolved oxygen probe averaging 8.4 ± 2.4 mg l⁻¹ for the duration of the experiment.

Results

Seed germination
Total germination of seeds was significantly affected by temperature for only Eucalyptus rudis (p=0.01), with a decrease in total germination at 15° C (Figure 8.1). However, rate of germination was affected by temperature for all species (Figure 8.2). For E. rudis, initial germination was rapid (one day) at 20, 25 and 30°C and for the higher temperatures at least 50% of seed germinated within this time. For the other species there was a delay from initial to median germination at all temperatures. Of the temperatures examined, 25° and 30° C were the optimum temperature for rapid germination in all species.

The effects on germination of increasing levels of salt concentration for Blackwood River species showed a significant reduction in total germination with increasing salinity of water in the petri dish (Figure 8.3). For all species, germination was not affected at 10 mS cm⁻¹ but a significant reduction in germination occurred with each subsequent increase in salt concentration. There was no significant increase in salinity tolerance with seed from saline environments for E. rudis or M. cuticularis. Germination rates were also affected by increasing salinity (Figure 8.4), with time to initial germination increasing with increased salinity even at 10 mS cm⁻¹.
Figure 8.1: Total germination percentage of seed subjected to four constant temperature treatments in growth cabinets. Species included *E. rudis* and *M. rhaphiophylla* from the Blackwood River and *E. camaldulensis* and *M. leucadendra* from the Ord River. Figures are the means (± SEM) of five replicates.
Figure 8.2: Speed of germination of the four selected species at different temperatures with initial germination speed ($1/T_{\text{int}}$) where $T_{\text{int}}$ is the time taken in days for at least one seed to germinate and $T_{50\%}$ is time taken for 50% of the total seeds to germinate.
Figure 8.3: Total germination percentage of seed watered with four different salt concentrations for species occurring on the Blackwood River including two ecotypes of *E. rudis* from freshwater area (Nannup) and saline area (Narrogin). Figures are the means (± SEM) of five replicates. Within each species, treatment means with the same letter are not significantly different (Fisher LSD, p = 0.05).
Figure 8.4: Speed of germination of four selected species at different salinities (mS/cm) with initial germination speed ($1/T_{int}$) where $T_{int}$ is the time taken in days for at least one seed to germinate and $T_{50\%}$ is time taken for 50% of the total seeds to germinate.
Seedling establishment

The majority of the Ord River seedling plots had loam to sandy soils (Figure 8.5a). When seedling density was compared for the different soil types, numbers of seedlings per m² was significantly higher in loam, loamy sand and sandy soils than in the clay and gravel soil types (H=15.87, p= 0.003). Frequency of plots was similar for the different microtopography sites with slightly more plots occurring on the river flat area but analysis of seedling density showed that plots in depressions, slopes and rises had significantly more seedlings per m² (H=13.28, p=0.004). Moist and dry sites had the greatest frequency of seedling plots but waterlogged sites had significantly greater density of seedlings than the other moisture-related parameters (H=9.74, p=0.02). There was no significant correlation between seedling density and distance to nearest seed tree, with a large group of plots in close proximity and another group at some distance (>200 m) from a seed tree. There was also no significant correlation between seedling density and percentage litter or percentage bare ground. Frequency of plots with 0-20% litter and 0-20% bare ground was much greater than for the other cover classes (Figure 8.5). There was a strong negative relationship between seedling density and elevation (r= 0.875, p=0.001), with most seedlings occurring at lower elevations (Figure 8.6a). There was, however, not a strong relationship between elevation and distance from the river (r=0.284, p=0.10).

The majority of Blackwood River seedling plots were loamy sand and sandy soils (Figure 8.5b). When seedling density was compared for the different soil types, numbers of seedlings per m² was significantly higher in loam, loamy sand and sandy soils than in the clay soil and no plots occurred in gravel soil (H=10.99, p= 0.011). Frequency of plots for microtopography showed more than 50% of plots occurring on the river flat, but analysis of seedling density showed river flat, depression and rise had significantly greater seedlings per m² than plots on a slope (H=11.66, p=0.0086). Moist sites had the greatest frequency of seedling plots with wet and moist sites having a significantly greater density of seedlings than did dry sites (H=10.47, p=0.0053). There was a significant correlation between seedling density and distance to nearest seed tree (r=0.470, p= 0.048) with most plots in close proximity to a seed tree and no plots >30 metres from a seed
There was no significant correlation between seedling density and percentage litter or percentage bare ground. Like the Ord River plots, frequency of plots with 0-20% litter and 0-20% bare ground was much greater than for the other cover classes (Figure 8.5b). There was a strong negative relationship between seedling density and elevation ($r = 0.758$, $p=0.001$), with most seedlings occurring at lower elevations (Figure 8.6b). There was also a significant relationship between elevation and distance from the river ($r=0.815$, $p=0.001$).

After initial germination of seed of *E. rudis* and *M. rhaphiophylla* in November 1996 seedling numbers declined along the seedling transects at Site 3 on the Blackwood River (Figure 8.7&8). For *E. rudis*, seedling numbers were greatest in the middle of the transect where conditions were moist but not waterlogged. Greatest loss of seedlings was over weeks 16 to 32, the time of highest salinity and lowest moisture (Figure 8.9). There were few seedlings at seven to eight metres and seed that did germinate rapidly died. There was steady growth of seedlings over the period, with rapid growth from week 40 to 48 with warmer temperatures and adequate moisture, except in the 0-2 m quadrats which were inundated and growth was negligible and some death occurred. *M. rhaphiophylla* had higher survival and better growth in plots closest to the water, although more seedlings initially established in the middle plots. The first quadrats (0-1 m) were underwater for 3.5 months (July to October) up to a depth of 0.5 m while the second quadrats (1-2 m) were inundated for two months (August -September). Moisture content was initially high before dropping to lowest levels in March-April after 16 weeks, then rising steadily with winter rains and rising river levels (Figure 8.9). Surface soil electrical conductivity along the transect peaked in May after initial rains following the summer drought period (when salts would accumulate at the soil surface through evaporation) but subsequently reduced after more substantial rains flushed out the salt.
Figure 8.5: Percentage of 1m x 1m seedling plots with particular environmental attributes for (a) the Ord River and (b) the Blackwood River.
Figure 8.6: Relationship between elevation from the river and number of seedlings in 1m x 1m plots for (a) the Ord River and (b) the Blackwood River.
Figure 8.7: Number of seedlings and growth of *Eucalyptus rudis* over a twelve month period in 1m x 1m quadrats on exposed sediment on the river foreshore at Site B2 on the Blackwood River. Monitoring from November 1996 (0 weeks) to November 1997 (48 weeks).
Figure 8.8: Number of seedlings and growth of *Melaleuca rhaphiophylla* over a twelve month period in 1m x 1m quadrats on exposed sediment on the river foreshore at Site B2b on the Blackwood River. Monitoring from November 1996 (0 weeks) to November 1997 (48 weeks).
Figure 8.9: a) Mean (±SE) gravimetric soil moisture content and b) soil electrical conductivity along seedling transects on exposed sediment on the river foreshore at Site B2b on the Blackwood River. Soil samples were taken at 2, 4 & 8 metres along the transects. Monitoring from November 1996 (0 weeks) to November 1997 (48 weeks).
Figure 8.10 : Mean density and growth of seedlings of *Melaleuca leucadendra* in ten 1m x 1m quadrats on sediment islands at two sites on the Ord River over a period of 80 weeks.
Monitoring of seedling plots on sediment islands on the Ord River at two sites indicated the greatest loss of seedlings was in the wet season when seedlings were inundated for two to three months and completely submerged for some of that time (Figure 8.10). There was also some loss of seedlings in the dry season with soil moisture content of 8.4% ± 0.7 in the mid dry season (August 1996) and 3.8% ± 0.4 in the late dry season (December 1997) for both sites combined. During the April 1997 and April 1998 measurements, sediment in the seedling plots was waterlogged. Growth of seedlings was steady over the study period with seedlings increasing in height by 2 m over a twenty month period at Site O1 and 1.4 m at Site O4. Relative growth rates were 0.044 cm cm yr\(^1\) for the dry season (April - November 1997) and 0.141 cm cm yr\(^1\) for the wet season (December 1997 - April 1998) at Site O1 and 0.0194 cm cm yr\(^1\) for the dry season and 0.171 cm cm yr\(^1\) for the wet season at Site O4.

Effects of flooding

After 12 weeks of the flooding experiment, survival of seedlings of *Melaleuca leucadendra* and *M. rhaphiophylla* was 100% for all treatments including total submersion. *Eucalyptus camaldulensis* seedlings had 100% survival in control and waterlogged treatments with 60%±12 for flooded and 73%±15 for submerged treatment. *E. rudis* had 100% survival in the control and waterlogged treatments, 71%±6 for flooded and 60%±9 for submerged treatments. Growth of seedlings showed the detrimental effects of flooding and submersion on the *Eucalyptus* spp. with significantly reduced mean dry weight of seedlings in flooded and submerged treatments after eight weeks (p= 0.03, Ec; p=0.063, Er) and 12 weeks (p=0.032, Ec; p=0.021, Er) (Figure 8.11). Growth of the *Melaleuca* spp. seedlings in the totally submerged treatment was significantly reduced after eight weeks (p= 0.033, Ml; p=0.031, Mr) and 12 weeks (p=0.022, Ml; p=0.015, Mr). Dry weights of seedlings in the flooded and waterlogged treatments were similar to those of seedlings in the control treatment. Measurement of seedling top height showed similar trends for each treatment as dry weights except for *M. rhaphiophylla* where there was no difference in mean seedling height for any treatment after 12 weeks (Figure 8.12). This indicated the
elongation of the stems of this species in trying to grow out of the water. Some seedlings of this species had grown out of the water in the submerged treatment by the ninth week. Mean relative growth rates over the 12 week period also demonstrated the superior growth of the *Melaleuca* spp. and the lack of a negative effect on growth rate of partial submersion in the flooded treatment (Figure 8.13). For the *Eucalyptus* spp. there was a clear separation of growth rates with treatment, although, as for dry weights, there was no difference between control and waterlogging treatments. Further adaptation of the *Melaleuca* spp. to flooding was evidenced by the formation of adventitious roots on the stems of 70% of seedlings by the fourth week. Root to shoot ratio dry weights did not differ significantly for any treatment for any of the species and at 12 weeks varied from 2.07 to 3.95 across all species.

Xylem pressure potential was significantly more negative than the control in the waterlogging, flooded and submerged treatments for *E. camaldulensis* (*p* = 0.023) and in the submerged treatment for *E. rudis* (*p* = 0.014) after 8 weeks (Figure 8.14). For *M. leucadendra* (*p* = 0.098) and *M. rhaphiophylla* (*p* = 0.0675) there was no significant difference between treatments at 8 weeks but after 12 weeks xylem pressure of seedlings of *M. rhaphiophylla* in the flooded and submerged treatments was significantly more negative (*p* = 0.025).
Figure 8.11: Mean dry weight of seedlings subjected to one of four flooding treatments over a twelve week period. Means (±SEM) are of three replicates for each treatment.
Figure 8.12: Mean top height of seedlings subjected to one of four flooding treatments over a twelve week period. Means (±SEM) are of three replicates for each treatment.
Figure 8.13: Relative growth rate of seedlings of each species for each of the four flooding treatments, over a 12 week period. Means (±SEM) are from three replicates and p values are from Kruskal-Wallis non-parametric ANOVA of treatment means for each species.
Figure 8.14: Xylem pressure of seedlings of each species for each of the four flooding treatments over a 12 week period. Means (±SE) are of three replicates for each species in each treatment.
Discussion

Field observation and experimental results presented here show the adaptation of the study species to their riparian environment. Temperature provides a cue to break innate dormancy of seed so that seeds are likely to germinate at the time of year with the greatest chance of seedling survival (Mott & Groves 1981; Bell et al. 1993; Britton & Brock 1994). As demonstrated in the previous Chapter this also correlates well with timing of maximum seedfall and river hydrology. Optimum temperature for germination of Ord and Blackwood river species was similar, despite very different climatic and hydrological conditions. This may be related to the common features of the riparian environments where moisture is readily available (Bell & Williams 1997). Position of seedlings in the riparian landscape is also strongly related to environmental conditions that provide adequate moisture but which protect seedlings from flooding and relates to dispersal of seed within the riparian zone (see Chapter 7). Of the study species, the Melaleuca species showed a greater degree of flooding tolerance than the Eucalyptus species, which is reflected in the position in the riparian landscape in which they occur. This provides an insight, at least for the species examined here, into the distribution of plants along the elevation gradient in the riparian zone described in Chapter 4.

Seed germination

Optimal germination temperatures for all four species tested was 25 - 30° C in terms of both total germination and germination speed. For the Ord River species (E. camaldulensis and M. leucadendra) this corresponds with mean diurnal temperatures experienced from March to May (see Chapter 3) which is also the time of receding high river flows and maximum seed fall (Chapter 6). These ambient temperatures also occur in October to November but successful recruitment is unlikely then because of insufficient seed storage, low moisture availability and the oncoming wet season which results in prolonged inundation of small seedlings and/or river flows scouring out seedling beds. Eucalyptus species from northern Australia are considered to have germination temperature optima of around 30° C (Bell & Williams 1997). Variation in
germination requirements of moisture and temperature of different provenances of *E. camaldulensis* is considered to be a consequence of adaptation to the environment in which they occur (Gibson & Bachelard 1987). Germination temperature optima for Blackwood River species (*E. rudis* and *M. rhaphiophylla*) is higher than would be expected for species occurring in the Mediterranean climate of south-western Australia (Bell *et al.* 1993; Bell & Williams 1997). However results presented here for *E. rudis* agree with those presented in a study on temperature effects on germination of native species used for mining rehabilitation (Bell & Bellairs 1992). It has been suggested that as *E. rudis* is a species of streams and wetland areas, germination temperatures are higher as soil moisture will be available longer into summer in these habitats (Bell & Williams 1997). This may also apply to the germination of *M. rhaphiophylla*. Germination of seed is also enhanced by high humidity (Battaglia & Reid 1993), which is a common feature of riparian environments and which may allow germination to continue later into the dry season. In addition, delaying germination to later in the year when temperatures are warmer allows germinating seed to avoid the period of flooding and waterlogged soils. Optimum germination temperature for *E. camaldulensis* on the Murray River in Victoria is reported as 35° C and this has been related to delaying germination until after winter floods (Dexter 1978). The very rapid germination of *E. rudis* at 25 and 30° C may provide a competitive advantage (Mott & Groves 1981) for this species in being able to quickly establish when conditions are optimal. The temperatures tested in this Chapter are limited and a greater range of temperatures would provide a more complete picture of the germination range for each species as it relates to temperature. In addition, it may be useful to create germination conditions that would be experienced by the seed *in situ*. This may include alternating light and dark conditions and corresponding changes in temperature. A regime of alternating wetting and drying periods may also affect germination patterns of seeds and may be useful to determine whether seeds can remain viable after imbibition followed by drying out (Gibson & Bachelard 1987). Testing germination under these conditions may shed some light on the viability of buried seed which was tested under field conditions in the previous Chapter.
Germinating seed of the Blackwood River species showed some tolerance at low levels of salinity (10 mScm⁻¹) but total germination and germination speed was severely affected at the higher salinity levels. Seed of *Melaleuca cuticularis* and the ecotype of *E. rudis* from saline environments showed no greater tolerance to higher water salinity. Tolerance to salinity at germination has been found not to correlate with the tolerance of seedlings (Pearce-Pinto *et al.* 1990) or of adult plants (Morris 1984). Imbibition of seeds may only take place when rainfall sufficiently dilutes surface and soil water salinity levels to more favourable external osmotic potentials (Bell & Williams 1997). Seed germination tolerance to salinity of riparian species on the Blackwood River may become important if these species are reliant on water from the river to initiate germination. Blackwood River salinity levels have been steadily rising at a rate of 52 mgl⁻¹ yr⁻¹ (Schofield *et al.* 1988) to present levels of 2069 mgl⁻¹ (five year moving average) at Site B1 on the lower Blackwood with higher levels for the upstream sections of the river (Water and Rivers Commission unpublished data).

**Seedling establishment**

For both rivers, the environmental conditions that appear to coincide with seedling establishment are similar. Most seedlings occur in river sediment of larger particle size of sandy to loam soils. Seedlings are also more dense at lower elevations and in microtopographic sites that are moisture-gaining but also where there is a slight rise. These rises are important for seedling establishment in creating safe sites to prevent waterlogging (Bren & Gibbs 1986; Skoglund & Verwijst 1989; Titus 1990). This highlights the importance of fluvial processes in recruitment. Moisture-gaining sites are important for sustaining seedlings through the dry part of the year. Greater emergence of seedlings of *E. delegatensis* in depressions was attributed to lower vapour pressure deficits in these microsites (Battaglia & Reid 1993). Litter levels and areas of bare sediment do not appear to be important for establishment of developing seedlings. These seedling plots were of older seedlings (>1 year old) and litter levels and area of bare ground may however be important for the successful initial establishment of germinating seed (Nilsson & Grelsson 1990; Greenway 1994; Johnson 1994). Seedling plots on the Ord River occurred at large distances from mature trees and therefore probably from an alternative source of seed.
This may indicate that seed can be dispersed by floodwaters. The presence of numerous open fruit in the flood debris lines indicate that seed is being transported in this way. Thus in large flows seed can be transported not only longitudinally down river, but also laterally away from the channel to areas which afford some protection from subsequent flooding after initial dispersal on floodwaters. In fact, for the Ord River, successful long term establishment may require a period without large floods. On the Blackwood River seedling density was closely related to distance to seed trees and no seedlings were found further than 30 metres from a potential seed tree. For *E. camaldulensis* on the Murray River in south-eastern Australia a similar close association between seedlings and seed trees was found (Dexter *et al.* 1986). This suggests that seeds are generally dispersed by wind with little dispersal on floodwaters. Germination trials on seeds of *E. rudis* indicate that seeds germinate rapidly after wetting (one to two days) and the majority of floating seed germinate within four to five days (Chapter 7), so that they may not have time to be dispersed by water. However, floating seed can be transported long distances very rapidly on floodwaters (Nilsson *et al.* 1993) so that seed do not need to remain viable for long to be effectively dispersed in this manner. Seed and fruit of *E. rudis* was found in debris samples on the Blackwood River (Table 7.5) with good viability of seed. It is most important for seed to be deposited in a safe site where conditions are conducive for survival and growth.

In seedling plots along the transect on the Blackwood River the greatest survival and growth of *E. rudis* was in the mid-slope position. Where seedlings were below this, flooding conditions caused high mortality and restricted growth and in the upper-most plots conditions were too dry with mortality and poor growth most likely caused by drought conditions in summer. For *M. rhaphiophylla* the zone of optimal survival and growth was lower on the transect. This reflects the greater tolerance to waterlogging of this species and also reflects the respective positions of the adults of these two species in the landscape with *M. rhaphiophylla* occupying the lower landscape position on the fringe of the high water level and *E. rudis* generally occupying the bank top and on to the floodplain. Greatest loss of seedlings for both species was at the dry time of year (late summer and autumn) when soil moisture levels are low and soil salinity is high. This indicates that surviving the summer drought may be more important in survival of seedlings.
than flooding in winter, which inhibits growth but to which plants are fairly tolerant, particularly *M. rhaphiophylla*. Replenishment of soil moisture is probably important for riparian seedlings in arid zone rivers. Roberts (1993) found a good correlation between recruitment and flood events which replenish soil water for *E. coolabah* seedlings on a semi-arid ephemeral creek in eastern Australia.

*M. leucadendra* seedling plots on deposition islands on the Ord River showed the greatest loss of seedlings in the wet season when they are completely submerged for up to two months. Although, owing to the 'flashy' nature of river flows on the Ord River, which may cause levels to rise and fall during this period, seedlings would have periods when at least some portion of the plant is exposed to the air so that photosynthesis, and therefore growth, can continue. This is supported by growth rates in the wet season are higher than in the dry season when lack of water may be limiting but is not great enough to cause widespread drought-death of seedlings.

**Effects of flooding**

The results of the flooding experiment correspond to field observations of the different positions in the landscape occupied by the *Melaleuca* and *Eucalyptus* species with the former occupying the lower landscape positions subject to greater frequency of inundation. Greater tolerance, at the seedling stage, to inundation has been used to explain the differences in distribution in the riparian zone of two rainforest species in Victoria (Melick 1990). The flooding experiment indicated that both *Melaleuca* species can survive even complete submergence for several months. Growth, however, is affected by total submergence as transpiration and photosynthesis shut down, severely affecting the energy budget of the plant (Ernst 1990). The *Melaleuca* species showed signs of adaptation to flooded conditions, such as elongation of the stem and the formation of adventitious roots. Elongation of the stem (controlled by the plant hormone ethylene) is important in flood tolerance as it allows plants to reach the water surface and maintain photosynthesis (Blom et al. 1990). This, coupled with the formation of aerenchyma tissue and the growth of adventitious roots allows better oxygen diffusion. Elongation of the stem or petiole is a common adaptation of flood tolerant aquatic plants (Blom & Voesnek 1996).
formation of adventitious roots and stomatal closure were considered important factors in the flooding tolerance of *Melaleuca quinquenervia* seedlings, a species of northern Australia (Senna-Gomes & Kozlowski 1980). For *Melaleuca halmatrorum* seedlings, survival was poor after six to nine weeks of total submergence, although elongation of the stems increased survival rates (Denton & Ganf 1994), indicating some flood tolerance in this species. Survival and growth of the *Eucalyptus* species was significantly affected by partial and total submersion. This may indicate an inability of these species to produce the physiological adaptations seen in the *Melaleuca* species. All of the species tested, including the eucalypts, did not show any detrimental effects of waterlogging, indicating adaptation to their environment where persistence in proximity to the river would require some tolerance to waterlogging. Waterlogging has been demonstrated experimentally not to effect the growth of *E. camaldulensis* seedlings (Akilan *et al.* 1997) nor leaf water potential (Pereira & Kozlowski 1977). Age of seedlings would also clearly affect tolerance to flooding. Seedlings tested here were more than six months old and younger seedlings may not show the same tolerance. However, flooding clearly affected the *Eucalyptus* species which suggests that these species require access to the air through the soil surface for survival and growth. Although in the flooding experiment some attempt was made to circulate water between the seedlings by pumping water through the tanks, providing less detrimental conditions than stagnant water (Kozlowski 1984), this was at a fairly slow rate and would not very well simulate the high flow rates that would be experienced in floodwaters. The physical effect of high flow rates on seedlings is likely to be substantial and therefore requires further examination to contribute to understanding of the mechanisms affecting survival and growth of seedlings in the riparian zone.

The previous Chapter examined the sources of seed in the riparian zone, including the development of seed and its release, the dispersal of seed in flood debris and the storage of seed in the soil seedbank as well as seed predation and long term viability. This Chapter has expanded this in investigating the optimum germination temperature of seed from the selected species and the environmental factors that affect establishment and growth of seedlings including soil type, microsite conditions and adaptation to flooding. The next chapter will look
at the factors affecting recruitment in the riparian zone by dealing with the population structure and spatial distribution of the selected species.
CHAPTER 9

POPULATION STRUCTURE AND SPATIAL DISTRIBUTION OF SELECTED SPECIES IN THE RIPARIAN ZONE.

Introduction

The previous chapter examined the ecological factors influencing the germination, survival and growth of seedlings of *E. rudis* and *M. rhaphiophylla* on the Blackwood River and *E. camaldulensis* and *M. leucadendra* on the Ord River. This Chapter will consider the age class structure of these species as well as their spatial distribution within the riparian zone. This will be done by inferring age by the size class structure of each species along transects on different river reaches. Recording the age class structure of a sample of a population can infer survivorship through time of cohorts of individuals (Hutchings 1997). This can be used to assess the population stability and successional trends or vegetation dynamics of these species (Veblen 1986). The spatial structure of the populations at these sites will also be related to the long term hydrologic records for these rivers.

Fluvial regime and river geomorphology are major influences on the spatial and temporal structure of riparian vegetation (Johnson 1994; Barnes 1997; Johnson 1997). The formation of sandbars, levee banks and river terraces as well as river bends, pools and riffle zones all make for a heterogeneous environment for the recruitment and establishment of riparian plants (Fonda 1974; Bell & del Moral 1977). Added to this is the regime of regular or irregular flooding. Large scale disturbances, such as high water flows and flooding, are likely to be important factors in the dynamics of the riparian community. Recruitment, establishment and survival of riparian
trees is thought to be closely tied to the hydrological regime (Barnes 1985; Bradley & Smith 1986; Johnson 1994). Flood-induced disturbance may instigate the transition from stable states of plant composition and population structure. It can be hypothesised therefore that river systems with frequent disturbance from high energy flood events will support riparian communities with long periods of transition and rather shorter stable states. That is, communities which are in a state of arrested succession (Webb et al. 1972) and which, in terms of individual populations of trees, rarely reach maturity and remain in a juvenile stage of development.

The present state of an ecosystem is the result of a particular history of disturbance, climatic factors and/or management. The regeneration process and longevity of the vegetation can also be critical in determining the stage and rate of transition states (Hobbs 1994). State and transition models have been suggested as a tool for rangeland management (Westoby et al. 1989; George et al. 1992), as an alternative to linear succession, to allow for different vegetation community composition (states), depending on the transition pattern. Non-equilibrium vegetation dynamics may be described by discrete states and definable transitions between states. Transitions are usually instigated by natural events and may occur quickly or over an extended period and change to a persistent state depending on events during the transition (George et al. 1992). This model may provide an appropriate framework for management of degraded riparian zones and assist in interpreting the response of riparian vegetation to disturbance in terms of possible states and transitions of riparian vegetation. The state and transition model generally describes non-equilibrium vegetation dynamics in communities but may be usefully applied to populations of particular species as in this case. With chronic to frequent flooding disturbances riparian forests are young, as vegetation patch development or individual populations are continually reset and remain in stand initiation or immature stages of development (Wissmar & Swanson 1990). In environments with low magnitude, seasonally predictable floods the vegetation or populations are likely to be more stable and more developed.

This chapter compares the size class distribution and spatial arrangement of the selected study species that occur in the riparian zone on the two river systems. This will give an indication of
the health of these populations in terms of the ability of the population to regenerate as the maintenance of a population is an expression of the population’s resilience. For example, if small size classes are absent and there is a large number of trees in large size classes this may indicate that there is a lack of recruitment and the population is senescent (Hutchings 1997). In contrast, if there is a majority of trees in smaller size classes and few large individuals it may suggest a building population after a disturbance (Szaro 1990). In addition, the presence of groups of even-aged individuals (cohorts) or a more even distribution of sizes will provide some evidence of whether recruitment patterns are episodic or continual (Harper 1977). The position these species occupy in the riparian zone will be considered as well as those areas which are favoured for seedling recruitment and establishment of mature trees. Vegetation dynamics will also be discussed in terms of a state and transition model for populations of these riparian species, in relation to the fluvial regime and the implications for riparian vegetation management. The information presented in this chapter on the development of the mature plant into the population provides the next step in understanding regeneration processes of these species in the riparian zone. This follows on from the previous Chapters which looked at the replacement stages of plants including production of seed, dispersal, germination and the establishment of seedlings. These elements incorporate the five factors which are considered important in the differentiation of the regeneration niche (Grubb 1977).

Methods

This Chapter uses the two most common overstorey species from each river system as described in the previous chapter. *Eucalyptus camaldulensis* occurs as a dominant riverine species on the Ord River. *E. rudis* is the only large tree that occurs in the riparian zone of south-west rivers including the Blackwood River. *Melaleuca leucadendra* on the Ord River and *M. rhaphiophylla* on the Blackwood River are also similar species and common overstorey or midstorey species with a high tolerance of waterlogged conditions.
At the five sites on the Ord River and Sites B1 and B2 on the Blackwood River (see Figure 3.1 & 2), three 10 m x 100-200 m belt transects were set up perpendicular to the river. The length of each transect varied with the width of the riparian zone at each site. Each transect was divided into 10 metre sections to give a series of contiguous 10 m x 10 m plots. Within each plot the diameter at breast height (1.5 m) (DBH) of all trees of the study species in the transect were measured. In addition, the distance (m) of each tree from the river dry season base flow level was measured. Relative elevation (m) above dry season river base flow level was taken along each transect at 5 m intervals using an automatic level and staff. Elevations were given as height above the lowest point along the transect, which was invariably the low water mark in the river channel. For all sites combined for each species on each river elevation was correlated with DBH to test if there was a pattern between tree size and position in the riparian landscape. Diameters of individuals of each species at each site were arranged in ascending order to visually identify cohorts of trees which would indicate past recruitment events. From this data trees were also arranged into size classes and the frequency of each size class was plotted along the transects along with elevation for each site on both rivers.

Historical flow records (1958-1995) of monthly river discharge (m³ s⁻¹) for the Blackwood River were obtained from the Water and Rivers Commission gauging station at Darradup, located near Site B1a. This station covers approximately the upper two thirds of the Blackwood River catchment and includes the two study sites on the Blackwood River. Historical flow records (1971-1993) of monthly river discharge (m³ s⁻¹) for the Ord river sites were obtained from Water and Rivers Commission gauging stations at Old Ord River Station for Site O5 and Mistake Creek station on the Negri River for Site O4. No records were available for Site O3 on the Behm River or for Site O2 which is on Lake Kununurra since the river was dammed in 1963. Average monthly flow levels for the Ord River below the diversion dam (Site O1) were obtained from the modelling of flow calculated by the Water and Rivers Commission (J. Ruprecht, unpublished data).
Aerial photographs (1:20 000) were used to map the approximate distribution of the study species in the riparian zone at each site on the Ord and Blackwood Rivers. Data from the transects was used to obtain tree density estimates and species distribution. Median tree diameter and density per hectare was derived from data measured in the 100 m² plots.

An indication of the relationship between stem diameter and tree age was developed by taking a transverse section of a sample of stems up to 10 cm in diameter, polishing the cut surface and counting the growth rings which were assumed to be laid down annually. For stems greater than 10 cm in diameter an increment borer (Sunnto, Finland) was used to obtain a stem core which was mounted and polished and examined under a stereo microscope to reveal the annual growth rings. A sample of stems of different sizes and in different locations was taken at each site for *E. rudis* and *M. rhaphiophylla* on the Blackwood River and *E. camaldulensis* and *M. leucadendra* on the Ord River. *M. rhaphiophylla* growth rings were not obvious so this species was not considered for age estimates as the relationship between size and tree age could not be reliably estimated. Estimates of annual growth ring count were correlated with stem diameter to test the relationship between stem diameter and age so that stem diameter could be used as a surrogate of age. This method provides only a relative indication of the age of plants and is not a dendrochronological study. This is because of the inherent problems of distinguishing annual growth rings in species from variable climates or where there are not distinct seasonal climatic patterns (Ogden 1978). Riparian species especially may be insensitive to seasonal drought, or flooding may affect growth, and rings may not necessarily be laid down annually (Schweingruber 1992). In a study of tropical eucalypts annual rings could be distinguished from each other by groups of even growth zones (Mucha 1979).
Results

Tree population structure

A summary of the total number of trees of *Eucalyptus rudis* and *Melaleuca rhaphiophylla* in the different size classes (DBH) for the Blackwood River sites is given in Figure 9.1. *E. rudis* was found in greater abundance for all sites and in all size classes, showing it to be the dominant tree at these sites. As highlighted in Chapter 6, the effects of livestock grazing can be seen in the lack of trees of smaller sizes at the sites where stock have free access to the riparian zone (Sites B1b & B2b). This is particularly evident for *E. rudis*, with no stems less than 10 cm diameter being recorded for these sites and with a large proportion of older mature trees indicating an over-mature population. On the ungrazed sites there is a large proportion of stems in the smaller size classes indicating that recruitment of these species is taking place. The spread of size classes, with the greatest proportion of smaller sizes and fewer large older trees, indicates a dynamic population. Where individual stems of each species at each site were arranged by increasing diameter no obvious cohorts of similar sized trees were recognisable (Figures 9.2 & 9.3). There may be some evidence of size cohorts, particularly for *E. rudis* at Sites B1a & B1b but there are many stems which fit between the groups. This may be due to continual recruitment of individuals into the population or may indicate the presence of suppressed or exceptional individuals.

Summary of size classes of *Eucalyptus camaldulensis* and *Melaleuca leucadendra* for all five sites on the Ord River showed the greatest number of stems in the smaller size classes and therefore younger trees (Figure 9.4).
Figure 9.1: Size class distribution of *Eucalyptus rudis* and *Melaleuca rhaphiophylla* at Sites B1 & B2 on the Blackwood River.
Figure 9.2: Diameter at breast height (cm) of individual trees measured along the transects at Site B1 on the Blackwood River.
Figure 9.3: Diameter at breast height (cm) of individual trees measured along the transects at Site B2 on the Blackwood River.
Figure 9.4: Size class distribution of *Eucalyptus camaldulensis* and *Melaleuca leucadendra* at Sites O1 to O5 on the Ord River.
At all sites, large numbers of seedlings and juvenile trees were recorded with few older, large diameter trees. At all sites except Site 05 *M. leucadendra* was more abundant than *E. camaldulensis*, indicating that it is the dominant tree species at these sites although *E. camaldulensis* grows to a larger size (most abundant in >50 cm size classes) and can be locally dominant. When individual trees were sorted by diameter, size (and therefore age) cohorts could be discerned for *E. camaldulensis* at all sites and for *M. leucadendra* at all sites except 01 (Figures 9.5, 9.6 & 9.7). At Site 01 stem diameters of *M. leucadendra* were continuous, with no obvious gap in size between groups of stems that would indicate an age difference. Distinguishable cohorts of size classes were particularly obvious for *E. camaldulensis* at Site 04 where diameters were in four size classes: <2 cm, which were all approximately 1 year old seedlings of around 30 cm in height; 2.1 to 4.8 cm diameter; 12.8 to 14.8 cm; and large trees >50 cm which were probably of several ages and ranged in diameter from 51.8 to 85 cm.

**Size class distribution**

A profile diagram on the Blackwood River at Sites B1a & B2a of *E. rudis* shows seedlings to be most abundant at the lower elevation near the river edge but large diameter trees are also abundant at these lower elevations. Size classes were generally evenly spread along the profile (Figures 9.8 & 9.9). *M. rhaphiophylla* tends to be confined to areas close to the water which are regularly inundated. In this area there is a wide range of size classes. Similar patterns of establishment along the profile was evident for Sites B1b & B2b, except for the lack of the smaller size classes. Along the profile at Site B2a & b, trees have also become established away from the river edge in a slight depression. For both sites for both *E. rudis* and *M. rhaphiophylla* there was no significant relationship between size class and elevation (Figure 9.10a & b).

Distribution of trees along the river reach at the Blackwood River sites show a greater density of trees closer to the summer water levels, with trees becoming much more sparse further from the river (Figure 9.11). Both sites are on long straight river pools and at Site B1 there is a steep bank on the western side with a much narrower riparian zone.
Figure 9.5: Diameter at breast height (cm) of individual trees measured along the transects at a) Site O1 & b) Site O2 on the Ord River.
Figure 9.6: Diameter at breast height (cm) of individual trees measured along the transects at a) Site O3 & b) Site O4 on the Ord River.
Figure 9.7: Diameter at breast height (cm) of individual trees measured along the transects at Site O5 on the Ord River.
Figure 9.8: Size class frequency and distribution of the two main overstorey species (*E. rudis* and *M. rhaphiophylla*) along a transverse profile from the water's edge at a) Site B1a and b) Site B1b on the Blackwood River. Frequencies are from 3 combined 10m x 10m plots. Histograms show tree size classes (DBH(cm)) by species for each plot.
Figure 9.9: Size class frequency and distribution of the two main overstorey species (*E. rudis* and *M. rhaphiophylla*) along a transverse profile from the water's edge at Site B2 a&b on the Blackwood River. Frequencies are from 3 combined 10m x 10m plots. Histograms show tree size classes (DBH(cm)) by species for each plot.
Figure 9.10: Relationship between tree size (diameter at breast height) and elevation from the river for the 4 selected riparian species on the Ord River (a & b) and the Blackwood River (c & d).
Figure 9.11: Plan view of the riparian zone at Sites B1 & B2 on the Blackwood River showing median tree diameter size class (cm) and approximate densities per hectare( /ha) for E. rudis (E.r) and M. rhaphiophylla (M.r).
On the eastern side the gradient is more gradual, allowing floodwater to flow out into this area where trees have established. At Site B1b and Sites B2a&b a second line of trees has established away from the river in a slight depression.

The profile diagrams for sites on the Ord River show the abundance of new (<1 year old) seedlings at lower elevations on the river flats and an abundance of smaller size classes throughout the profile (Figures 9.12, 9.13, 9.14 & 9.15). Frequency of larger size classes is greatest at the higher elevations and greater distance from the river, especially for *E. camaldulensis*. All *M. leucadendra* size classes tend to be at the lower elevations closer to the rivers edge. For all sites combined there was a significant correlation between diameter at breast height and elevation for both *E. camaldulensis* and *M. leucadendra* (Figure 9.10 c&d). At Site O2 on the shores of Lake Kununurra, where water levels do not fluctuate more than a metre each year, there is a large number of seedlings and smaller size classes at the water’s edge. There is also a large number of larger trees of *M. leucadendra* at lower elevations that is now permanently inundated (Figure 9.13). At sites O3, O4 & O5 there are large numbers of seedlings on sandy moist sediments on river flats where water levels are receding. On the steep banks (e.g. west bank, Site O5) larger trees occur closer to the water and there are no seedlings as there is no suitable habitat except in a slight depression upslope where there are some smaller size class stems (Figures 9.14, & 9.15). The river reach where Site O1 on the Ord River is located is on a river bend (Figure 9.16a). This shows the occurrence of new seedlings on sandbars on the insides of the bend (depositional) and the steep slope where only larger trees occur on the outsides of the bend (erosional). Establishment of younger trees has also occurred on the edge of the depositional flat where sediments have been deposited when high flows have flooded out across this area. At Site O2 the riparian zone is confined to a narrow strip of new recruitment where lake levels fluctuate and there is virtually no flow at this site (Figure 9.16b). Below this area mature *M. leucadendra* trees are permanently flooded, with many trees (~60%) having fallen over. Upslope, mature *E. camaldulensis* are now in a terrestrial environment.
Figure 9.12: Size class frequency and distribution of the two main overstorey species (E. camaldulensis and M. leucadendra) along a transverse profile at Site 01 on the Ord River. Frequencies are from 3 combined 10m x 10m plots. Histograms show tree size classes (DBH(cm)) by species for each plot.
Figure 9.13: Size class frequency and distribution of the two main overstorey species (*E. camaldulensis* and *M. leucadendra*) along a transverse profile at Site O2 on the Ord River. Frequencies are from 3 combined 10m x 10m plots. Histograms show tree size classes (DBH(cm)) by species for each plot.
Figure 9.14: Size class frequency and distribution of the two main overstorey species (E. camaldulensis and M. leucadendra) along a transverse profile at a) Site O3 & b) Site O4 on the Ord River. Frequencies are from 3 combined 10m x 10m plots. Histograms show tree size classes (DBH(cm)) by species for each plot.
Figure 9.15: Size class frequency and distribution of the main overstorey species (*E. camaldulensis* and *M. leucadendra* & *E. gymnotales*) along a transverse profile at Site O5 on the Ord River. Frequencies are from 3 combined 10m x 10m plots. Histograms show tree size classes (DBH(cm)) by species for each plot.
Figure 9.16: Plan view of the riparian zone at Sites O1 & O2 on the Ord River showing the median tree diameter size class (cm) and the approximate densities per hectare (/ha) for *E. camaldulensis* (E.c.) and *Melaleuca leucadendra* (M.l.).
Figure 9.17: Plan view of the riparian zone at Sites O3 & O4 on the Ord River showing median tree diameter size classes (cm) and approximate densities per hectare(/ha) for *E. camaldulensis* (E.c.) and *Melaleuca leucadendra* (M.l.).
Site O5

E. camaldulensis (E.c.)
- 20-30; 20/ha
- 2-10; 20/ha

Melaleuca leucadendra (M.l.)
- 2-10; 100/ha
- <2; 1000/ha

Figure 9.18: Plan view of the riparian zone at Site O5 on the Ord River showing median tree diameter size classes (cm) and approximate densities per hectare(/ha) for *E. camaldulensis* (E.c.) and *Melaleuca leucadendra* (M.l.).
At Sites 03 and 04 river water levels dry up to a small stream and eventually to isolated pools around which most seedlings are located (Figure 9.17a&b). Juvenile trees in smaller size classes occur in bands on the flood-out depositional area on the inside of the bend, with mature trees occurring on the steeper banks of the erosional area of the outside of the river bend. A similar pattern is seen at Site 05 (Figure 9.18), with large trees on the steeper western bank and juvenile trees occurring on the gradual slope of the flood-out area, and with occasional larger *E. camaldulensis* and *E. gymnotales* at the top of the slope.

**Long term hydrograph**

Over a 37 year period maximum discharge on the Blackwood River consistently occurred in the winter in the wet part of the year between July and August. Peak flows were regular events each year occurring with the regular winter rains. The one exception was an extremely large flood event in January 1982 caused by a cyclonic feature drifting down from the tropics into the southwest land division (Figure 9.19). Maximum discharge levels are much smaller and less variable than those seen on the Ord River, with a mean maximum discharge of 161 $\text{m}^3\text{s}^{-1} \pm 24.5$. Even the exceptional event in January 1982 (with a peak flow of 1187 $\text{m}^3\text{s}^{-1}$) was much smaller than average maximum discharge on the Ord River. Average monthly discharge shows a peak in July with river levels usually receding by September.

Over a 19 year period on the Ord River large river flows have been confined to the wet season with 100% of discharges greater than 500 $\text{m}^3\text{s}^{-1}$ occurring between November and March. Recorded flows have only occurred 3 times outside this wet season period in June 1978, May 1979 and October 1988 (Figure 9.20a). Magnitude of peak flows is highly variable, with maximum discharge of $>15000$ $\text{m}^3\text{s}^{-1}$ occurring 4 times over the 19 year period and 4 years having a discharge $<1000$ $\text{m}^3\text{s}^{-1}$, with only 375 $\text{m}^3\text{s}^{-1}$ in 1992. Average maximum discharge ($\pm$ SE) for the period from November to March is 5565 $\text{m}^3\text{s}^{-1} \pm 1475$, with January having the highest mean discharge and March the lowest. For the lower Ord River below the diversion dam (near Site O1) the river flow regime prior to river regulation has been modelled from rainfall and runoff data (J. Ruprecht, unpublished data) and compared with the current flow regime (Figure 9.21). This
shows that variation in monthly flows has been much reduced, with a large reduction in wet season flows and greatly increased dry season base flows where, prior to regulation, the river would dry up to a series of pools.

Tree age and hydrology

Growth ring counts from stem sections and cores showed a significant relationship between number of rings and stem diameter for *E. rudis* on the Blackwood River and *E. camaldulensis* and *M. leucadendra* on the Ord River (Figure 9.22 a,b&c). Using this relationship, an estimate of the age of the trees can be made from stem diameter alone. At Site B1b on the Blackwood River a stand of trees growing in a slight depression 50 m from the water with a mean DBH of 14.3 cm in 1996 (Figure 8.8c) would be approximately 16 years old. This fairly well coincides with the very large, unseasonal flow event in January 1982 (Figure 8.19), 14 years earlier. The establishment of these trees at this time has been confirmed by the local landowner. On the Ord River at Site O4 the establishment of cohorts of *E. camaldulensis* at 8 and 20 years ago (Figure 9.6c) coincide with a year of high flow followed by several years of low flow (Figure 9.20b). This would create the conditions suitable for seedling establishment and allow several years without severe flooding in which to develop.

Discussion

Population structure of the Blackwood River species indicates that stable populations with a range of sizes occur in ungrazed areas. In areas that are grazed by livestock there is a lack of smaller size classes, indicating stagnant or senescent populations. On the Blackwood River sites trees develop to maturity throughout the river profile, from the river channel to the extent of the riparian zone and there is fairly even frequency distribution of size classes, suggesting non-episodic recruitment.
Figure 9.19: Maximum monthly river discharge over a 37 year period for the upper two thirds of the Blackwood River catchment from a recording station near Site B1a.
Figure 9.20: Maximum monthly river discharge over a twenty year period at (a) Site O5, for the upper half of the Ord river catchment and at (b) Site O4, on the Negri River (see map, Figure 3.1). Note different scale on the y axis.
Figure 9.21: Monthly river flow (GL) for the lower Ord River at Carlton Crossing below the diversion dam. Natural flows are for the river prior to dam construction in 1963 and is calculated from modelling. Regulated flows are the present flows experienced with Stage I of the Ord River irrigation district.
Figure 9.22: Relationship between tree diameter at breast height (1.5m) and tree age estimated from counting annual growth rings for (a) *Eucalyptus rudis* on the Blackwood River (b) *Melaleuca leucadendra* on the Ord River and (c) *Eucalyptus camaldulensis* on the Ord River.
On the Ord River tree populations are more dynamic, with large numbers of individuals in the <2 cm diameter size class and an uneven distribution of size classes. There are obvious cohorts of individuals which implies that environmental disturbances are affecting recruitment which is likely to be episodic (Bradley & Smith 1986). These differences in population structures and spatial distribution in the riparian zone and the very different hydrologic regimes suggest a need for different vegetation dynamics models for the two rivers. On the Blackwood River recruitment appears to generally occur continually, with biotic processes such as competition being important. The population structure of these species can be viewed as consisting of long stable states with a short transition between states. In contrast, on the Ord River, recruitment is most likely episodic and is driven by abiotic processes such as high river flows, with the population structure described in terms of long periods of transition and short relatively stable states.

**Population structure**

On the Blackwood River *E. rudis* is the major overstorey species (Marchant *et al.* 1987) and the much greater numbers seen on the transects measured here confirm this. At the sites that are subject to stock grazing the effects on tree population structure is obvious, with no stems under 10 cm DBH recorded. This suggests that there has been no recruitment into the population for around 15 years, and with the greatest proportion of stems in the large size classes (mature trees), it would also indicate that the population is in decline (Johnson 1994). Although seed germination is taking place at these sites (see Chapter 8) seedlings are not surviving, mainly due to grazing by livestock (see Chapter 6). The understorey at these sites is also highly modified (see Chapter 4), with extensive invasion of exotic grasses which may also contribute to poor survival of seedlings through competition (De Steven 1991). Free from livestock grazing, recruitment is taking place, with large numbers of stems in the smaller size classes indicating a more stable population (Johnson 1994). For *E. rudis* there are no obvious cohorts of similar sized trees which would indicate that episodic events such as flooding are not an important mechanism for recruitment and that continuous recruitment takes place for this species. Anecdotal evidence (corroborated by tree ring counts at Site 1B) does suggest however that after large unusual
disturbance events, such as the exceptional flood in January 1982, large recruitment events can also occur. Results here also indicate that *E. rudis* can establish and mature anywhere throughout the profile, including at low elevations near the water's edge, and that establishing trees are not unduly affected by floodwaters.

*M. rhaphiophylla* at the sites surveyed on the Blackwood River is usually a mid-storey species to *E. rudis* but can become locally dominant (Marchant *et al.* 1987). It is mainly restricted to the wetter areas of the riparian zone and usually occurs on the littoral fringe of the river between summer and winter water levels. It does occur further from the river in moisture gaining depressions and this is probably related to waterlogging tolerance and/or lack of drought tolerance. Population structure of *M. rhaphiophylla* on the Blackwood River shows similar patterns to *E. rudis* with an effect on recruitment with livestock grazing but a stable population at ungrazed sites. This species is restricted to closer to the river and does not grow as large as *E. rudis* but within this zone there is an even spread of size classes. The better adaptation to inundation at the seedling stage in *M. rhaphiophylla* was demonstrated in the flooding experiment in the previous chapter and may partly explain their distribution closer to the river channel than *E. rudis*. Greater tolerance, at the seedling stage, to inundation has been used to explain the differences in distribution in the riparian zone of two rainforest species in Victoria (Melick 1990).

For *E. camaldulensis* on the Ord River the greater proportion in the smaller size classes and few larger mature trees suggest a building population (Harper 1977). The cohorts of trees identified indicate that recruitment is most likely episodic with some background recruitment. However stems of intermediate size between cohorts may also represent suppressed or exceptional individuals. There was also clearly a relationship between elevation and tree size, with no large mature trees at low elevations. This is also related to river geomorphology, with larger trees occurring at higher elevations near the river on eroding inside river bends, whereas on depositional outside bends and flood-out areas at low elevations only smaller trees occur. Therefore, while germination is more common at the lower elevations where moist open
sediments provide ideal sites for seedlings, growth to maturity is more likely at higher elevations which are less likely to be flooded (Jones et al. 1994). Lack of stability of soils at lower elevations due to the movement of floodwaters is likely to be a factor in the poor survival to maturity. This lack of soil stability preventing the development of mature populations has been reported for shrubs and trees on the floodplain in a arid zone catchment (Friedel et al. 1993).

The most abundant species at the Ord River sites was *M. leucadendra*. Population structure was similar to *E. camaldulensis* with an abundance of young stems and few large mature trees again indicating a building population. Like *M. rhaphiophylla* on the Blackwood River it is confined to the wetter areas, usually close to the river, and is therefore better adapted to inundated conditions, such as through the formation of adventitious roots under anoxic conditions during inundation (Boland et al. 1989). As for the Blackwood River species, the better adaptation of *M. leucadendra* to inundation at the seedling stage was demonstrated in Chapter 8.

**Tree age**

Estimating tree age by counting tree rings is a common technique used in determining tree population structure (Bradley & Smith 1986; Duncan 1993; Johnson 1994) or past environmental disturbances (Baker 1990; Villalba & Veblen 1997). However, there are some limitations to this approach due to technical difficulties and confounding effects (Villalba & Veblen 1997). For example, there can be large variations in the size within a cohort due to habitat heterogeneity and competition between individuals (Hutchings 1997). Also, most of this work has been done in the northern hemisphere in climates with strong seasonality which make the detection of annual rings much easier (Ogden 1978). More work is needed to develop a reliable dendrochronological technique for Australian plants but this is beyond the scope of the present study. Therefore aging of trees by ring counts in the present study must be interpreted with some caution. It does indicate however that establishment of trees is related to past hydrological events. For the Ord River this may involve the germination of seed at higher elevations after a large flow event in the wet season which would enhance seed transport through hydrochory and recharge soil moisture (Roberts 1993). Lower flows in subsequent years would prevent the
seedlings from being scoured out or inundated at least until they had become established. Unseasonal dry season rainfall in at least the first year after seed germination would also enhance survival. This link between tree recruitment and particular flow events has been established in many studies of riparian trees (e.g. Bradley & Smith 1986; Baker 1988; Johnson 1994).

Tree vegetation dynamics

Fluvial processes on the Ord River are dominated by fairly frequent, large, high energy floods that are capable of scouring out the soil, destroying the existing riparian vegetation community and preventing the establishment of stable mature stands. This is evidenced by the existence of large mature trees on these river reaches only at high elevations, in protected river bends or far from the river where only extreme floods can reach. In the years between large flood events large stands of seedlings and saplings develop but these generally do not reach maturity before they are destroyed in the next large flood. High frequency flooding can keep the vegetation in an early stage of succession (Naiman et al. 1998). Failure to reach later successional stages due to high frequency flood disturbance has been documented for New Zealand Podocarp forest (Duncan 1993). In this way, single catastrophic events change the ecosystem to an extent which is inconsistent with the theory of climax communities (George et al. 1992). These high magnitude wet season floods are, however, highly episodic and in the intervening years smaller floods allow the development of the existing trees and the recruitment of younger age classes. This regime of intermittent high frequency large disturbances prevents the establishment of stable states and in terms of the state and transition model the ecosystem is characterised by long periods of transition between short-lived stable states. This riparian ecosystem is thus driven by physical (allogenic) processes rather than by vegetation successional (autogenic) processes (Baker & Walford 1995). In contrast, lower energy seasonal flooding on the Blackwood River allows mature stands of trees to develop throughout the river profile. Recruitment is continual, although species can also respond to large flood events. This disturbance regime results in long periods of stable states with short periods of transition. Therefore the vegetation is subjected to longer periods of autogenic processes and, because of lower frequency flooding disturbance, shorter
periods of allogenic processes. Where flooding disturbances are chronic to frequent, riparian forests are young, as vegetation patch development is continually reset and remains in stand initiation and exclusion successional stages (Wissmar & Swanson 1990). In environments with low magnitude, seasonally predictable floods the vegetation is likely to be more stable and more developed. The fact that no cohorts of trees were discerned at Site O1 on the regulated section of the Ord River suggests a change in dynamics of these species to a regime of continual recruitment brought about by the reduction in flooding disturbance. Large dense stands of younger aged trees now occur in a narrow band close to the river. Without large flood disturbance thinning out these stands strong competition may prevent the development of larger size trees. At Site O2 on Lake Kununurra where river flows no longer occur and the riparian zone now acts like a lentic system and water levels are permanently much higher, there are two distinct populations of trees. There are relics of larger older trees of the former riparian system and a cohort of young saplings developing on the newly created narrow littoral zone where the lake levels fluctuate. This has created a new niche of exposed moist bare sediments suitable for seed germination. Given that this area is no longer subjected to disturbance from large floods, it would be expected that population structure would become more stable at this site as saplings develop to maturity and there is less opportunity for recruitment.

The hydrological regimes for the Ord and Blackwood rivers are vastly different despite similar rainfall and catchment size. This is mainly due to the different geology of the catchments (Department of Mines 1972) and rainfall patterns. The Ord River catchment is subject to high intensity rainfall events mainly generated from sub-tropical monsoons. These are confined almost entirely to the wet season between October and March and contribute high levels of runoff into the river. For the Blackwood River, although it has a strong winter (June-August) rainfall maximum, events are less intense and runoff is not as high (see Chapter 3).

These results highlight the very different fluvial regimes that exist on these two rivers and their effect on the respective models of vegetation dynamics for the overstorey species. This is despite the species compared on the two rivers being functionally very similar. Management of
the riparian vegetation should therefore take into account the frequency of change in the vegetation and that the disturbed states and long periods of transition between states are part of the natural process. This would suggest that altering the natural flow regimes, such as through river regulation, will have significant effects on riparian vegetation dynamics. This is particularly so for the effects on long term recruitment in terms of reproductive phenology and seedling survival (Bren 1992; Johnson 1997). In the case of regulation on high disturbance rivers such as the Ord River, riparian vegetation dynamics may be significantly altered to long periods of stable states with much reduced transitions. This has important implications for the long term structure and functioning of these communities.

This Chapter has shown the differences in population structure and vegetation dynamics of the study species and the strong link with river hydrology, particularly for the Ord River where recruitment appears to be episodic and development of the population is continually reset by the destructiveness of large flows. Recruitment of species on the Blackwood River appears to be more subtle and not as closely linked to the river hydrology, but possibly influenced also by biotic factors. This can also be related to other elements of regeneration discussed in the preceding chapters, such as seed production and dispersal, the timing of seed release to river flows and the annual release of seed of the Ord River species.
An overall aim of this thesis has been to provide information on the processes involved in the regeneration and recruitment of riparian vegetation, using examples from two contrasting river systems. There is a general paucity of basic ecological studies on riparian vegetation in Australia (Dexter 1978; Bren & Gibbs 1986; Roberts & Ludwig 1991; Roberts 1993; Walker et al. 1994). This thesis is therefore broad in scope and provides a general picture of regeneration processes on the study rivers and establishes a starting point for more detailed work in this area. The two rivers chosen for study, despite being very different in terms of hydrology and climate, show similarities in vegetation processes which can be more generally applied. Species selected for more detailed study are functionally similar and therefore can be used to clarify ecological adaptations of each to their particular environments. Riparian landscapes are formed by the interaction of hydrologic, geomorphic and ecological processes (Malanson 1993) and consequently regeneration mechanisms are likely to be somewhat different for each river. The combination of specific knowledge of natural flow regimes and an understanding of vegetation dynamics is therefore required when planning for the effective management of riparian vegetation. The interaction of elements that have been found to influence the recruitment of riparian vegetation on the study rivers is summarised in Figure 10.1.

The thesis has been structured to look firstly at the community level of riparian vegetation on both rivers. From this, particular species (Eucalyptus rudis and Melaleuca rhaphiophylla on the Blackwood River and E. camaldulensis and M. leucadendra on the Ord River) have been selected for more detailed investigation of their population structure and ecology and of the influence of environmental factors (particularly hydrology) on their recruitment. In Chapter 4 a general description of the vegetation included patterns of species richness, diversity and spatial distribution of the plant communities in the riparian zone as well as key functional groups in
terms of life form and species origin. From this Chapter the importance of trees in the riparian zone became evident and their key functional role is well documented (Malanson 1993; Bunn 1993; Naiman et al. 1998), so that this life form became the obvious choice for more detailed investigation in later Chapters. It is also clear that livestock grazing has a major impact on riparian vegetation, particularly on the Blackwood River. Chapter 5 describes the relationship that exists between historical river flows for the Ord and Blackwood rivers and aspects of riparian vegetation ecology. It provides an example of how historical flow records can be used to develop a picture of the natural flow regime which can then be related to existing patterns of vegetation development and plant community patterns in the riparian zone. An assessment of the effects of livestock grazing on riparian vegetation was made and the initial response of the communities to the exclusion of livestock is examined in Chapter 6. This indicates that grazing has a major impact on the recruitment of tree species on the Blackwood River but this effect is not obvious on the Ord River. The reason for this difference is most likely the differences in the process of seedling recruitment on the two rivers but it may also be influenced by differences in stocking rates. These differences in the processes of seedling recruitment are explored in the next three chapters. From the examination of sources of seed in Chapter 7 it appears that the soil seedbank is only important for annual species and that, in particular, predation and poor survival of seed in the soil of the examined overstorey species reduces their likelihood of persisting in the soil seedbank. The fact that the reproductive phenology of the two target species on each river is timed to river flows and that seed is found in flood debris indicates that these are a more likely source of seed for recruitment. The question of whether this timing to river flows also applies to recruitment of seedlings is examined in Chapter 8. This includes determination of the optimum temperature requirements for germination of seed of these species, the site conditions likely to allow successful early establishment of seedlings and the level of tolerance over time to various degrees of flooding. Whether these findings can be related to the existing population structure and spatial distribution is explored in Chapter 9. The population structure and spatial distribution in the riparian zone of the target species suggests that different models of vegetation dynamics operate on the two rivers and these can be related to fluvial regime. From these results the general hypothesis stated in Chapter 1, that the fluvial regime
has a strong influence on the vegetation dynamics in the riparian zone has not been rejected. How the fluvial regime influences various aspects of the riparian vegetation is detailed in the following sections.

Figure 10.1: Interaction of the elements important in recruitment of riparian vegetation.

Riparian vegetation communities

Describing the riparian vegetation community and the range of different plant life forms that occur is an effective way of identifying the important functional groups and the range of regeneration strategies of vegetation of the riparian zone of these rivers. Chapter 4 highlights the dominance of trees in the riparian zone on both rivers. On the Blackwood River the understorey is dominated by annual herbs and grasses, particularly at sites that are subject to livestock grazing, while perennial grasses are the dominant feature of the understorey on the Ord River. Greatest diversity on the Ord River was in the number of overstorey species, with the
understorey tending to be dominated by only a few species. Species diversity on the Blackwood River was most influenced by the understorey species which, particularly on the ungrazed sites, was composed of a high diversity of shrubs and perennial herbs. The overstorey was composed of almost exclusively *Eucalyptus rudis*. For the study rivers there was a high proportion of disturbance tolerators (ruderals), such as annual and perennial grasses, and low numbers of stress tolerators which are commonly woody perennial species (Grime 1979). This would indicate that disturbance has had a strong influence on the composition of both vegetation communities, although stress is also an important contributing factor in the form of waterlogging and drought.

For the two rivers species richness tended to increase with distance from the river and therefore with lower frequency of flooding. In particular, a sharp decline in species richness is seen in plots near the water's edge in the littoral zone which is subject to the greatest flooding disturbance and greatest stress. This is generally the zone of helophytes or emergent macrophytes such as from the Cyperaceae family. Vegetation patterns, and therefore species richness and diversity, in the high disturbance riparian zone are strongly influenced by species colonising ability (White 1979). The high frequency disturbance regime and the harsh (high stress) environment precludes many species as plants need to be able to tolerate extreme conditions such as flooding in the wet season and prolonged periods of drought in the dry season. The intermediate disturbance hypothesis (Fox 1979; Huston 1979; Ward & Stanford 1983) states that greatest species richness occurs in areas where frequency of disturbance is high enough to create gaps for species establishment but not so high as to exclude species (such as through the scouring of the river banks). Clearly, the heterogeneous environment of the riparian zone allows many species to persist under these conditions and the impact along the gradient of disturbance and stress can be modified by small spatial scale variations (e.g. microtopography) (Pollock *et al.* 1998). Further work is required to measure species diversity differences between the riparian zone, the surrounding floodplain and the terrestrial environment. This would examine, for Western Australian rivers, whether the riparian zone is an area of high species richness and follows the generally accepted idea of the riparian zone being a transition zone of higher species richness as the river collects propagules of species throughout the watershed (Nilsson *et al.* 1994).
The fluvial regime and the influence on riparian vegetation

Characterising the river fluvial regime of the study rivers is an essential first step in determining the relationship with the riparian vegetation. Many aspects of the ecology of riparian vegetation are similar to those of vegetation in other environments such as wetlands, floodplains and even terrestrial environments. Flowing water and its effect on riparian vegetation is what makes this community type unique (Malanson 1993). This study has highlighted the importance of the fluvial regime in shaping vegetation community structure and floristics, as well as in determining the distribution and abundance of species. The fluvial regime impacts upon the dispersal of propagules, the reproductive phenology of particular species, germination of seed and the establishment of seedlings and plant community population dynamics. River flows shape the structure of the riparian habitat and contribute to the redistribution of soils and soil nutrients. Replenishment of soil water and groundwater across a gradient are also influenced by the duration and frequency of flows into the riparian zone.

Other ecological factors obviously also influence vegetation dynamics in the riparian zone. For example, climate (including seasonality and variation in rainfall and temperature) has a strong influence on the floristics of a region (Groves 1994). This is evident in the very different floras of the two rivers in this study and from the ordination of vegetation plots in Chapter 4, which clearly shows the influence of amount of rainfall on longitudinal changes in the vegetation community along each river. Fire, as a form of disturbance, can also affect vegetation community development (Gill 1981), and specifically in the riparian zone (Douglas 1999; Busch 1995). Another disturbance which impacts on many Australian plant communities is livestock grazing (Wilson 1990), which is implicated in the degradation of the riparian zone on many rivers (CEPA 1992). These latter factors operating separately, or more likely, through interaction, create patchiness (mosaics) in the vegetation of the riparian zone across gradients (zonation), which is driven by the fluvial regime. Identifying the flow regime, in terms of variability, predictability, constancy and contingency (Colwell 1974), from the historical hydrological...
records, can therefore be useful in describing the vegetation dynamics of a particular river (Wissmar & Swanson 1990; Naiman et al. 1998). An example of this was provided in Chapter 5.

Livestock grazing and fire

Grazing by domestic livestock is a human-induced disturbance that clearly has the potential to impact on recruitment in the riparian zone. Responses of the riparian vegetation to livestock grazing were very different for the two rivers in this study. Large sections of the riparian zone of the Blackwood River occur within a matrix of agricultural land cleared for improved pasture and cereal cropping. Native understorey species have been effectively cleared by high intensity livestock grazing and replaced with introduced pasture species and pasture weeds. Increased fire frequency can also contribute to this process (Leigh et al. 1991; Hobbs & Huenneke 1992). Invasion of exotic species has also probably been aided by the transport of propagules in floodwaters. The combination of removal of native species, increased nutrient levels (Cale & Hobbs 1991; Scougall et al. 1993) and a high disturbance riparian environment (flooding) has provided ideal conditions for ruderals which are generally exotic annual species (Grime 1979). Grazing has also prevented the recruitment of overstorey species which constitute the 'skeleton' of the riparian vegetation, but because of the long life span of these species the effects will take a long time to became apparent (Pettit et al. 1998). Livestock grazing effects on the Ord River, in contrast, are not as easily detected. Low stocking rates, the fact that the riparian zone occurs in a matrix of predominantly natural vegetation that has not been cleared and the grassy woodland nature of the vegetation contribute to the apparent reduced impact. All areas of the Ord River have been exposed to cattle grazing, so it was not possible to compare current vegetation community composition with riparian sites that have never been grazed. In fact, only a few very isolated rivers in the Kimberley region have not been subjected to some degree of livestock grazing (Water & Rivers Commission 1997). Size class analysis of overstorey species has suggested that some recruitment of these species is taking place. Long term monitoring of exclosure plots will give some indication as to whether species richness, vegetation cover and number of shrubs is lower due to livestock grazing. Further work is required to clearly establish the vegetation
composition prior to grazing as is an expansion of the grazing exclusion trials with a long term monitoring programme.

The response of a plant community to grazing varies with community type and evolutionary history of grazing (Milchunas & Lauenroth 1993). In environments that have had a long history of grazing, herbivore grazing is considered essential for maintaining species diversity and in many communities species diversity has decreased when grazing has ceased (Carr & Turner 1959; McNaughton 1985; Noy-Meir et al. 1989; Smith & Rushton 1994). Such communities are generally dominated by grasses and forbs, whereas in vegetation communities dominated by woody perennial species, species diversity decreases with livestock grazing (Williams & Ashton 1987). Severe over-grazing will clearly have a substantial impact on riparian vegetation, with widespread loss of plant cover and subsequent erosion problems such as have occurred in areas of the Ord River catchment (Fitzgerald 1967; de Salis 1993). The nature of the different drivers of vegetation dynamics operating in the two rivers may also contribute to this difference in response to livestock grazing, with allogenic or physical processes (such as the flooding regime) being important on the Ord River and autogenic or vegetation successional processes being dominant on the Blackwood River.

Exclosure experiments on the Blackwood River show little improvement after 3 years, with only minor increases in the occurrence and cover of native species. Exclosure experiments in riparian zones in the United States have shown an increase in cover and number of species of woody perennial plants with relief from grazing (Shultz & Leininger 1990) and an increase in competition with rapid vegetative growth of strong competitors (Kauffman et al. 1983). The exclosure plots in the present study are highly degraded and perhaps do not contain sufficient storage of vegetative and sexual reproductive material of native species, such as underground storage organs or a soil seedbank, to support natural regeneration. Such sites may require intervention in the form of weed removal and reseeding or replanting to re-establish native species. Establishment in these species may be restricted by the current abundance of exotic grasses and annual herbs which have increased in cover in the absence of grazing. The effects of
competition from exotic weeds on the germination and establishment of riparian overstorey species is an area that requires further study. For exclosure experiments, a much longer period of observation is required to fully understand the vegetation dynamics and successional processes, particularly for long-lived perennial species such as the overstorey species. Pioneer species such as annuals may eventually be replaced by another suite of species depending on future disturbance and management (Onans & Parsons 1980; Wahren et al. 1994). For example, some episodic disturbances such as a large flood and/or particular climatic conditions may be required for a successful recruitment event to take place.

As for other vegetation communities, frequent fire can have a significant influence on riparian vegetation communities. In south-west Australian rivers such as the Blackwood River, fire, as a disturbance, together with livestock grazing, can lead to greater degradation of the vegetation (Leigh et al. 1991). This is chiefly through the increased invasion of exotic ruderal species which are better adapted to this combined disturbance regime. Burning may enhance the germination of seed of native overstorey species and improve short term survival by creating areas of bare ground suitable for seed germination (Wellington & Noble 1985b) but once the biomass of annual species recover these may quickly reduce survival of seedlings. In tropical savanna in northern Australia season of fire appears very important in shaping community structure in the riparian zone (Douglas 1999). Annual late dry season burning results in significantly less diverse and abundant riparian communities and recovery is slower than after burning early in the dry season. Frequent (annual) fires in the riparian zone may also lead to the loss of rainforest type species such as lianas.

Sources of seed for regeneration

Strategies for regeneration of riparian vegetation include aspects of the reproductive phenology, dispersal of propagules, and the storage of mature seed ready for germination when conditions are suitable. This study indicates that the soil seedbank may be important for annual species of herbs and grasses but of only minor significance for perennial species. In lentic wetlands, the seedbank can be important in determining the vegetation community (Schneider & Sharitz 1986;
Thompson 1987; Brock et al. 1994) and determination of the composition of the soil seedbank is used to predict the outcome of succession after a disturbance (van der Valk 1981). Little work has been done on the role of the soil seedbank in lotic systems, however the highly disturbed nature of the riparian zone and the unstable nature of soil sediments indicate that the role would be minimal (Malanson 1993). A comprehensive survey of the soil seedbank in the riparian zone, including looking at the seedbank in different habitats (such as pool and riffle areas and erosion and depositional bends and floodplain wetlands), would provide a more complete picture of the role of the seedbank in the riparian zone. This could also include sampling at different times of the year to discern the long term from the transient seedbank. Storage of seed on the plant (serotiny) can provide another effective seedbank (Lamont et al. 1991) and in Australia many species in the Proteaceae and Myrtaceae families use this mechanism (Enright & Lamont 1989; Beardsell et al. 1993). *Eucalyptus* spp in general show a varying degree of serotiny. However, eucalypt seed is rarely held in the canopy for more than 3 or 4 years (House 1997). Of the overstorey species examined in this study only *Melaleuca rhaphiophylla* appears to use this device.

Reproductive phenology of the four species studied reflects their adaptation to their environment and in particular to the fluvial regime. For *E. camaldulensis*, *M. leucadendra* and *E. rudis* the period of greatest seedfall is timed to coincide with receding floodwaters, when moist sediments favourable for seed germination and survival are exposed. This adaptation has been reported for riparian species of *Populus* and *Salix* in the U.S. (Bradley & Smith 1986; Johnson 1994). The Ord River species release the majority of their seed over a short period at the end of the wet season, this being the only opportunity for recruitment for the year. Other northern Australian *Eucalyptus* spp have been reported to display a similar reproductive phenology (Bowman et al. 1991; Fensham 1992; Setterfield & Williams 1996). For many temperate *Eucalyptus* spp, including *E. rudis* on the Blackwood River, seeds are retained in the capsules with a continuous low level of seed release occurring which is accelerated by dry conditions (Cunningham 1957; Wellington & Noble 1985a; Davies & Myerscough 1991). For *E. rudis*, with a ready supply of seed available in the canopy, there is also potential for explosive recruitment
after a major flood event coinciding with other favourable environmental conditions. Many species show a high degree of variability in reproductive phenology and trees need to be monitored over a much longer time to confirm the results reported here.

Although wind dispersal was found to be the most common primary means of propagule dispersal, enhanced or secondary dispersal by floating downstream or laterally within the riparian zone or with flood debris is clearly a consequential recruitment mechanism (Barrat-Segretain 1996). In rivers in Sweden, floodwaters carrying seed greatly extended the dispersal range of wind-dispersed species, depending on the ability of the seed to float and the length of time they could float (Skoglund 1990). Floating time can also be important for dispersal distance, with larger, heavier seeds establishing closer to the point of release (Nilsson et al. 1993). Lateral transport of propagules on floodwaters can also be important in depositing seed at higher elevations thus affording some protection for developing seedlings from subsequent flooding. The presence of seed of many common riparian species in debris samples in this study indicates the importance of secondary dispersal of seed by water. This has been reported for other riparian habitats (Schneider & Sharitz 1988; Johansson et al. 1996). Seed and fruit of many terrestrial species were also found in debris samples, indicating that overland flow tends to concentrate species in the riparian zone (Nilsson et al. 1994).

**Mechanisms of seedling recruitment**

Temperature and moisture play a critical role in providing the stimulus for seed germination. This is largely determined by climatic conditions, with many plants having evolved to germinate when conditions are most favourable for survival (Mott & Groves 1981). Optimum temperature for germination was similar for Ord River and Blackwood River species despite very different climatic and hydrological conditions. This may be related to the common features of riparian environments where moisture is readily available (Bell & Williams 1997). Position of seedlings within the riparian landscape is also strongly related to environmental conditions that would provide adequate moisture but protect seedlings from flooding. Microtopographical rises, or areas of slightly higher elevation, are important for seedling establishment in creating
safe sites to prevent prolonged submersion and waterlogging (Bren & Gibbs 1986; Skoglund & Verwijst 1989; Titus 1990). Ideally, these rises should also be slightly concave to allow collection of vital moisture from dry season rainfall events. Of the study species, the *Melaleuca* spp. showed a greater degree of flooding tolerance than the *Eucalyptus* spp., which reflects the position in the riparian landscape in which they occur. The formation of adventitious roots and stomatal closure were considered important factors in the flooding tolerance of *Melaleuca quinqueneroia* seedlings, a species of northern Australia (Senna Gomes & Kozlowski 1980). Waterlogging has been demonstrated experimentally not to affect the growth or leaf water potential of *E. camaldulensis* seedlings (Pereira & Kozlowski 1977; Akilan et al. 1997).

Vegetative resprouting is particularly common in communities which receive frequent periodic disturbance (James 1984), such as in many wetlands and rivers (van der Valk 1992). The importance of vegetative propagation for species is therefore mainly to allow them to persist at a site after a disturbance. The rapid recovery of established resprouters gives them a competitive advantage over seedlings so that resprouting species may dominate the post-disturbance habitat (Malanson & O'Leary 1982). In highly disturbed riparian habitats, the ability to resprout as well as to produce large quantities of seed would be highly advantageous. Many species that occur in riparian habitats in North America, such as *Salix* spp. and *Populus* spp., possess the ability to resprout and to produce large quantities of seed (Johnson 1994). This is also seen in some of the riparian trees in Australia, including *Eucalyptus camaldulensis* and *Melaleuca leucadendra* on the Ord River and *E. rudis* and *M. rhaphiophylla* on the Blackwood River. Seedlings that establish on new substrates must be able to withstand high water flows in the following or subsequent seasons which could damage and defoliate the plants. An ability to resprout also enables mature plants to survive physical damage caused by flooding. However, in large floods where trees are destroyed by the scouring of sediments, recovery can only be from seed.
Vegetation dynamics and population structure in the riparian zone

A clear insight into vegetation dynamics is essential in understanding the processes of regeneration in plant communities such as the riparian zone. Changing views of vegetation dynamics suggest that changes seen after a disturbance may not be unidirectional and that successional models may be too simplistic in describing vegetation patterns (Hobbs 1994). The present state of an ecosystem is the result of a particular history of disturbance, climatic factors and/or management. The resultant mosaic of disturbance patches and successional stages in a landscape has been described in terms of multiple stable states (Forman & Godron 1981). The regeneration process and longevity of the vegetation can be critical in determining the stage and rate of transition between stable states (Hobbs 1994). Therefore, non-equilibrium vegetation dynamics described as discrete states and definable transitions between states may better reflect vegetation communities, particularly in highly disturbed environments. State and transition models described for rangeland management (Westoby et al. 1989; Friedel 1991; Laycock 1991; George et al. 1992) allow for different vegetation community composition (states) depending on the pattern of transition. In the riparian zone the high level of disturbance can result in a mosaic of vegetation communities (Kallida & Puhakka 1988) which directional succession theories do not adequately describe because of the complex nature of the interactions taking place (Szaro 1990; Baker & Walford 1995). The state and transition model may provide an appropriate framework for interpreting the response of riparian vegetation to disturbance. The results of this study do suggest that this model may more accurately describe the vegetation dynamics on these very different rivers. Fluvial processes on the Ord River are dominated by frequent, large, high energy floods that are capable of destroying the existing riparian vegetation community and preventing the establishment of stable mature stands. These high magnitude wet season floods are, however, highly episodic and in the intervening years smaller floods allow the development of existing trees and the recruitment of younger age classes. This regime of high frequency large disturbances restricts the establishment of stable states and the ecosystem is characterised by long periods of transition between short-lived stable states. This riparian ecosystem is thus driven by abiotic or allogenic processes rather than by biotic (autogenic) processes. In contrast, lower energy, seasonal flooding on the Blackwood River allows mature
stands of trees to develop throughout the river profile (Figure 10.2). Recruitment is continual, although species can also respond to large flood events. This disturbance regime results in long periods of stable states with short periods of transition. The vegetation is subjected to longer periods of autogenic processes and, because of lower frequency flooding disturbance, shorter periods of allogenic processes.

Figure 10.2: Pathways of vegetation development and recovery in the riparian zone in response to a) high frequency fluvial disturbance as experienced on the Ord River and b) infrequent fluvial disturbance as experienced on the Blackwood River. (adapted from Wissmar & Swanson 1990).

Such a non-equilibrium model may provide an appropriate framework for management of degraded riparian zones and has been applied to riparian vegetation dynamics on a montane river in the U.S.A. (Baker & Walford 1995). Large scale disturbances, such as high water flows and flooding, are likely to be important factors in the dynamics of the riparian community. Recruitment, establishment and survival of riparian trees is thought to be closely tied to the hydrological regime (Barnes 1985; Bradley & Smith 1986; Wissmar & Swanson 1990; Johnson
Flood-induced disturbance may instigate the transition between stable states of plant composition and population structure. It can be hypothesised therefore, that river systems with frequent high energy flood events will support riparian communities with long periods of transition and rather shorter stable states. There may of course be islands of stability, in a general mosaic of differing states of transition, depending on where flooding has caused most damage. This may be along a gradient within the riparian zone, from low elevation high disturbance areas to areas at higher elevations with low frequency disturbance.

A description of the population structure of particular species within the riparian zone can be used to assess population stability and successional trends or vegetation dynamics (Veblen 1986). In many instances, large numbers of seedlings germinate each year but there is a high mortality rate (100% in some years). Therefore, while germination is more common at lower elevations where moist open sediments provide ideal sites for seedlings, growth to maturity is more likely at higher elevations which are less likely to be flooded (Jones et al. 1994). The distribution of plant communities in the riparian zone can be related to the gradient away from the river, with water being the most important factor. This includes the frequency of flooding, length of time that areas are inundated and groundwater and soil water replenishment. Lateral patterns of the riparian vegetation on low terraces and floodplains are mostly influenced by abiotic factors such as moisture gradients and flooding. On higher terraces and slopes the vegetation is more influenced by biotic factors such as competition and herbivory, although water stress may also become important as conditions become more xeric. Population structures on rivers with a high frequency of disturbance, such as occurs on the Ord River, reflect this fluvial regime. Results highlight the very different fluvial regimes that exist on the Ord and Blackwood Rivers and their effect on vegetation dynamics for the overstorey species. This is despite the species compared on the two rivers being functionally very similar. Management of the riparian vegetation should therefore take into account the frequency of change in the vegetation and that the disturbed states and long periods of transition between states are part of the natural process. This would suggest that altering the natural flow regimes, such as through river regulation, will have different effects on riparian vegetation dynamics on different rivers.
Management implications

This work has relevance to several aspects of riparian zone vegetation, including management of natural systems unaffected by man-made disturbances, for systems affected by livestock grazing and erosion and for areas requiring rehabilitation on regulated rivers. It highlights the importance of fluvial processes to riparian vegetation and indicates that understanding the natural flow regime of a target river is a critical first step in the management of riparian vegetation and planning of riparian zone rehabilitation. Where the riparian zone is highly modified, for example, by livestock grazing and/or weed invasion, natural regeneration of the riparian vegetation may be a long-term process. If intervention through direct seeding or replanting with seedlings is appropriate, care should be taken that species selected are adapted to particular site conditions such as flooding regime, landscape position and river geomorphology. Plants used for rehabilitation should also be adapted to the wet and dry cycle experienced in the riparian zone (Pautou & Decamps 1985) and have a reproductive cycle adapted to flowing water. Ideally, plants that are endemic to the riparian zone of the river that is to be rehabilitated should be used. There are many prescriptions for rehabilitation of riparian zones. These generally include a precise statement of objectives, good study design, collection of baseline data, monitoring before and after implementing the project, flexibility to change the procedure based on results of on-going monitoring and wide reporting of results (both successes and failures) (Henry & Amoros 1995; Kondolf 1995; O'Donnell 1995; Hancock et al. 1996).

Natural regeneration of riparian zones may not always be successful because of changes to the environment. Invasion of early successional species, such as exotic annual grasses, may prevent establishment of seedlings of native perennial species through competition for light and moisture. Erosion of top soil and trampling of the soil by livestock may make conditions inhospitable for germination and establishment. There may also be a lack of propagules in the surviving vegetation. In these circumstances, natural regeneration may need to be enhanced by such methods as herbicide spraying to eliminate weeds, spreading seeds of local species and
replanting areas with seedlings of local species. If replanting is to be done, care should be taken with species selection to match the various types of plant communities that occur in the riparian zone. For example, different plant communities would occur adjacent to pools or areas of rapids or riffle zones, on the levee banks, in abandoned channels and on the floodplain. The high natural disturbance levels occurring in riparian zones may mean that there are particular requirements and adaptations of species necessary to achieve successful establishment. For example, protection of seedlings from strong flows and woody debris in floodwaters may be required for several years until seedlings are strong enough to withstand this disturbance (Hancock et al. 1996). Different sections of a river, such as reaches and pools, riffle zones, erosion bends and depositional areas, flood plains and narrow, steep-sided sections may have different requirements for regeneration. This highlights the importance of individual responses of species to the environment and to chance events following disturbance (Gleason 1927). This aspect requires further research.

The impact on riparian vegetation of river regulation has been widely studied (e.g. Nilsson et al. 1991a; Walker et al. 1994; Barnes 1997; Johnson 1997). The majority of the world's rivers are regulated (Petts 1984) and in the northern third of the world 77% of total discharge of the 139 largest rivers are affected by some form of regulation (Dynesius & Nilsson 1994). Understanding the vegetation dynamics and the mechanisms of recruitment under natural (unregulated) flow conditions is critical to understanding or anticipating the effects of river flow regulation on riparian vegetation (Nilsson et al. 1997). Water resource policy in Australia requires setting a provision of water for the environment in regulated systems (Arthington & Zalucki 1998). Setting of environmental water requirements by documenting the variability in the natural flow regime of a river and matching this to ecologically critical flow requirements of in-stream biota has been used to define a schedule of flow releases for the North Dandalup and Harvey Rivers in south-western Australia (Davies et al. 1998). Based on the results from this study, this holistic approach (Arthington 1998) can be extended to include provisions for the riparian vegetation using quantitative vegetation data as shown in the example in Chapter 5. This would refine the setting of environmental water requirements on regulated rivers.
The common thread that appears to influence all aspects of the vegetation replacement processes examined in this thesis is the fluvial regime. The strong relationship between fluvial regime and vegetation dynamics is important in developing the unique character of riparian vegetation (Wissmar & Swanson 1990; Naiman et al. 1998). River flows, and particularly the disturbance of large floods, affect vegetation community structure and spatial distribution, seed dispersal, seedling recruitment and population structure. The species which were examined in detail provide good examples of adaptations to conditions in the riparian zone, including reproductive phenology synchronised to seasonal flows, floating ability of seed to facilitate dispersal and tolerance of seedlings to flooding. Other aspects are also important in determining riparian vegetation community structure, including biotic (e.g. competition, livestock grazing) and abiotic (e.g. soils, topography and fire) factors, with the influence of each depending to a large extent on the interaction with the hydrology. This influence is obviously different for the two study rivers, with the riparian vegetation on the Ord River strongly influenced by the fluvial regime whereas on the Blackwood River the effects are more subtle and other factors have a stronger influence on vegetation dynamics. In terms of river restoration, this emphasises the importance of gaining a sound understanding of the fluvial regime for a particular river, along with other abiotic factors, such as soils and topography, and relating this to the biology of the vegetation community.
REFERENCES


APPENDIX 1

List of species found at the study sites on the Blackwood River.

A total of 226 species, including 44 exotic species, were recorded for the Blackwood River sites during the study. These species came from 54 families and 163 genera. The most common families were Poaceae (29 species from 22 genera), Asteraceae (22 species from 20 genera), Cyperaceae (20 species from 10 genera) and Myrtaceae (17 species from 8 genera). Common species that were found at all five sites included the exotic annual herbs *Hypochaeris glabra* and *Romulea rosea*, the exotic annual grass *Lolium rigidum* and the native riparian tree *Eucalyptus rudis*. *Melaleuca rhaphiophylla* also occurred at all sites other than the saline site (B3).

Location of sites in the Blackwood River catchment are shown on the map in Figure 3.2 and include:

- B1a - ungrazed site near the town of Nannup at the downstream end of the middle catchment.
- B1b - grazed site near the town of Nannup at the downstream end of the middle catchment.
- B2a - ungrazed site near the town of Boyup Brook in the centre middle catchment.
- B2b - grazed site near the town of Boyup Brook in the centre middle catchment.
- B3a - ungrazed site on the Beaufort River in the upper catchment.
- B3b - ungrazed site on the Beaufort River in the upper catchment.
- B4 - grazed site in the middle catchment.
- B5 - grazed site in the middle catchment.

* Exotic species

<table>
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<th>SPECIES NAME</th>
<th>SITES</th>
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<td><em>Ptilotus manglesii</em> (Lindley) F. Muell.</td>
<td>B3a, B3b</td>
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</tr>
<tr>
<td></td>
<td><em>Arthropodium preissii</em> Endl.</td>
<td>B1a, B1b</td>
</tr>
<tr>
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<td><em>Chamaescilla corymbosa</em> (R. Br.) F. Muell ex Benth.</td>
<td>B2a, B2b, B3b, B4, B5</td>
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<tr>
<td></td>
<td><em>Corynotheca micrantha</em> (Lindley) J.F. MacBride</td>
<td>B5</td>
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<tr>
<td></td>
<td><em>Hodgsoniola junciformis</em> F. Muell.</td>
<td>B1b, B2a, B2b, B4</td>
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<td></td>
<td><em>Laxmannia grandiflora</em> Lindley</td>
<td>B3b</td>
</tr>
<tr>
<td></td>
<td><em>Thysanotus multiflorus</em> R. Br.</td>
<td>B1a</td>
</tr>
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<td>Family</td>
<td>Species</td>
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<td>--------------------------------------------------------------------------</td>
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<td>Apiaceae</td>
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<td>Eryngium rostratum Cav.</td>
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<td>Asparagaceae</td>
<td>Asparagus asparagoides (L.) Wight</td>
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<td>Asteraceae</td>
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<td>Arctotheca calendula (L.) Levyns.*</td>
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<td></td>
<td>Aster subulatus Michaux*</td>
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<td></td>
<td>Calocephalus angianthoides (Steetz) Beth.</td>
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<td>Caradus pycocephalus L.*</td>
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<td></td>
<td>Circium vulgare (Savi) Ten.*</td>
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<td></td>
<td>Cotula turbinata L.*</td>
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<td></td>
<td>Ditrichia graveolens (L.) Greuter*</td>
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<td></td>
<td>Gnaphalium sphaericium Willd.*</td>
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<td>Hyalosperma cotula (Benth.) P.G. Wilson</td>
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<td>Hypochaeris glabra L.*</td>
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<td>Podolepis lessonii (Cass.) Benth.</td>
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<td>Psuedognaphalium lutealbum (L.)</td>
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<td>Hilliard &amp; B.L. Burtt*</td>
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<tr>
<td></td>
<td>Quineta urvillei Cass.</td>
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<td>Siloxerus humifusus Labill.</td>
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<td>Sonchus asper Hill*</td>
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<td>Sonchus oleraceus L.*</td>
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<td>Cerastium glomeratum Thuill.*</td>
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<td>Sagina apetala Ard.*</td>
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<td></td>
<td>Spargularia salina J.S. Presl &amp; C. Presl*</td>
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<td>Casuarinaceae</td>
<td>Casuarina obesa Miq.</td>
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<tr>
<td></td>
<td>Chenopodium album L.*</td>
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<td>Chenopodaceae</td>
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<tr>
<td>Chenopodaceae</td>
<td>Halosarcia lepidosperma Paul G. Wilson</td>
<td></td>
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</tbody>
</table>

Note: The table lists species with their respective families and authors, along with references and other relevant information.
Crassulaceae
\textit{Crassula alata} (Viv.) Berger*
\textit{Crassula glomerata} P. Bergius*

Cyperaceae
\textit{Carex appressa} R. Br.
\textit{Chorizandra enodis} Nees
\textit{Cyathochaeta avenacea} Benth.
\textit{Cyperus} sp. L.
\textit{Gahnia} sp Forst. & Forst.
\textit{Gahnia} trifida Labill.
\textit{Isolepis cernua} (M. Vahl) Roemer & Schultes
\textit{Isolepis nodosa} (Rottb.) R. Br.
\textit{Lepidosperma angustatum} R. Br.
\textit{Lepidosperma drummondii} Benth.
\textit{Lepidosperma effusum} Benth.
\textit{Lepidosperma leptostacyum} Benth.
\textit{Lepidosperma longitundinale} Labill.
\textit{Lepidosperma squamatum} Labill.
\textit{Lepidosperma tenue} Benth.
\textit{Mesomelaena tetragona} (R. Br.) Benth.
\textit{Schoenus elegans} S.T.Blake
\textit{Schoenus nanus} (Nees) Benth.
\textit{Schoenus} sp.L.
\textit{Tetraria octandra} (Nees) Kuek.

Dasypogonaceae
\textit{Lomandra micrantha} (Endl.) Ewart
\textit{Lomandra sericea} (Endl.) Ewart

Dilleniaceae
\textit{Hibbertia montana} Steudel

Droseraceae
\textit{Drosera gigantea} Lindley
\textit{Drosera glanduligera} Lehm.
\textit{Drosera macrantha} Endl.
\textit{Drosera pallida} Lindley

Epacridaceae
\textit{Astroloma drummondii} Sonder
\textit{Astroloma pallidum} R. Br.
\textit{Leucopogon propinquis} R. Br.

Euphorbiaceae
\textit{Euphorbia australis} Boiss.*
\textit{Phyllanthus calycinus} Labill.
\textit{Poranthera microphylla} Brongn.

Gentianaceae
\textit{Centaurium erthryrea} Rafn.*

Geraniaceae
\textit{Erodium botryus} (Cav.) Bertol.*
\textit{Geranium retrorsum} L’Her. ex DC.

\textbf{B3a, B3b, B5}
\textbf{B5}
\textbf{B2a}
\textbf{B2a, B3a, B3b, B4, B5}
\textbf{B5}
\textbf{B1a, B1b}
\textbf{B2a, B4}
\textbf{B3a, B3b}
\textbf{B2a, B2b, B5}
\textbf{B5}
\textbf{B1a, B2a}
\textbf{B2a}
\textbf{B2a}
\textbf{B2a}
\textbf{B2a, B3b}
\textbf{B2a, B3b}
\textbf{B2a, B2a, B5}
\textbf{B2a}
\textbf{B1a}
\textbf{B2a}
\textbf{B3b}
\textbf{B5}
\textbf{B2a, B2a}
\textbf{B1a}
\textbf{B1a, B2a}
\textbf{B1a}
\textbf{B3b}
\textbf{B1a}
\textbf{B1a}
\textbf{B4}
\textbf{B1a}
\textbf{B1a, B1b, B2a, B5}
\textbf{B1a, B1b, B2a, B5}
\textbf{B1a, B1b, B4, B5}
\textbf{B1a}
\textbf{B1a, B2a}
\textbf{B4}
\textbf{B1a}
Haemodoraceae  
- *Conostylis aculeata* R. Br.  
- *Conostylis setosa* Lindley  
- *Haemodorum laxum* R. Br.  
- *Haemodorum spicatum* R. Br.

Hypoxidaceae  
- *Hypoxis glabella* R. Br.

Iridaceae  
- *Hesperantha falcata* (L. f.) Ker Gawler  
- *Hexaglottis lewisiae* Goldblatt*  
- *Homeria flaccida* Sweet*  
- *Patersonia occidentalis* R. Br.  
- *Patersonia umbrosa* Endl.  
- *Romulea rosea* (L.) Eckl.*  

Juncaceae  
- *Juncus bufonius* L.*  
- *Juncus capitatus* Weigel *  
- *Juncus pallidus* R. Br.  
- *Juncus pauciflorus* R.Br.  
- *Juncus subsecundus* Wakef.

Lamiaceae  
- *Mentha pulegium* L.*  
- *Cassytha racemosa* R. Br.

Lauraceae  
- *Villarsia capitata* Nees

Lobeliaceae  
- *Lobelia alata* Labill.

Menyanthaceae  
- *Monopsis deblis* (L.f.) C. Presl.*  

Mimoaceae  
- *Acacia pulchella* R. Br.  
- *Acacia acuminata* Benth.

Myoporaceae  
- *Myoporum caprarioides* Benth.

Myrtaceae  
- *Astartea fasicularis* (Labill.) DC.  

Myrtaceae  
- *Eucalyptus marginata* Donn ex Smith  
- *Eucalyptus rudis* Endl.

Mimaceae  
- *Eucalyptus wandoo* Blakely  
- *Hypocalymma angustifolium* Endl.

Kunzea ericifolia* (Smith) Heynh.
Lhotskya acutifolia Lindl.
Melaleuca acuminata F. Muell.
Melaleuca hamulosa Turcz.
Melaleuca incana R. Br.
Melaleuca lateriflora Benth.
Melaleuca rhaphiophylla Schauer

Melaleuca uncinata R. Br.
Melaleuca urceolaris F. Muell. ex Benth.
Melaleuca viminea Lindley
Verticordia densiflora Lindley

Epilobium billardierianum Ser.

Elythranthera brunonis (Endl.) A.S. George
Diuris longifolia R. Br.
Microtis unifolia (G. Forster) H.G. Reichb.
Monadenia bracteata (SW.) T. Durand & Schinz*
Pterostylis nana R. Br.

Thelymitra antennifera (Lindl.) J.D. Hook.

Oxalis corniculata L.*
Oxalis hirta L.*
Oxalis pes-caprae L.*

Brachysera celsianum Lemaire
Bossiaea linophylla R.Br.
Davesia horrida Priess ex Meissner
Gastrolobium bilobum R. Br.
Gonophlobium marginatum R.Br.
Hovea trisperma Benth.
Jacksonia furcellata (Bonpl.) DC
Jacksonia sternbergiana Huegel
Lotus suaveolens Pers.*
Lupinus angustifolius L.

Trifolium angustifolium L.*
Trifolium campestris Schreber *

Trifolium repens L.*
Trifolium subterraneum L.*
Viminaria juncea (Schrader & Wendl.) Hofsgg.

Philydrella pygmeae (R. Br.) Caruel

B3
B2a
B3a
B2a
B3a
B1a, B1b, B2a, B2b, B4, B5
B3a
B3a
B1a
B3a
B2b, B3b, B4
B3b
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B1a
B3b
Phorminaceae
Dianella divaricata R. Br.

Pittosporaceae
Stypandra glauca R. Br.
Billardiera floribunda (Putterl.)F. Muell.
Sollya heterophylla Lindley

Plantaginaceae
Plantago lanceolata L.*

Poaceae
Aira caryophyllea L.*
Amphipogon turbinatus R. Br.
Astrostipa compressa (R. Br.) S. W. L. Jacobs & J. Everett
Austrostipa elegantissima Labill. S. W. L. Jacobs & J. Everett
Astrostipa semibarbata R. Br.
Avena fatua L.*
Briza maxima L.*
Briza minor L.*

Bromus diandrus Roth*
Bromus hordeaceus L.*
Bromus madritensis L.*
Cynodon dactylon (L.) Pers.

Danthonia caespitosa Gaudich.
Ehrharta calycina Smith*
Ehrharta longiflora Smith*
Holcus lanatus L.*
Hordeum leporinum Link*
Lolium perenne L.*
Lolium rigidum Gaudin*

Microlaena stipoides (Labill.) R. Br.
Neurachne alopecuroidea R. Br.

Parapholis incurva (L.) C. E. Hubb.*
Pennisetum cladestinum Hochst. ex Chiov.*
Pentaschistis airiodes (Nees) Stapf *
Phalaris minor Retz.*
Polypogon monspeliensis (L.) Desf.*

B1a, B1b, B2a, B3a, B4
B2a, B3a
B1a
B1a, B2a
B1a, B3b, B4
B1a, B1b, B2a, B2b, B3a, B3b, B4, B5
B1a
B2a, B2b
B1a, B2a, B2b, B4, B5
B2a, B2b, B3a, B3b, B4, B5
B1a
B3a, B3b
Polygalaceae

Sporobolus virginicus (L.) Kunth*

Polygonaceae

Muehlenbeckia adpressa (Labill.) Meissner

Primulaceae

Anagallis arvensis L.*

Proteaceae

Banksia seminuda (A.S.George) B.L.Rye

Ranunculaceae

Ranunculus muricatus L.*

Restionaceae

Meeboldina coangustata (Nees) B.G.Briggs & L.A.S. Johnson

Rosaceae

Rubus discolor Weihe & Nees *

Rubiaceae

Galium diaricatum Pourret ex Lam.*

Santalaceae

Exocarpos sparteus R. Br.

Scrophulariaceae

Bellardia trixago (L.) All.*

Stylidiaceae

Levenhookia pusilla R. Br.

B3b
B1b
B1a, B1b, B2a, B4, B5
B1a
B1a, B1b, B4
B4, B5
B1a, B2a, B2b, B4, B5
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<td>Zaminaceae</td>
<td>Macrozamia</td>
<td>reidii (Fischer ex Gaudich.) C. Gardner</td>
<td></td>
<td>B1a, B2a</td>
</tr>
</tbody>
</table>
A total of 151 species, including 23 exotic species, were recorded for the Ord River sites during the study. These species came from 46 families and 104 genera. The most common families were Poaceae (24 species from 18 genera), Cyperaceae (19 species from 5 genera), Papilionaceae (12 species from 7 genera) and Myrtaceae (10 species from 4 genera). Common species that were found at all five sites included the trees *Eucalyptus camaldulensis, Melaleuca leucadendra, Lysiphyllum cunninghamii* and *Pandanus spiralis* and the exotic creeper *Passiflora foetida*.

Location of sites in the Ord River catchment are shown on the map in Figure 3.1 and include:

O1 - Lower Ord River upstream of Carlton crossing.
O2 - Lake Kununurra near the settlement of Crossing Falls
O3 - Upper Ord on the Behn River near the Duncan Rd crossing.
O4 - Upper Ord on the Negri River near the Duncan Rd Crossing
O5 - Upper Ord at the Water and Rivers Commission gauging site at Old Ord River Station.

* Exotic species

<table>
<thead>
<tr>
<th>FAMILY</th>
<th>SPECIES NAME</th>
<th>SITES</th>
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<td>Amaranthaceae</td>
<td><em>Achyrantes aspera</em> L.</td>
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</tr>
<tr>
<td></td>
<td><em>Aerva javanica</em> (Burm.f.) Juss.ex Schultes*</td>
<td>O4, O5</td>
</tr>
<tr>
<td></td>
<td><em>Alternanthera nana</em> R.Br.</td>
<td>O1</td>
</tr>
<tr>
<td></td>
<td><em>Alternanthera nodiflora</em> R.Br.</td>
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<tr>
<td></td>
<td><em>Gomphrena affinis</em> F. Muell. ex Benth</td>
<td>O4, O5</td>
</tr>
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<td></td>
<td><em>Ptilotus exaltatus</em> Nees</td>
<td>O5</td>
</tr>
<tr>
<td>Asclepiadaceae</td>
<td><em>Calotropis procera</em> (Aiton) W.T. Aiton*</td>
<td>O5</td>
</tr>
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<td></td>
<td><em>Marsdenia viridiflora</em> R.Br.</td>
<td>O1</td>
</tr>
<tr>
<td></td>
<td><em>Sarcostemma esulentum</em> (L.f.) Holm</td>
<td>O1</td>
</tr>
<tr>
<td></td>
<td><em>Tylophora flexuosa</em> R.Br.</td>
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</tr>
<tr>
<td>Asteraceae</td>
<td><em>Bidens pilosa</em> L.*</td>
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</tr>
<tr>
<td></td>
<td><em>Blumea axillaris</em> (Lam) DC.</td>
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</tr>
<tr>
<td></td>
<td><em>Blumea diffusa</em> R. Br ex Benth.</td>
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</tr>
<tr>
<td></td>
<td><em>Flaveria australasica</em> Hook.</td>
<td>O5</td>
</tr>
<tr>
<td></td>
<td><em>Vernonia cinerea</em> (L.) Less.</td>
<td>O2</td>
</tr>
<tr>
<td>Asteraceae</td>
<td><em>Xanthium occidentale</em> Bertol.*</td>
<td>O1</td>
</tr>
</tbody>
</table>
Bixaceae  Cochlospermum fraseri Planchon
Bombacaceae  Adansonia gregorii F. Muell.
Boraginaceae  Heliotropium indicum L.*
Heliotropium sp L.
Caesalpiniaceae  Lysiphyllum cunninghamii (Benth.) de Wit
Parkinsonia aculeata L.*
Capparaceae  Cleome viscosa L.*
Centrolepidaceae  Centrolepis exserta (R.Br.) Roemer & Schultes
Chenopodiaceae  Dysphania plantaginella F. Meull.
Salsola kali L.*
Combretaceae  Terminalia canescens (DC.) Radlk.ex T.Durand
Terminalia hadleyana W. Fitzg.
Terminalia oblongata F. Muell.
Terminalia platyphylla F.Muell.
Commelinaceae  Commelina ciliata T.D. Stanley
Commelina ensifolia R.Br.
Convolvulaceae  Ipomoea muelleri Benth.
Jacquemontia browniana Ooststr.
Cucurbitaceae  Luffa graveolens Roxb.
Cyperaceae  Bulbostylis barbata (Rottb.) C.B.Clarke
Cyperus breviculmus R.Br.
Cyperus castaneus Willd.
Cyperus conicus (R.Br.) Boeckler
Cyperus cunninghamii (C.B.Clarke) C.Gardner
Cyperus cuspidatus Kunth
Cyperus difformis L.
Cyperus holoschoenus R. Br.
Cyperus sp L.
Cyperus vaginatus R.Br.
Eleocharis atropurpurea Kunth
Eleocharis sp A
Fimbristylis caespitosa R. Br.
Fimbristylis littoralis Gaudich.
Fimbristylis phaeoleuca S.T.Blake
Fimbristylis punctata R.Br.
Fimbristylis sp Vahl
Schoenoplectus dissanchanthus (S.T.Blake) Raynal

O1, 02, 03, 04, 05
O3, 04
O5
O3, 04, 05
O1, 05
O1
O5
O3
O1
O5
O1
O3
O2
O2
O1
O5
O1
O5
O2

Schoenoplectus littoralis (Schrader) Pall  
*Euphorbia hirta* L.*  
*Euphorbia australis* Boiss.  
Excoecaria parvifolia Muell. Arg.  
*Flueggea virosa* (Roxb. ex Willd.) Voigt  
*Petalostigma pubescens* Domin  
*Phyllanthus maderaspatensis* L.  

**Euphorbiaceae**  
Gyrocarpus americanus Jacq.  
*Hyptis suaveolens* (L.) Poit.*  
*Barringtonia acutangula* (L.) Gaertner  
*Abelmoschus ficulneus* (L.) Wight & Arn. ex Wight  
*Abutilon indicum* (L.) Sweet  
*Abutilon ovocarpum* F.Muell.  
*Abutilon oxyacarpum* (F. Muell.) F.Muell.exBenth.  
*Hibiscus sabdariffa* L.*  
*Malvastrum americanum* (L.) Torrey*  
*Sida acuta* Burrm. f.*  
*Sida fibulifera* Lindley  
*Sida spinosa* L.  

**Hernandiaceae**  
*Barringtonia acutangula* (L.) Gaertner  

**Lamiaceae**  
*Melastoma affine* D.Don  
*Melia azedarach* L.  
*Tinospora smilacina* Benth.  
*Acacia farnesiana* (L.)Willd.*  
*Acacia holosericea* Cunn. ex Don  
*Calthormion umbellatum* (Vahl)Kosterm.  
*Dichrostachys spicata* (F. Muell.)C. Gardner  
*Neptunia monosperma* F. Muell.  

**Meliaceae**  
*Ficus coronulata* Miq.  
*Ficus opposita* Miq.  
*Ficus racemosa* L.  

**Menispermaceae**  
*Nepeta opposita* Miq.  

**Mimoseaceae**  
*Acacia farnesiana* (L.)Willd.*  
*Acacia holosericea* Cunn. ex Don  
*Calthormion umbellatum* (Vahl)Kosterm.  
*Neptunia monosperma* F. Muell.  

**Moraceae**  
*Ficus coronulata* Miq.  
*Ficus opposita* Miq.  
*Ficus racemosa* L.  

**Myrtaceae**  
*Eucalyptus camaldulensis* Dehnh.  
*Eucalyptus gymnoteles* L.A.S. Johnson & K.D.Hill  
*Eucalyptus houseana* W. Fitzg. ex Maiden  
*Eucalyptus microtheca* F. Muell.  
*Lophostemon grandiflorus* (Benth.) P.G.Wilson & J.T.Waterhouse  
*Melaleuca argentea* W. Fitzg.  

**Myrtaceae**
<table>
<thead>
<tr>
<th>Family</th>
<th>Genus and Species</th>
<th>Page Numbers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Melaleuca</td>
<td>leucadendra (L.) L.</td>
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<tr>
<td>Melaleuca</td>
<td>minutifolia F.Muell.</td>
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<td>Melaleuca</td>
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<td>Syzygium</td>
<td>eucalyptoides (F.Muell.) B. Hyland</td>
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<tr>
<td>Nymphaeaceae</td>
<td>Nymphaea violacea Lehm.</td>
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<tr>
<td>Oleaceae</td>
<td>Jasminum didymum G. Forster</td>
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<td>Onagraceae</td>
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<td>Opiliaceae</td>
<td>Opilia amentacea Roxb.</td>
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<td>Papilionaceae</td>
<td>Abrus precatorius L.</td>
<td>O1, O2</td>
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<tr>
<td></td>
<td>Aeschynomone indica L.</td>
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<td>Clitoria ternatea L.*</td>
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<td>Crotalaria medicaginea L.am.</td>
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<td>Crotalaria nova-hollandiae D.C.</td>
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<td>Crotalaria retusa L.</td>
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<tr>
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<td>Erythrina vespertilio Benth.</td>
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<td>Indigofera linifolia (L.f.)Retz.</td>
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<td>Indigofera parviflora Heyne ex Wight &amp; Arn.</td>
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<td>Sesbania cannabina (Retz.) Poiret</td>
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<td>Sesbania formosa (F.Muell.) N.Burb.</td>
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<td>Sesbania simpliciuscula F.Muell. ex Benth.</td>
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<td>Poaceae</td>
<td>Aristida hygrometrica R.Br.</td>
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<td>Bothriochloa bladhii (Retz.) S.T.Blake</td>
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<td>Brachyachne convergens (F. Muell.) Stapf</td>
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<td>Cenchrus citaris L.*</td>
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<td>Cenchrus setiger Vahl*</td>
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<tr>
<td>Poaceae</td>
<td>Chionachne hubbardiana Henrard</td>
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<td>Chloris barbata Sw.</td>
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<td>Chrysopogon fallax S.T. Blake</td>
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<td>Cynodon dactylon (L.) Pers.</td>
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<td>Dichanthium sericeum (R.Br.) A. Camus</td>
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<td>Echinochloa colona (L.) Link*</td>
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<td>Eragrostis cummgi Steudel</td>
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</table>
Polygonaceae

Eragrostis falcata (Gaudich.) Gaudich. ex Steudel O4, O5
Eragrostis tenellula (Kunth) Stuedel O5
Eulalia aurea (Bory) Kunth O4, O5
Heteropogon contortus (L.) P. Beauv. ex Roemer & Schultes O3, O4, O5
Iseilema vaginiflorum Domin O1
Panicum decompositum R. Br. O1
Panicum mindanaense Merr. O1
Panicum seminudum Domin O1
Paspalidium jubiflorum (Trin.) Hughes O1
Phragmites karka (Retz.) Trin. O1, O5
Whiteochloa airoides (R. Br.) Lazarides O1

Portulacaceae

Persicaria attenuata (R. Br.) Sojak O1, O4, O5
Calandrinia quadriovis F. Muell. O1
Portulaca oleracea L. O4, O5

Rhamnaceae

Ziziphus quadrifoliolus F. Muell. O4

Rubiaceae

Nauclea orientalis L. O1, O3, O4, O5

Santalaceae

Santalum lanceolatum R. Br. O5

Sapindaceae

Cardiospermum halicacabum L.* O1
Atalaya hemiglauca (F. Muell.) F. Muell. ex Benth. O1

Solanaceae

Datura inoxia Miller* O5
Physalis minima L.* O4, O5
Solanum lucani F. Muell. O1

Tiliaceae

Grewia breviflora Benth. O1

Typhaceae

Typha domingensis Pers. O1, O2, O5

Violaceae

Hybanthus euneaspermus (L.) F. Muell. O1

Vitaceae

Cissus adnata Roxb. O1
Appendix 3

List of submitted publications and conference presentations related to the thesis topic.


Appendix 4

Copy of Manuscript accepted for publication in Wetland Ecology and Management.

(due for publication in September 2000)
Variability in flood disturbance and the impact on riparian tree recruitment in two contrasting river systems

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Centre for Ecosystem Management, Edith Cowan University, Joondalup, Western Australia 6027

Received 15 March 1999; accepted in revised form 20 December 1999

Key words: flood disturbance, riparian vegetation, tree recruitment, water regime

Abstract

The vegetation within the riparian zone performs an important ecological function for in-stream processes. In Australia, riparian zones are regarded as the most degraded natural resource zone due to disturbances such as river regulation and livestock grazing. This study looks at factors influencing vegetation dynamics of riparian tree species on two contrasting river systems in Western Australia. The Blackwood River in south-western Australia is influenced by a Mediterranean type climate with regular seasonal winter flows. The Ord River in north-western Australia is characterized by low winter base flows and episodic, extreme flows influenced by monsoon rains in the summer. For both rivers, reproductive phenology of studied overstory species is timed to coincide with seasonal river hydrology and rainfall. An even distribution of size classes of trees on the Blackwood River indicated recruitment into the population is continual and related to the regular predictable seasonal river flows and rainfall. In contrast, on the Ord River tree size class distribution was clustered, indicating episodic recruitment. On both rivers tree establishment is also influenced by elevation above the river, microtopography, moisture status and soil type. In terms of vegetation dynamics riparian vegetation on the Ord River consists of long periods of transition with short lived stable states in contrast to the Blackwood river where tree population structure is characterized by long periods of stable states with short transitions.

Introduction

In most countries, changes to land use in river catchments have had a major impact on riparian zones. Impacts and activities include industrial and urban pollution (Jeffries and Mills, 1990), agriculture and forestry (Abido, 1985; Shah and Thames, 1985; Fleischner, 1994). In Australia, riparian zones are regarded as the most degraded natural resource zone (CEPA, 1992). These ecosystems are important in terms of overall landscape ecology and for the protection and maintenance of the instream river ecosystem (Bunn, 1993). In order to manage these systems knowledge of the ecological processes that are important for regeneration of the riparian vegetation is required.

Ecological studies on the regeneration of plant communities have been done for many types of plant communities including grasslands (Grime and Hillier, 1992; McIntyre et al., 1995), heath (Bell et al., 1982), and forest (Bell and Koch, 1980) as well as lentic wetlands (van der Valk, 1981; Boutin and Keddy, 1993; Hills et al., 1994). However, little work has been done specifically on riparian vegetation (Barnes, 1985; Baker, 1988; Baker, 1990; Nilsson et al., 1994) and especially not in Australia (Dexter, 1978; Breen and Gibbs, 1986; Breen, 1992; Roberts, 1993). In many areas of Australia there is a high level of community interest in restoration of rivers. However there is a lack of ecologically-based knowledge of the processes of regeneration within riparian vegetation.

Traditional 'Clemensian' successional models have been found to be inappropriate for many vegetation communities (Glenn-Lewin and van der Maarel, 1992). Rather than unidirectional succession, dynamics within vegetation communities create a series of patches made up of transitions between more or less stable states mediated by disturbance, climate or management (Hobbs, 1994). The present state of an
ecosystem is the result of a particular history of disturbance, climatic factors and/or management. The regeneration process and longevity of vegetation can also be critical in determining the stage and rate of transition states.

State and transition models have been suggested as a tool for rangeland management (Westoby et al., 1989; George et al., 1992), as an alternative to linear succession, to allow for different vegetation community composition (states) depending on the transitions pattern. Non-equilibrium vegetation dynamics may be described by discrete states and definable transitions between states. Transitions are usually instigated by natural events and may occur quickly or over an extended period and change to a persistent state depending on events during the transition (George et al., 1992). This model may provide an appropriate framework for management of degraded riparian zones and assist in interpreting the response of riparian vegetation to disturbance in terms of possible states and transitions of riparian vegetation.

Large scale disturbances, such as high water flows and flooding, are likely to be important factors in the dynamics of the riparian community. Recruitment, establishment and survival of riparian trees has been thought to be closely tied to the hydrological regime (Barnes, 1985; Bradley and Smith, 1986; Johnson, 1994). Flood induced disturbance may instigate the transition from stable states of plant composition and population structure. It can be hypothesized therefore, that river systems with frequent high energy flood events will support riparian communities with long periods of transition and rather shorter stable states.

The Ord River, in the tropical north-west of Australia, is affected by seasonal monsoon rains during the wet season, when episodic high intensity events result in high river flows. For the rest of the year virtually no rain falls and the river, especially those sections draining the semi-arid interior, dry up completely or to a series of permanent pools. The Blackwood River is one of the largest rivers in south-western Australia and drains the low rainfall agricultural area before flowing through forest and entering the sea on the southwest corner of the continent. River flows are influenced by the Mediterranean climate with regular high seasonal winter flows and low summer base flows. Two dominant overstory species from each river system have been chosen for this study. *Eucalyptus camaldulensis* occurs as a dominant riverine species throughout continental Australia except for the south west where it is replaced by *E. rudis* which is a closely related spe-

cies that is known to hybridize with *E. camaldulensis* (Boland et al., 1989). *Melaleuca leucadendra* on the Ord River and *M. rhaphiophylla* on the Blackwood River are also similar species with a high tolerance of waterlogged conditions. By studying functionally equivalent riparian tree species in two contrasting river systems and climatic zones, the influence of the different physical environments on vegetation persistence and recruitment in the riparian zone can be elucidated.

This paper compares recruitment patterns of functionally similar overstory species that occur on two contrasting river systems. These patterns will be discussed in terms of a state and transition model for populations of these riparian species and the implications for riparian vegetation management.

**Methods**

**Study sites**

The study sites are located in the south-west (Blackwood River) and in the Kimberley region of the north-west of Western Australia (Ord River) (Figure 1). The Blackwood river was chosen as being representative of temperate river systems in the south-west of Western Australia while in contrast the Ord is a sub-tropical northern Australian river with flows greatly affected by monsoon rains resulting in large seasonal flows. The riparian zone of each of these rivers has, at least in some sections, become degraded by livestock grazing and as a consequence of agricultural clearing.

**Blackwood River**

The Blackwood River originates in the low rainfall area and flows westward to enter the sea at the south west tip of the continent. The river is approximately 300 km long and carries the largest flow of any river in the south west. Rainfall in the catchment varies from 400 mm yr⁻¹ in the east to 1200 mm yr⁻¹ near the coast. The upper and middle reaches are greatly influenced by large areas of cleared agricultural land with many areas having been cleared for 100 years and with livestock grazing taking place right up to the river’s edge (Olsen and Skitmore, 1991). Clearing in the naturally highly saline soils of the upper catchment has resulted in rising salinity levels of the river with the waters of the upper Blackwood tributaries (Arthur and Beaufort Rivers) being saline to brackish (Schofield et al., 1988). Water in the middle to lower sections which are drained by mainly forested areas is marginal
to fresh before becoming influenced by the salt wedge as the river nears the coast.

**Ord River**

The Ord River stretches from its source north-west of Halls Creek to empty into Cambridge Gulf north-west of Kununurra. Vegetation in the catchment is predominately open grassy woodland (Beard, 1979) which is grazed by cattle. On the Ord River plains in the upper catchment degradation of the vegetation through a long history of overgrazing has resulted in severe erosion problems and extremely high sediment loads in the river. On large areas, such as Ord River Station, rehabilitation through fencing and de-stocking has taken place (Fitzgerald, 1967). The river has been dammed in two places which results in three discrete sections. Upstream from the Ord River Dam and Lake Argyle the river flow is essentially natural with flows influenced by the climate, consisting of a distinct wet season (December to March) with monsoon rainfall initiating high river flows and a dry season when the river dries up to a series of pools. In the middle section of the river, between the Ord River Dam and the diversion dam at Kununurra, the river has become permanent and water levels alter little throughout the year. Downstream from the diversion dam, water flows are artificially regulated to provide water for irrigation.
Tree species

Eucalyptus camaldulensis and E. rudis (in the informal subgenus Symphyomyrtus (Boland et al., 1989)) are taxonomically and functionally very similar species. Both are riverine trees which grow to 20 m tall and fill the same ecological niche in the riparian zone, occupying the river bank and in some instances the adjacent floodplain. E. camaldulensis is widespread throughout mainland Australia having essentially a linear geographic distribution along watercourses. E. rudis has a much more restricted distribution to south western Australia where it replaces E. camaldulensis as the main riparian species. Both species are tolerant of periodic inundation and waterlogged conditions. Melaleuca leucadendra on the Ord River can be co-dominant with E. camaldulensis but tends to occupy the wetter littoral edges of the riparian zone probably due to greater waterlogging tolerance. Similarly M. rhaphiophylla on the Blackwood River occurs with E. rudis and is a small tree which tends to persist on the fringe of the littoral zone and in other areas where prolonged inundation can exclude other species.

Survey methods

For each river long term climate and river flow data were collected from nearby climate and stream gauging stations operated by the Waters and Rivers Commission of Western Australia. Sites were selected at two areas on reaches of both rivers. The river reach scale was considered the appropriate scale for this study as it includes a range of disturbance patches of different ages but in close proximity to reduce other environmental sources of variation such as changes in geology. At the study sites on the upper Ord river in the unregulated section and on the middle section of the Blackwood River (Figure 1) six 5 m x 200 m belt transects where set up (in, 1996) perpendicular to the river. Along each transect the diameter at breast height (1.3 m) of all trees of the study species in the transect were measured as well as their elevation (using an auto-level and staff) relative to the river dry season base flow level and distance from river base flow. In addition, reproductive status of each tree was recorded. Sites were revisited regularly to record reproductive phenology.

One m square seedling quadrats were randomly laid out adjacent to the transects and on two additional transects where seedlings occurred. Within each quadrat, heights of all 1 year old seedlings were recorded. For each quadrat a number of environmental parameters were recorded including surface soil type, microtopography, surface soil moisture status, elevation above river base flow level, bare ground, litter, distance to water and distance to nearest seed tree. Frequency of seedling plots for each environmental parameter was collated. For quantitative parameters (elevation, litter, distance to water and distance to nearest seed tree) correlation analysis against seedling density was performed. For each categorical parameter (soil type, microtopography, surface soil moisture status) a Krussall-Wallis test (non-parametric ANOVA analog) was conducted for seedling density to test if there were a significant difference between categories for each parameter. As there was unequal numbers of quadrats in the categories for each parameter the five seedling density scores around the median score were used for the analysis.

Results

Long term hydrograph and climate

On the Ord River over the, 1975 to, 1993 period large river flows have been confined to the wet season with 100% of discharges greater than 500 m$^3$/s occurring between November and March. Recorded flows have only occurred 3 times outside this period in June, 1978, May, 1979 and October, 1988 (Figure 2a). Magnitude of peak flows are highly variable with maximum discharges of >15000 m$^3$/s occurring 4 times over the, 19 year period with 4 years having a discharge <1000 m$^3$/s with only 375 m$^3$/s in, 1992. Average maximum discharge (± SE) for the period from November to March is 5565 m$^3$/s ± 1475 with January having the highest mean discharge and March the lowest. Rainfall is also confined to the wet season with 87% falling in this period with dry season falls of >10mm having occurred only 6 times in the, 19 year period. Rainfall magnitude is also very variable and there is a significant correlation between discharge and rainfall (r = 0.632, p = 0.01). A very close correlation would not be expected between discharge and rainfall as isolated intense rainfall events in other parts of the catchment may affect discharge at the site of the stream gauging station where data were collected.

In contrast, on the Blackwood River over a 37 year period maximum discharge consistently occurs in the winter in the wet part of the year between July and August. Peak flows are regular events each year occurring with the regular winter rains. The one exception
was an extremely large flood event in January, 1982 caused by a cyclonic feature drifting down from the tropics in to the south-west land division (Figure 2a). Maximum discharge levels are much smaller and less variable than those seen on the Ord River with a mean maximum discharge of 161 m$^3$/s ± 24.5. Even the exceptional event in January, 1982 with a peak flow of 1187 m$^3$/s is much smaller than average maximum discharge on the Ord River. Average monthly discharge shows a peak in July with river levels usually receding by September. Rainfall patterns in the lower Blackwood show a regular and distinct winter (June-August) maximum but with summer rainfall events of > 10 mm quite common (Figure 2b). There was a strong correlation between maximum discharge and rainfall for the Blackwood river ($r = 0.741, p = 0.01$) if the out-

Figure 2. Monthly river discharge and monthly rainfall data over a 18 year period for the (a) Ord River and the (b) Blackwood River.
lier event in January is removed. This is because the greatest amount of rainfall fell in the upper part of the catchment.

**Tree reproductive phenology**

Seasonal reproductive phenology for *Eucalyptus camaldulensis* and *Melaleuca leucadendra* on the Ord River and *E. rudis* and *M. rhaphiophylla* on the Blackwood River has been summarized for a 12 month period and compared with mean monthly river discharge (Figures 3a and b). For both *Eucalyptus* species seedfall appears to be timed to coincide with that period of the year when river water levels are receding. That is, March, April for *E. camaldulensis* and September to November for *E. rudis*. For *E. camaldulensis* flowering and seedfall occur in a single annual cycle with fruit maturing and releasing seed with little seed appearing to remain in the canopy. In contrast *E. rudis* flowers from August to November with fruit and seed...
developing over summer. Greatest seed release is not from these matured capsules until the following early summer period. Seed is therefore retained on the tree so that some seed may be released throughout the year with a peak in the early summer period.

A similar contrast is seen for the *Melaleuca* species with *M. leucadendra* on the Ord River releasing all its seed from February to April, the period after flowering and fruit development from August to January the previous year. *M. rhaphiophylla* on the Blackwood River flowers in September to November. Fruit development occurs over summer and autumn and the woody fruit and seed are retained on the plant for several years. Seed release appears to be opportunistic after the desiccation of the fruit.

**Seedling establishment**

In the Ord River seedling plots the majority had loam to sandy soils (Figure 4a). When seedling density was compared for the different soil types, numbers of seedlings/m² was significantly higher in loam, loamy sand and sandy soils than in the clay and gravel soil types (*H* = 15.87, *p* = 0.003). Frequency of plots was fairly similar for the different microtopography sites with slightly more plots occurring on the river flat area but analysis of seedling density showed that plots in depressions, slopes and rises had significantly more seedlings/m² (*H* = 13.28, *p* = 0.004). Moist and dry sites had the greatest frequency of seedling plots but waterlogged sites had significantly greater density of seedlings than the other moisture-related parameters (*H* = 9.74, *p* = 0.02). There was no significant correlation between seedling density and distance to nearest seed tree with a large group of plots in close proximity and another group at some distance (>200 m) from a seed tree. There was also no significant correlation between seedling density and litter or bare ground. Frequency of plots with 0–20% litter and 0–20% bare ground was much greater than the other cover classes (Figure 4b). There was a strong negative relationship between seedling density and elevation (*r* = 0.758, *p* = 0.001) with most seedlings occurring at lower elevations (Figure 5b). There was also a significant relationship between elevation and distance from the river (*r* = 0.815, *p* = 0.001).

**Size class distribution**

A profile diagram of an Ord river transect shows abundance of new (<1 year old) seedlings at the lower elevations on the river flats and an abundance of smaller size classes throughout the profile (Figure 6a). Frequency of larger size classes is greatest at the higher elevations and greater distance from the river, especially for *E. camaldulensis*. All *M. leucadendra* size classes tend to be at the lower elevations closer to the rivers edge. There was a significant correlation between diameter at breast height and elevation for both *E. camaldulensis* and *M. leucadendra* (Figure 7a and b). For *E. rudis* on the Blackwood River the profile diagram shows seedlings most abundant at the lower elevation near the river edge but large diameter trees are also most abundant at these lower elevations. Size classes were generally more evenly spread along the profile (Figure 6b). *M. rhaphiophylla* tends to be confined to areas close to the water which are regularly inundated. In this area there is a wide range of size classes. For both *E. rudis* and *M. rhaphiophylla* there was no significant relationship between size class and elevation (Figure 7c and d).
Figure 4. Percentage of $1 \times 1 \text{ m}$ seedling plots with particular environmental attributes for (a) the Ord River and (b) the Blackwood River.

**Discussion**

This study highlights the vastly different hydrological regimes of the Ord and Blackwood rivers despite similar rainfall and catchment size. This is mainly due to the different geology of the catchments (Department of Mines, 1972) and rainfall patterns. The Ord River catchment is subject to high intensity rainfall events mainly generated from sub-tropical monsoons. These are confined almost entirely to the wet season between October and March and contribute high levels of runoff into the river. The Blackwood River, although it has a strong winter (June–August) rainfall maximum, events are less intense and run-off not as high.

Fluvial processes on the Ord River are dominated by fairly frequent large high energy floods that...
Figure 5. Relationship between elevation from the river and number of seedlings in 1 m x 1 m plots for (a) the Ord River and (b) the Blackwood River.

are capable of destroying the existing riparian vegetation community and preventing the establishment of stable mature stands. This is evidenced by the existence of large mature trees on these river reaches only at high elevations, in protected river bends or far from the river where only extreme floods can reach. In the years between large flood events large stands of seedlings and saplings develop but these generally do not reach maturity before they are destroyed in the next large flood. Failure to reach later successional stage due to high frequency flood disturbance has been documented for New Zealand Podocarp forest (Duncan, 1993). In this way single catastrophic events change the ecosystem to an extent which is inconsistent with the theory of climax communities (George et al., 1992). These high magnitude wet season floods are, however, highly episodic and in the intervening years smaller floods allow the development of the existing trees and the recruitment of younger age classes. This regime of intermittent high frequency large disturbances prevents the establishment of stable states and in terms of the state and transition model the ecosystem is characterized by long periods of transition between short-lived stable states. This riparian ecosystem is thus driven by allogenic or physical processes rather than vegetation successional (autogenic) processes (Baker and Walford, 1995). In contrast, lower energy seasonal flooding on the Blackwood River allows mature stands of trees to develop throughout the river profile. Recruitment is continual although species can also respond to large flood events. This disturbance regime results in long periods of stable states with short periods of transition. Therefore the vegetation is subjected to longer periods of autogenic processes and because of lower frequency flooding disturbance, shorter periods of allogenic processes.
For both rivers the environmental conditions that appear to correlate with seedling establishment are similar, with most seedlings occurring in river sediment of larger particle size of sandy to loam soils. Seedlings are also more dense at lower elevations and in microtopographic sites where moisture is gaining and there is a slight rise. These rises are important for seedling establishment by creating a safe site to prevent waterlogging (Bren and Gibbs, 1986; Skoglund and Verwijst, 1989; Titus, 1990). This once again highlights the importance of fluvial processes in recruitment. Litter levels and areas of bare sediment do not appear to be important for establishment of seedlings. These elements may however become important for the successful initial establishment of germinating seed (Nilsson and Gunnell, 1990; Greenway, 1994; Johnson, 1994). Seedling plots on the Ord River can occur at large distances from mature trees and therefore from a source of seed. This may indicate that seed can be dispersed by flood waters. Observations of flood debris lines indicate that seed is being transported in this way as evidenced by the presence of numerous open fruit and newly germinated seed. Thus seed can be transported to areas which afford some protection from subsequent flooding. In fact, for the Ord River successful long term establishment to a stable state may require a period of no large floods. On the Blackwood River seedling density was closely related to distance to seed trees and no seedlings were found further than 30 m from a potential seed tree. For *E. camaldulensis* on the Murray River in south-eastern Australia a similar close association between seedlings and seed trees was found (Dexter et al., 1986). This suggests that seeds are generally dispersed by wind with little dispersal on floodwaters. Germination tests on seeds of *E. rudis* indicate that the seed germinate rapidly after wetting (1 to 2 days) so that they may not have time to be dispersed by water. Seed or fruit of *E. rudis* was not found in any debris samples. However, all species appear capable of responding to floods with large recruitment events but the mechanisms for doing so appear different. For example there was a large recruitment event of *E. rudis* after the unseasonal extreme flood in January, 1982. Roberts (1993) found a good correlation between recruitment and flood events, which replenish soil water for *E. coolibah* on a semi-arid ephemeral creek in eastern Australia.

Reproductive phenology of the four species studied also reflects their adaptation to their environment.
Maturation of flowers and seed takes place within a couple of months in many tropical eucalypts (Brooker and Kleinig, 1983; Eldridge et al., 1993) as opposed to more than two years in some southern eucalypts (Ashton, 1975). For _E. camaldulensis_, _M. leucodendra_ and _E. rudis_ the period of greatest seedfall is timed to coincide with receding floodwaters when moist sediments favorable for seed germination and survival are exposed. This adaptation has been reported for riparian species of _Populus_ and _Salix_ in the U.S. (Bradley and Smith, 1986; Johnson, 1994). Indeed phenological events in many species are thought to be timed to abiotic conditions (Estabrook et al., 1982). The Ord river species release the majority of their seed over a short period of time at the end of the wet season which provides their only opportunity for annual recruitment. Other northern Australian _Eucalyptus_ spp. have been reported to display a similar reproductive phenology (Bowman et al., 1991; Fensham, 1992; Setterfield and Williams, 1996). The small seed of these species do not survive long in the soil and therefore do not become incorporated into the soil seedbank (N. Pettit, unpublished data). Therefore post-dispersal conditions may limit recruitment and if subsequent conditions are not favorable the community will remain in transition. _E. rudis_ on the Blackwood River retains mature seed in the canopy for at least 12 months. Although there is a time of peak seed release, some seed is released all year round so that there is potential for germination of seed whenever conditions are favorable thus providing continuous recruitment into the stable community. For many temperate eucalypts seed maturation can take several months and seeds are retained in the capsules with a continuous low level of seed release occurring which is accelerated by dry conditions (Cunningham, 1957; Wellington and Noble, 1985; Davies and Myerscough, 1991). Interestingly, reproductive phenology of _E. camaldulensis_ occurring on the Murray River in south-eastern Australia is similar to that documented here for _E. rudis_ on the Blackwood River (Dexter et al., 1986). These rivers have similar fluvial regimes and climatic conditions. _M. rhaphiophylla_ retains mature fruit on the tree and appears to only release seed with the desiccation of the woody fruit. This can

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Figure 7. Relationship between tree size (diameter at breast height) and elevation from the river for the 4 selected riparian species on the Ord River (a & b) and the Blackwood River (c & d).
happen through disturbance such as flooding where branches are commonly broken off or during strong winds. This may result in the release of seed when conditions are most favorable for successful germination such as when flood waters are receding. Fire may also result in the release of seed (Proend et al., 1993).

These results highlight the very different fluvial regimes that exist on these two rivers and their effect on the vegetation dynamics for the overstory species. This is despite the species compared on the two rivers being functionally very similar. Management of the riparian vegetation should therefore take into account the frequency of change in the vegetation and that the disturbed states and long periods of transition between states are part of the natural process. This would suggest that altering the natural flow regimes, such as through river regulation will have significant effects on riparian vegetation dynamics. This is particularly so for the effects on long term recruitment in terms of reproductive phenology and seedling survival (Bren, 1992; Johnson, 1994). In the case of regulation on high disturbance rivers such as the Ord River, riparian vegetation dynamics may be significantly altered to long periods of stable states with much reduced transitions. This has important implications for the long term structure and functioning of these communities.

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References


