Eucalypt regeneration on the Lower Murray floodplain, South Australia

by

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ABSTRACT

Vegetation along the River Murray floodplains has been shown to be in a severe state of decline. This decline is amplified by the impositions of river regulation. In South Australia, where vegetation losses have been great, regeneration is limited and may result in not only individual tree losses but also widespread population decline. This study aimed to examine the relationship between river flows and the regeneration process in populations of *Eucalyptus camaldulensis* and *Eucalyptus largiflorens*.

The current structure of the populations was examined to determine if a viable number of varying age-classed trees were present. Tree surveys conducted at Banrock Station determined that while densities were low for both species, *E. camaldulensis* had a more sustainable population structure than *E. largiflorens*. Growth stages for both species illustrated highly clumped distribution, which is believed to correspond with river flooding magnitudes and frequencies.

To address the potential link between tree distribution and flooding within the River Murray, a hydrological analysis was conducted for Banrock Station using river flows at the South Australian border from 1900 to 2003. The amount of time growth stages for each species were inundated was found to be greatly reduced under regulated flows compared to natural flows. This has resulted in shifted localized regeneration patterns corresponding with *E. camaldulensis'* greater demand for inundation than *E. largiflorens*. Moderate magnitude flows have been most impacted by regulation, and consequently these are the very flows needed for floodplain tree population maintenance.

Flowering and seed fall for *E. camaldulensis* and *E. largiflorens* were monitored at Banrock Station for 22 months to identify losses in reproductive potential resulting from tree decline. While seed viability was not affected by vigour, trees with visually reduced vigour were found to produce less fruit and had reduced seed fall, as well as a reduced rate of fruit development.

Dendrochronological techniques were applied to floodplain trees. Age and size relationships could be established, implying that such techniques can be applied in South Australia to high quality sites. Growth responses within cohorts were similar and easily matched between individuals illustrating cyclic, but not necessarily seasonal correlations. This work verified the preferential selection of younger trees for dendroecological studies, and identified a relationship between on moderate flows and measurable girth expansion in both floodplain tree species.

DECLARATION OF ORIGINALITY

I certify that this thesis does not incorporate without acknowledgement any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

I consent to a copy of my thesis being available for loan and photocopy once deposited in the University Library.

Amy Kathryn George

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Chapter 1 Introduction

1.1 Introduction

Flooding plays a vital role in floodplain rivers (Sparks *et al.*, 1990), so that the ecological effects of regulation are likely to be profound (Junk *et al.*, 1989). This is particularly so in dry regions, where the disparity between natural and regulated regimes is most pronounced (e.g. Walker 1992). In general, the hydrological effects of regulation are indicated by the frequency, magnitude, duration and timing of floods, including in-channel and overbank flows, and by the rates of rise and fall of floods (e.g. Maheshwari *et al.*, 1995).

In the Murray-Darling Basin, south-eastern Australia, floodplain vegetation is degraded and dieback is widespread (MPPL, 1990; Webb and Nichols, 1997). About 30% (335,000 ha) of native vegetation has been lost in the past 200 years. Some 18,000 ha of ‘severely degraded’ vegetation have been identified, with 93% (16,726 ha) occurring along the River Murray (MPPL, 1990). The decline is evident in tree condition, and in the lack of regeneration (MPPL, 1990; Jolly and Walker, 1996).

Most of the degradation is occurring in river red gum and box (yellow, grey, black) woodlands. This is of particular concern in South Australia (MPPL, 1990), which has the lowest area (in hectares) of vegetation, but the most degradation. Regeneration is exceptionally poor compared to other States (MPPL, 1990). Clearly, if individual trees fail to reproduce, at a rate sufficient to compensate for dispersal, mortality, climatic variations and other factors, the population will decline. Regeneration includes flowering, seed set, seed dispersal, germination, seedling survival and establishment.

1.2 Significance

Regeneration is the natural process by which plant populations are maintained over time. With the expansion of river regulation (e.g. Petts, 1984) and its impacts on riparian trees, new trees are not surviving in sufficient numbers to replace older stands. Environmental flow programs attempt to reinstate natural ecological responses, but they generally are not designed to stimulate and maintain regeneration (e.g. Ward and Stanford, 1995; Petts, 1996; Hughes *et al.*, 2001). Although it is often supposed that a single flood event will be sufficient to reinstate natural responses, different stages of the regeneration process rely on different aspects of the natural flood regime. For trees, a single flood event may stimulate seed set, but another flood is necessary, 9 months later, for germination, and another is required one year later to maintain seedlings that are yet to develop sinker roots. For environmental flows to be effective, a programmed sequence of flows is required.

1.3 Research Aims

This thesis concerns the regeneration of river red gum (*Eucalyptus camaldulensis* Dehnh.) and black box (*Eucalyptus largiflorens* F. Muell.), the two dominant species of trees on the floodplain of the Lower River Murray, South Australia. The aims are to identify the impacts of reduced flooding on the regeneration process, and to investigate how these impacts affect growth, establishment and survival of the trees.

Each chapter will include comparisons between *E. largiflorens* and *E. camaldulensis* to elucidate the species specific role in the floodplain environment. For example, the species are differentiated by elevational preferences that may affect how each tree tolerates different stresses. *E. largiflorens*, typically located in more elevated areas, may be a poor competitor in flood-prone areas, and therefore only have advanced successional growth stages on outer edges of the floodplain. Conversely, *E. camaldulensis*, preferring areas frequently inundated may show greater numbers of individuals and cohorts in lower elevation areas. These comparisons offer insights into the nature of the processes underlying regeneration. One goal of this study is to provide information regarding the environmental flow requirements of riparian woodlands on the Murray.

1.4 Thesis Outline

Chapter 2 presents a review of the literature outlining the present condition of vegetation within the Murray-Darling Basin and the impacts on the system. The biology and ecology of red gum and black box trees are discussed with an emphasis on reproduction and regeneration. The final section of the literature review presents a conceptual model of the regeneration process for floodplain eucalypts. The model discusses regeneration stages throughout the tree life-cycle and potential limitations to each stage.

The current demography of floodplain eucalypts is examined in Chapter 3. While the demographic structure of populations does not directly limit regeneration, it indicates long-term sustainability. Demography is a balance between mortality and regeneration. Thus, knowledge of regeneration and population structure highlight the effects of reduced flooding. Structure incorporates the primary growth stages concentrating on regeneration stages VIII - X, described later (Section 2.4).

The association between flooding and tree growth stages suggested in Chapter 2 is further developed within Chapter 4. Trees depend on available moisture to induce germination and recruitment. The current distribution of floodplain trees could be used to identify flood magnitudes and frequencies necessary to promote regeneration, growth and survival. Information derived from flow hydrographs will be used to examine the relationship between various age classes or growth stages with flows occurring during the time of germination and establishment. Attempts will be made to extrapolate this information for application of environmental flows.

Regeneration cannot occur if seeds are unavailable, and seed availability begins with the parent trees. Chapter 5 addresses this issue by monitoring phenological processes in ‘healthy’ and ‘unhealthy’ trees. While tree health has been assessed on the floodplains, no correlations have been made between health and reproductive potential. If flowering and seed production are reduced in an unhealthy tree, there is less chance that trees will replace themselves or contribute to the long-term sustainability of the population.

Chapter 6 applies dendroecological techniques to floodplain trees. Ambiguities resulting from the demography study required a closer examination of the age/size relationship for floodplain trees. Tree ring analysis could also provide a quantitative measure of water requirements for active tree growth, thus providing a way of prescribing necessary flow allocations. Finally, Chapter 7 reiterates the conclusions from the previous chapters and summarises the primary findings.

Chapter 2 Literature Review

2.1 Introduction

Thirty percent of the world's land area is occupied by arid and semi-arid regions, characterised by irregular, generally low rainfall (Heathcote, 1983; Thomas, 1997). In these regions, water conservation mechanisms are a prerequisite for the survival of biota. Biodiversity may be considerably enhanced by floodplain rivers rising in adjacent, better-watered regions. For example, the River Murray in Australia is fed by winter precipitation in SE New South Wales and Victoria, but most of its 2560 km course is through semi-arid regions where rainfall is too sparse and erratic to sustain perennial streams (Walker, 1992). The composition and diversity of communities in the corridor formed by the Murray and its floodplain are distinct from those in surrounding regions (e.g. MPPL, 1990).

Floodplain rivers are also corridors for human industry. They have sustained irrigated agriculture in dryland regions since the beginning of recorded history (e.g. Petts, 1984), and today more than half of the global human population now lives in those regions (Thomas, 1997). Virtually all dryland rivers are exploited for irrigation; other forms of consumptive water use are small by comparison. In the Murray, more than 80% of annual water diversions are for agricultural use (Crabb, 1997). Technological advances in water distribution systems, land management and crop horticulture offer improved water use efficiency and less environmental impact, but their implementation is often undermined by short-term economic considerations (e.g. Davidson, 1969).

The environmental effects of irrigation and water diversions go beyond excessive water use. Aside from effects on groundwater, land and water salinisation, vegetation clearance, soil degradation and chemical use (e.g. Jolly, 1996), the most pervasive changes are those affecting the volume and pattern of river flows. Changes to in-channel and overbank flows are manifest in the frequency, magnitude, duration and timing of floods, and by the rates of rise and fall of floods (Maheshwari *et al.*, 1995). The magnitude of these changes is well recognized. For example, regulation affects nearly 77% of the total water discharged in the Northern Hemisphere (Dynesius and Nilsson, 1994). Such high levels of regulation have wide-ranging ecological effects on associated riparian species.

The ecological effects of flow regulation are most apparent in woody vegetation in floodplain wetlands and woodlands. The relationship between flow regulation and woody vegetation are well understood in North America, since severe population declines have prompted extensive research. For example, along the San Pedro River in the American south-west, reduced stream flows, lowered water tables and changed flood timing have generated conditions that favour exotic saltcedar (*Tamarix chinensis*) over native Fremont cottonwood (*Populus fremontii*) and willows (*Salix* spp.) (Stromberg, 1998). Consequently, in many areas tree diversity is shifting and saltcedar is replacing native forests. Similar conditions are found along the Milk River in southern Alberta and northern Montana. Downstream of the Fresno Dam, densities of plains cottonwood (*Populus deltoides* var. *occidentalis* Rydb.) are significantly reduced because of the reduction in flood magnitudes and frequencies resulting from the dam (Bradley and Smith, 1986). The impacts of regulation on groundwater are also illustrated. Stromberg *et al.* (1996) found that impacts of groundwater decline reduced not only tree establishment, but also cover of herbaceous species on floodplain terraces.

No fewer examples are found in other parts of the world. *Acacia* tree populations, below a dammed section of ephemeral streams, in Southern Negev, Israel were found to have mortality rates 2.3 times greater and regeneration rates 4.1 times lower than the unaltered streams (BenDavid-Novak and Schick, 1997). In floodplain forests of the Alsace Plain in France, species richness and diversity have both decreased as a result of extensive regulation along the Rhine River (Deiller *et al.*, 2001). River regulatory structures have isolated the floodplain forests and allowed for the introduction of flood-intolerant species and reduced regeneration.

Each of these studies, and others (e.g. Rood and Mahoney, 1990; Cordes *et al.*, 1997; Hampe and Arroyo, 2002; Rooney *et al.*, 2002), examined the effects of altered flows on trees and the regeneration process. All of these studies found a correlation between altered flows and tree loss as well as disruption to regeneration and establishment. Here, the term ‘regeneration’ is intended to include flowering, seed set, seed dispersal, germination, seedling survival and establishment. It thereby extends beyond the traditional botanical concept of *recruitment*, referring to establishment of a seedling from a seed (Harper, 1977).

In Australia, similar studies have been conducted in Western Australia. The relationship between flows and riparian vegetation was described for the Blackwood River in south-western Australia and the Ord River in north-western Australia. Different from the North American studies, Pettit *et al.* (2001) found that along the Blackwood River, flooding did not influence tree seedling germination, but size class of tree species increased with flooding. Along the Ord River there was no relationship between flooding and seedling establishment, but tree size class decreased with flooding. Further, Pettit and Froend (2001) examined aspects of reproduction in riparian vegetation along these two rivers and found that dispersal and successful germination were enhanced by flows. These studies illustrate that the processes driving regeneration and population dynamics in the Northern Hemisphere may not be wholly validated in Australia.

An early study, focused on regeneration of *Eucalyptus salmonophloia*, illustrated that regeneration in fragmented forests of Western Australia was driven by landscape-scale disturbances of fire, flood, or storm (Yates *et al.*, 1994b). The study emphasized the difficulties of identifying processes contributing to long-term persistence of natural ecosystems within highly fragmented landscapes such as is found throughout Australia. Continuing work was targeted at identifying particular factors limiting recruitment (Yates *et al.*, 1994a; Yates *et al.*, 1995; Yates *et al.*, 1996). The studies indicated that neither the availability of seed nor unfavourable germination conditions was limiting recruitment (Yates *et al.*, 1994a; Yates *et al.*, 1996). The authors determined that recruitment was likely limited by both the absence of a soil seed bank resulting from short-term seed viability and seed predation by ants (Yates *et al.*, 1995). The largest limitation in fragmented forests was speculated to be changes in resources available following disturbance (Yates *et al.*, 1996).

Along the Murray River, the processes associated with regeneration of woody species are surprisingly less understood. Studies of regeneration along the Murray have been limited to forested areas along the middle reaches of the Murray. Dexter (1967, 1970) first examined regeneration of *Eucalyptus camaldulensis* in the Barmah State Forest. He determined that seedling establishment occurred mainly at sites that were disturbed, bare, or burnt. Lack of flooding was indicated as a possible limitation to regeneration in this area. This study prompted extensive work into the flooding requirements of forest eucalypts and the impacts of regulation on flooding. Bren and Gibbs (1986) determined that vegetation type and site quality were both statistically dependent on flood frequency, suggesting that changes in flood frequency may be reflected in vegetation distribution and community composition. Studies continued to examine the duration of inundation (Bren, 1987) and flow characteristics necessary for red gum forests (Bren, 1988b; Bren *et al.*, 1988; Bren, 1991).

The eucalypt forests of the middle Murray, however, are unlike the woodlands on the Murray floodplain in South Australia (see Section 2.3). The eucalypt forests have trees greater than 20 m in height and exhibit canopy closure from overlapping tree cover (exceeding 30%), while woodland trees of South Australia rarely extend beyond 20 m in height and characteristically have canopy cover less than 30% (Brooker and Kleinig, 1999). Further, the studies along the middle Murray have focused on frequency and duration evaluation relative to entire populations without relating the flooding requirements to various life or growth stages.

While the same general effects of reduced regeneration and population decline have been observed in South Australia (MPPL, 1990), diagnoses are based upon fragmentary observations concentrating not on the effects of altered flows, but on water use patterns and salinity effects (e.g. Mensforth *et al.*, 1994; Overton *et al.*, 1995; GR Walker *et al.*, 1996 and papers therein). These fragmentary observations also rely on *mature* woody vegetation, failing to mention or address younger growth stages. The status of mature trees, however, may not reliably indicate the status of populations. If individuals fail to reproduce themselves at a rate sufficient to compensate for dispersal, mortality, climatic variations and other factors, the population will decline.

This review concerns present knowledge of floodplain vegetation on the River Murray, particularly the 830-km tract below the Darling junction ('the Lower Murray'). It describes the Murray-Darling Basin environment and the physiological and ecological nature of the riparian vegetation, and outlines historical changes related to land clearance, flow regulation and salinisation. This information is assembled as a conceptual model that identifies the stages in regeneration and the key environmental modifiers impacting the transition between stages. The model is a framework for development of research questions, including those addressed in subsequent chapters. These include potential applications of Geographic Information Systems and the concepts of landscape ecology to the vegetation of the Lower Murray. The model also proposes a scheme to evaluate the long-term 'health' of eucalypt stands by incorporating the role of regeneration in sustaining populations.

2.2 The Murray-Darling Basin

2.2.1 General description

The Murray-Darling Basin extends over 1.073 million km^2, from latitude 24-37^{o}S and longitude 138-151^{o}E (Figure 2-1), with climates that range from subtropical in the north, cool and humid in the east, temperate in the south to dry and hot inland (Walker, 1992). Annual rainfall patterns vary accordingly, from <300 to 1400 mm. Annual rainfall is highly variable and generally less than evaporation.

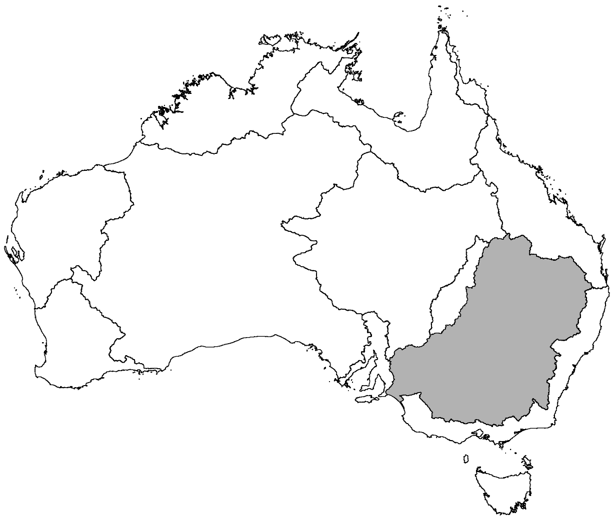

Figure 2-1 Australian drainage basins with the Murray-Darling Basin in grey.

The Murray-Darling Basin began forming over 50 million years ago by a gradual subsidence of the original land surface (Davis, 1978). Since its formation, the sea has frequently inundated large parts of the basin, leaving deposits of limestone and sands. After the sea retreated, a large lake covered parts of the basin (Rutherfurd, 1990) depositing clays and silts over the remaining marine sediments. The basin now consists of largely flat plains which hold Quaternary and Tertiary sediments on a hard impervious rock base from the Palaeozoic Age.

The Murray is the principal river, extending 2560 km westward from its source in the Snowy Mountains near Mount Kosciusko (2251 m ASL), New South Wales, to the sea near Goolwa, South Australia. It is joined by the Darling at Wentworth, New South Wales, 830 river km from the mouth. It is a low-gradient river, with an average bed slope of only 1-5 cm km^{-1} in South Australia (Walker and Thoms 1993). The river provides water for 16 cities and more than 40% of the water resources for South Australia.

The river travels through five distinct regions (Mackay, 1990). The Headwaters stretch for 450 river kilometres (rv km) providing water mostly from snowmelt in the Snowy Mountains. The Riverine Plains have shallow branching channels across 800 rv km of flat plains. The wider plains of marine origins comprise the Mallee Trench, providing another 850 rv km with a single well-defined channel. The Trench is followed by the Mallee Gorge (280 rv km), where steep cliffs result from the river cutting through limestone. Within the Lakes and Coorong Region, the Murray empties into Lakes Alexandrina and Albert before entering the Coorong where salt water from the Southern Ocean mixes with fresh river water.

The Lower Murray is the area below the Murray-Darling junction. It is a separate and unique region (Walker, 1992; Crabb, 1997) with a semi-arid climate, high evaporation and low rainfall. Because of the component marine sediments of the Mallee Trench, soils of the Lower Murray are more naturally saline than in other areas of the basin.

2.2.2 Hydrology

Runoff in the Murray-Darling basin is low by global standards (McMahon *et al.*, 1992). The mean annual runoff is 14 mm, and only about 3% of the average annual rainfall (Walker, 1992). Most runoff originates from the upper reaches of the Murray, from rainfall and snow, and decreases as the river flows westward. The middle reaches of the Murray are supplemented by flows from the Ovens, Goulburn and Murrumbidgee rivers, but the Lower Murray, below the Darling River junction, has no significant tributaries. Flows from the Darling are unreliable because they are fed by erratic summer monsoonal rains that contribute only 10-12% to the long-term mean annual discharge of the basin (10,090 GL in 1894 – 1993) (Walker, 1986; Walker, 1992; Walker *et al.*, 1995).

2.2.2.1 Natural flow regime

Comparisons of natural and regulated flows are facilitated by the Monthly Simulation Model developed by the Murray-Darling Basin Commission (MDBC, 2002). The model incorporates historical tributary flows, rainfall, evaporation and transpiration losses, diversions, river channel losses and regulations for storage and water sharing (Maheshwari *et al.*, 1995) to examine changes in the flow regime.

Under natural flow conditions (1894 – 1993), average annual flows varied between 4750 GL at Albury to approximately 13,000 GL in the lower reaches (Maheshwari *et al.*, 1995). Annual flows (1930 – 1991) would have been 2500 – 20,000 GL 95% of the time (Thomson, 1992). Flows were erratic and highly variable. In the upper reaches, variability was lowest during September, with variability in the lower reaches lowest one month later in October. Flows peaked in spring quickly reducing and remaining at the lowest levels during late summer and autumn (Close, 1990). Flow magnitudes of 1000 GL month^{-1} occurred during 45% of months and slightly higher magnitudes (1500 GL month^{-1}) only decreased to 25% of months (Close, 1990).

On a few occasions, under natural conditions, flows ceased as in 1915, but there was generally some flow that continued to the mouth of the river, keeping Lake Alexandrina fresh (Close, 1990). Low flows decreased downstream, but the duration of low flows was similar along the length of the river (Maheshwari *et al.*, 1995). Low flows (<5000 GL) occurred approximately 7% of the time during 1930 – 1991 (Thomson, 1992). The duration of low flows was also relatively short, thus when low flows occurred they did not remain low for extensive periods (Maheshwari *et al.*, 1995).

2.2.2.2 Regulated flow regime

The erratic and variable flows encouraged intensive flow regulation. River regulatory structures were proposed to meet two purposes. Large storages were intended to provide water during drought or low flow periods, whilst locks and weirs were designed to supply water for irrigation and to ensure that the Murray was permanently navigable (Jacobs, 1990). Following a century of development, the River Murray and its tributaries now hold an extensive system of regulatory structures including, for example, 13 locks and weirs, 5 barrages, and more than 100 dams. The Murray-Darling Basin Commission manages flows in the system and allocates water to four states including Queensland, New South Wales, Victoria, and South Australia (Jacobs, 1990).

Intensive regulation has resulted in alteration of the spatial and temporal patterns of flow as well as the duration, timing, frequency, magnitude, and rate of recession of floods (Davies *et al.*, 1994). Substantial changes in monthly and annual average flows and flow variability are consistent with the altered conditions (Maheshwari *et al.*, 1995; Walker, 2000). In 1994, flows at the mouth of the river were only 21% of the natural flow and the natural median flow is now only exceeded 8% of the time (Walker, 2000). Flow duration is similar along the length of the river, but has generally decreased with regulation, as illustrated by the steep recession limb of current flood hydrographs (Jolly, 1996).

Extreme flow characteristics have also been affected by development and regulation. The largest impact is seen on the frequency of mid-range flows (exceeded 20-80% of the time) (Maheshwari *et al.*, 1995; Walker, 2000). Flows of 1000 GL/month or more are only expected in 15% of months compared to the 45% of months under natural flows (Close, 1990). Further, the expected frequency of flows in excess of 1500/GL month has been decreased from 25% to 5% of months. Average annual floods have been reduced by over 50%, and low flows are generally more frequent under regulated condition (Maheshwari *et al.*, 1995).

2.2.2.3 Hydrological characteristics of the Lower Murray

The Lower Murray is hydrologically distinctive because this section of the river receives no significant tributaries other than the Darling River, flowing from the northern regions of the Basin (Walker and Thoms, 1993). The Darling's contribution is generally low and does little to increase flow magnitudes in the Murray. Peak flows in the Darling occur during summer when flows in the Murray are lowest, thus flows do not supplement existing flows but simply maintain flows at capacities similar to regulation stages. The Lower Murray is more turbid than upstream sections primarily because of the inputs from the Darling River. The Darling carries high levels of suspended sediments that are carried through the lower reaches after the confluence of the two rivers.

Despite having no large storages on the Lower Murray, this region is characterized by a series of ten locks and weirs constructed between 1922 and 1935 (Walker and Thoms, 1993). Where once extreme levels of high and low flows were common, now a series of pools maintained at near bank full capacity prevail (Maheshwari *et al.*, 1995; Walker, 2000), and the river banks are breached only during large flood events (Close, 1990). The locks and weirs augment the effects from upstream storages and maintain the river as a series of pools. Such regulatory structures have contributed to the altered flows in the Lower Murray as well as to changes in channel and floodplain conditions. Problems of channel erosion, sediment deposition from the weirs, vegetation decline, and salinisation are common in this section (Maheshwari *et al.*, 1995).

2.2.3 Salinisation

The Lower Murray Basin has naturally saline soils and groundwater as a result of marine incursions during the Tertiary Period (Mackay, 1990). Irrigation, weirs, and vegetation clearance have altered the hydrological balance and increased the quantity and rate of accession of salt to the river and floodplain by raising the level of groundwater (Jolly, 1996), resulting in dryland salinity in non-irrigated areas and salinisation in irrigated regions. Rising groundwater levels force water into the upper soil profile dissolving stored salts and concentrating salts from the water as evaporation occurs. The chemical and physical properties of saline soils may also degrade as sodium ions react with clay particles producing sodic soils. Sodic soils become compacted and salts cannot be flushed from the profile (Grieve, 1987). The concentration of salts is further accentuated by the reduction in dilution flows that, under natural flow conditions, kept river salinity in check (MDBC, 1995; GR Walker *et al.*, 1996). Salinity increases, such as the magnitude found in the Chowilla floodplain of South Australia, have severe effects on riparian vegetation (e.g. Jolly *et al.*, 1993; Sun and Dickinson, 1995; Slavich *et al.*, 1999a; Slavich *et al.*, 1999b). Physiological dynamics can be limited by salinity. Munns and Termaat (1986) determined that long-term responses to increased salinity included limited leaf expansion in developing leaves and water deficits in mature leaves. Both of these lower the photosynthetic area, resulting in decline since plants are unable to produce sufficient amounts of carbohydrate to support growth. Water uptake can also be greatly impacted under saline conditions. Saline conditions at Monoman Island resulted in limited water uptake in *E. largiflorens* and restricted the trees from using saline groundwater when surface water was unavailable (Streeter *et al.*, 1996).

2.2.4 Impact of flow regulation on vegetation

In 1990, a perceived decline in the health of floodplain vegetation prompted a survey of the Murray-Darling Basin to assess the status of the riverine vegetation and the range of anthropogenic impacts (MPPL, 1990). The study area was divided into eight regions following regional descriptions from Pressey (1986) (Figure 2-2). The sections are delineated by hydrologic, geomorphic and climatic differences.

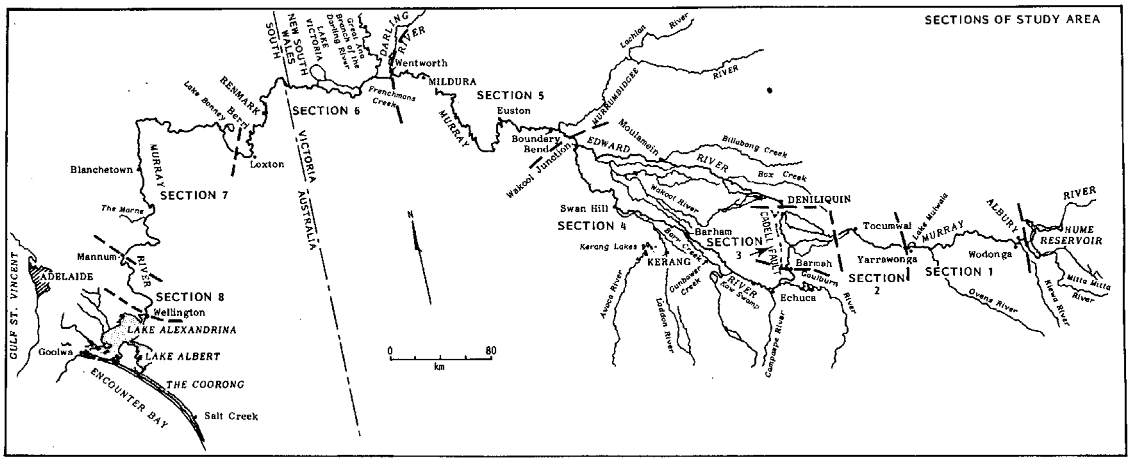

Figure 2-2 Floodplain of the River Murray and its tributaries from below Hume Dam to the upper end of Lake Alexandrina (From MPPL 1990). The sections follow Pressey (1986) and are based on differences in hydrology, geomorphology, and climate, which result in variation in vegetation communities.

The Murray-Darling Basin has been extensively altered from its pre-European state. Agriculture is the dominant economic activity. Crops and grazing supply 41% of the nation's gross agricultural production, with 82% of the total area of the basin used for grazing and 4.4% for crops (Garmen, 1983 cited in Crabb, 1997). Such high intensity agriculture has resulted in a 30% (335,000 ha) loss of native vegetation, mostly in riparian areas, over the last 200 years (MPPL, 1990). A survey, conducted by (MPPL, 1990), identified some 18,000 ha of 'severely degraded' vegetation throughout the basin, with 93% (16,726 ha) along the River Murray. A general pattern of decline in tree condition was evident (MPPL, 1990; Jolly, 1996).

Impacts related to river regulation were implicated as the overall cause of declining vegetation (Table 2-1), with salt identified as the largest single factor. The largest degraded areas were the red gum and box woodlands along the river. Forty-two percent (6947 ha) of the degraded sites were in red gum forests and woodlands, with 27% (4508 ha) in box woodlands (yellow, grey, and black) (MPPL, 1990).

Table 2-1 Factors affecting vegetation condition by area and percent of impact along the River Murray (after MPPL 1990).

Factors	Area (ha)	Percent of area Impacted
Salt	8783	52.5%
Drowning/Waterlogging	3207	19.2%
Drowned	2956	17.7%
Water stress	1038	6.2%
Grazing	277	1.7%
Fire	9	0.1%
Clearing	314	1.9%
Recreation	35	0.2%
Unexplained	107	0.6%
Total	**16726**	

The MPPL survey further identified that for the total area of the Murray-Darling Basin approximately 17.1% of the river red gum woodlands were in *severe* decline. The red gum woodlands in the Mildura and Renmark/Loxton irrigation areas of Section 6, as well as the black box woodlands in Section 5 were most affected. Additionally, the Mallee form of black box (*E. largiflorens*) was particularly degraded in the lower reaches of the basin (Figure 2-2) (MPPL, 1990). These affected areas are within, or in close proximity to, South Australia, suggesting that South Australia, with the lowest total area of vegetation but the greatest area of degradation (Table 2-2), should be especially concerned.

Table 2-2 Total area of vegetation (ha) by state, compared with the total area of degraded vegetation from (MPPL 1990).

State	Area of vegetation class	Area of degraded vegetation
South Australia	255,346	6544
New South Wales	648,762	4796
Victoria	405,660	5386

Regeneration was poorest in South Australia (MPPL, 1990), where only 60 regenerates ha^{-1} were found in 13 (400-m^2) plots, compared to 750 ha^{-1} in seven plots in other States. While these data suggest that stand survival may be prejudiced, especially in South Australia, the conclusions are open to challenge. The MPPL study was a preliminary survey, and the use of aerial photographs only allowed for the delineation of vegetation patches or communities (a ground survey was not considered practical). It is impossible to assess the extent of regeneration using aerial photographs, because the scale of the photograph will not reveal the earliest growth stages. Therefore, the conclusions are based on incomplete data that did not fully incorporate various regeneration stages. Furthermore, extrapolating from a limited number of field sites for regeneration counts provides unequal scales of comparison for the extent of vegetation on aerial photographs. The field site counts also included only seedlings and saplings, excluding other stages of regeneration that could provide valuable information regarding stand dynamics.

Despite the limitations of these data, correlations were apparent between regeneration patches and the health status of the surrounding vegetation. Thus, regeneration is reduced in areas where vegetation is in decline or severely degraded. This implies that there may be a problem of stand survival and long-term sustainability.

Bren (1991) demonstrated that changes in river hydrology have affected the growth and regeneration of river red gum forests along the middle Murray, supporting the (MPPL, 1990) survey. Yet, studies determining which factors promote recruitment in South Australia still have not been initiated. The majority of research in the lower Murray has focused on tree water use and salinity impacts (e.g. Eldridge, 1991; Eldridge *et al.*, 1993; Webb and Nichols, 1997; Slavich *et al.*, 1999b). While salinity impacts have been shown to cause dieback and tree death (Roberts and Marston, 2000), disruption to regeneration and recruitment patterns and processes, which may result from these impacts, remains unrecognised.

Further studies, using Geographic Information Systems (GIS) and landscape ecology, of the health status of riparian trees along the lower River Murray were initiated from the original

MPPL vegetation survey. Landscape ecology studies the effects of such large-scale disturbances on ecosystems as drought or flooding on forest and woodland dynamics (Yates *et al.*, 1994b). It interprets spatial and temporal patterns to better understand ecological processes across large areas.

For the Lower River Murray, GIS databases have been developed primarily for the evaluation of floodplain tree health (e.g. Hodgson, 1993; Taylor, 1993; Overton *et al.*, 1994a; MDBC, 1995; Taylor *et al.*, 1996). The first of such databases was created for Chowilla floodplain and provided useful information for evaluating the status of the floodplain vegetation in relation to the salinity and groundwater problems on the floodplain (Hodgson, 1993; Taylor, 1993). The GIS was further used to model the vegetation health in response to such conditions as saline soil and groundwater (Taylor *et al.*, 1996), as well as examining the effects of potential management procedures such as flow management for the Chowilla floodplain (Overton *et al.*, 1994b).

Local Action Planning (LAP) Groups for the Renmark to Border and the Loxton to Bookpurnong reaches of the river in South Australia have also created GIS vegetation surveys for vegetation health (PPK Environment & Infrastructure Pty Ltd., 1997; AGC Woodward-Clyde Pty Limited, 1999; Australian Water Environments, 2000). Each of these surveys examines historical changes in vegetation communities by field reconnaissance to identify vegetation communities present on the most recent aerial photography. The vegetation was then classified for community structure on aerial photographs from 1945, 1972, and 1996. An important use of GIS, as presented by the LAP vegetation reports, coupled with groundwater modelling is the assessment of potential management schemes on vegetation health. The LAP groups used the GIS data in just this manner to conclude that continued irrigation within these districts under the current management scheme will result in further declines in vegetation.

One of the primary limitations to the existing data is that they only partially evaluate the status of riparian vegetation regeneration. Since mapping of regeneration was not the primary objective, information concerning regeneration was limited to areas where significant regeneration was occurring and the health of the regeneration could be clearly established using the same techniques applied to the mature stands of trees. Expansion of the existing GIS data to include more detailed information on tree regeneration could provide a better understanding of long-term population effects of altered flow regimes.

2.3 Eucalypts

Woodlands are characterized by widely-spaced trees with foliage cover of less than 30% (Roberts and Marston, 2000; Yates and Hobbs, 2000). In floodplain environments, few species are present, and are distinguished by differences in elevation or soil types. Along the Lower Murray floodplain, the River Red Gum (*Eucalyptus camaldulensis*) and Black Box or River Box (*E. largiflorens*) are co-dominants.

2.3.1 Taxonomy

River red gum and black box are members of the Myrtaceae, which includes over 3000 species in about 155 genera (Turnbull and Doran, 1987). Members of this family have simple, entire leaves that are firm and leathery and dotted with glands containing aromatic oil. An operculum covers the floral buds, and the lack of petals distinguishes eucalypts (subfamily Leptospermoideae, genus *Eucalyptus*) from other Myrtaceae. Both species are members of the subgenus *Symphyomyrtus*, but separate at the Section level. Black box taxonomic classification derives from distribution and flower characteristics, while red gum taxonomy relates to fruit and leaves (Table 2-3) The taxonomic name for red gum (*E. camaldulensis*) comes from Camaldoli in Italy where the type material was grown (Nicolle, 1997). The name for black box (*E. largiflorens*) relates to the flower structures and means ‘abundant flowers’.

Table 2-3 Taxonomy of red gum and black box trees (Nicolle, 1997; Brooker and Kleinig, 1999).

E. camaldulensis		***E. largiflorens***	
Subgenus *Symphyomyrtus*		Subgenus *Symphyomyrtus*	
Section *Exsertaria*	Exserted valves on fruit	Section *Adnataria*	Adnate anthers
Series *Exsertae*	Seedling leaves lanceolate	Subsection *Apicales*	Erect anthers
		Series *Buxeales*	Eastern and Southern distribution
		Subseries *Amissae*	Outer operculum lost early
		Subraspecies *Opacae*	Dull leaves

2.3.2 Distribution

River red gum is one of the most widespread tree species in Australia (Roberts and Marston, 2000), and is found in all mainland states (Figure 2-3) (Pryor, 1976), covering approximately 196,900 ha along the River Murray (MPPL, 1990). It grows extensively on grey, heavy clay soils, but may occur on sandier soils when associated with black box. Red gums generally grow as ribbon stands along riverbanks and on low-lying areas subject to frequent flooding (MPPL, 1990; Cunningham *et al.*, 1992), but can extend over areas of regularly flooded flats across a wide range of flood conditions even within a single floodplain (Roberts and Marston, 2000).

Black box has a more limited distribution, but occurs throughout Queensland, Victoria, New South Wales, and South Australia (Figure 2-3) (Pryor, 1981). Like red gum, it grows on heavy clay soils, but along more elevated positions of the floodplain which may be only periodically flooded (MPPL, 1990; Cunningham *et al.*, 1992) They tend to grow in monospecific stands, but often grow in association with red gum when there are variable elevations (Cunningham *et al.*, 1992).

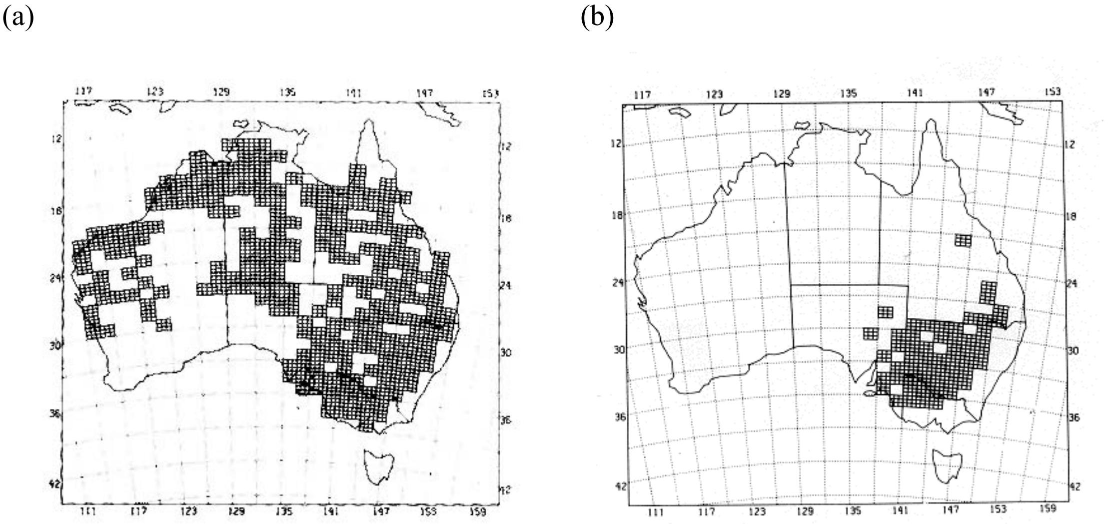

Figure 2-3 Distribution of (a) river red gum (*Eucalyptus camaldulensis*) and (b) black box (*E. largiflorens*) in Australia (From (Chippendale and Wolf, 1981).

2.3.3 Phenology

Phenological processes (season, timing, duration, and intensity of flowering and fruiting) underpin the reproductive success of eucalypts (House, 1997). Few studies have directly compared species, but information can be collected that may examine co-occurring species. Such studies are found for red gum and black box which identify the similarities and differences between the two species. This study is mostly concerned with the timing and extent of the events and their coincidence with abiotic environmental conditions that promote reproductive success.

Flowering in red gum and black box is regulated not by seasonal conditions within the year but rather on environmental conditions from previous years. For red gums, flowering occurs in most years from late spring to mid-summer (Dexter, 1967) particularly December to February (Boland *et al.*, 1981), generally following flooding (Roberts and Marston, 2000). Characteristic with the variability of semi-arid regions, the intensity of flowering varies widely and unpredictably (Dexter, 1978). Flowering in red gum does not occur every year and mast, or prolific production occurs approximately every 2 years (Cunningham *et al.*, 1992). Yet, heavy flowering does not imply a heavy seed crop. Dexter (1967) found that a heavy flowering period was often followed by a light or negligible seed crop primarily because approximately 45% of flowers failed to mature (Dexter 1978).

Flowering in black box reportedly occurs primarily between August and January (Boland *et al.*, 1981) and references therein), similar to red gum. Yet, flowering of black box on Chowilla floodplain in South Australia, may occur from May to October (Roberts unpublished data in (Roberts and Marston, 2000). This places the peak flowering time in South Australia between the northern Australia flowering and western regions, yet this has not been studied in any detail. Also similar to red gum, black box produce abundant flowers (Cunningham *et al.*, 1992), but studies of flower yield in relation to environmental conditions are lacking.

Eucalypts produce large numbers of small seeds that are shed from the capsule in a mixture of viable seed and chaff (unfertilised ovules and ovulodes) (Turnbull and Doran, 1987). The mean number of viable seed per 10 grams for red gum is 6052 (SD±2727) and for black box 4952 (SD±0) (Gunn, 2001). Many eucalypts shed their seed within months of maturity, but others retain it for two or more years, building a large store of seed within the crown. This store is thought to counteract the year-to-year variations in seed set and ensure that some seed will be available for regeneration following disturbance at any time.

Seeds are freely produced in red gums (Cunningham *et al.*, 1992). As with most eucalypts, seeds are retained on the tree in capsules until conditions for seed fall occur (Dexter, 1967). Seeds shed naturally throughout the year beginning nine months after flowering ends (Dexter, 1967; Dexter, 1978). Red gum peak seed dissemination occurs in spring and early summer when water is readily available from winter floods (Dexter *et al.*, 1986), with the lowest dissemination during winter (Dexter, 1978). From this pattern, Dexter (1967, 1970) concluded the extreme summer temperatures and the recession of winter floods triggered seed fall. Seed disperses laterally at a distance equal in height to the tree (Boomsma, 1950) with few seeds travelling a greater distance than twice the height of the tree (Cremer, 1977).

Data for black box seed are more limited, reflecting the lower commercial value of the species. While red gum are grown in plantations for commercial use, the principal commercial value of black box is as fence posts and firewood, due to the short growth form (Beadle, 1981; Cunningham *et al.*, 1992). Seed matures only a few months after flowering, unlike that of red gum, and is best harvested between February and April (Boland *et al.*, 1981). The duration of seed fall and factors inducing seed fall are not known.

2.3.4 Reproductive biology

Reproduction in eucalypts is initiated by the presence of an inflorescence (flowers arranged on a stem) (Turnbull and Doran, 1987). Following pollination and seed maturation, seed is dispersed. Turnbull and Doran (1987) cite wind as the primary agent of seed dispersal in eucalypts, with most seed spread in the direction of prevailing local winds. While wind may play a conclusive role in dispersal for many eucalypts, hydrochory (dispersal by water) may be more important for trees intimately associated with rivers and floodplains, such as red gum and black box. Seedlings of red gum and black box are often found in litter deposited at the maximum extent of a flood (Roberts and Marston, 2000). Flooding also stimulates regeneration in red gum by providing the appropriate microsite variables and water for promoting germination and establishment (e.g. Dexter, 1967; Dexter, 1978).

While germination generally follows flooding, flooding alone is not sufficient. Viable eucalypt seeds lack endosperm and must be sustained by the photosynthetic cotyledons that emerge from the soil (Turnbull and Doran, 1987). Therefore, for regeneration to be prompted, it is essential that the requirements of moisture, warm temperature, oxygen and light be met. For red gum and black box trees flooding is the primary source of moisture for germination, but germination may occur following excessive rainfall. Extreme summer temperatures and the recession of winter floods during spring provide the most beneficial conditions for seed germination in red gums (Dexter, 1967; Dexter, 1978). Early germination studies found that both river red gums and black box germinated best at an optimum temperature of 35^{o}C (Grose and Zimmer, 1958), but germination can also be prompted at 30^{o}C (Turnbull and Doran, 1987). Unlike many other eucalypts, light is also required for successful germination, with the role of light becoming more important as the temperature departs from the optimum (unpubl. data cited in Grose and Zimmer (1957).

2.3.5 Physiological ecology

As with other dryland species, river red gums and black box have wide tolerances. They have the ability to switch between different water sources, and to use water of varying quality (Mensforth *et al.*, 1994; Thorburn and Walker, 1994; Slavich *et al.*, 1999b; Roberts and Marston, 2000). Red gums have survived dry conditions for approximately 18 months as in the 1982 drought (Roberts and Marston, 2000). Bren *et al*. (1987) indicate that this is not unusual and has occurred four times over the last century, in 1904, 1915, 1944, and 1967. Red gums minimise the effects of drought by having sinker roots that penetrate greater than 10 meters (Bacon *et al.*, 1993), and shedding leaves during dry conditions (Roberts and Marston, 2000). There are no fewer examples of flooding tolerance in red gums and black box (see Dexter, 1967; Dexter, 1970; Sena Gomes and Kozlowski, 1980; Heinrich, 1990; McEvoy, 1992). *Eucalyptus camaldulensis* seedlings in the Barmah Forest survived 6-7 weeks of flooding during winter/spring without damage (Dexter, 1970). Seedlings from 1-60 cm in height exposed to 12 weeks of partial submergence followed by 2 weeks fully submerged also survived with the only response being shedding of lower leaves. In a related study, Heinrich (1990) examined growth and water relations of *E. camaldulensis* and *E. largiflorens* seedlings from the Barmah Forest. In response to flooding, *E. camaldulensis* seedlings modified their physiology by producing aerenchymatous root and stem tissue, which reduced water stress. Seedlings of *E. largiflorens* did not alter their physiology and consequently were more susceptible to water stress from flooding. This study conclusively illustrated that black box tend to be less tolerant of flooding but more tolerant of dry conditions than red gum (Roberts and Marston, 2000). This supports the findings of Dexter (1970) that topographic positions during flooding could impact mortality and stem damage (*i.e.* lower topographic positions were flooded for longer periods and by deeper water, thus for plants to survive they must be predisposed to these conditions).

2.4 Conceptual model

To better understand the direct limitations to regeneration, there is a need to identify stages in the regeneration process that may be impacted by the current altered flood regimes found in the Murray. Table 2-4 shows the key stages of regeneration. While the timing and frequency of stages may differ between species, it is presumed that the processes and limitations are similar given the co-dominance of red gum and black box on the river floodplains.

Table 2-4 Theoretical regeneration process from parent to mature offspring for both eucalypt species.

Growth Stage	Regeneration Stage	Characteristics of stage	Duration	Potential limitations to stage
Parent Tree	I	Flowering	4 months	Reduction in tree health; Reduced pollination
	II	Seed storage in the tree canopy	1-2 years	Excessive temperatures; Poor tree health;
	III	Seed fall	Year round	Reduced flood regime
	IV	Seed dispersal	Year round by wind; Coinciding with flooding	Ant predation; Reduced flood regime
Seedling	V	Germination	Year round with rainfall and flooding	Moisture stress; Reduced flood duration; Extreme temperatures; Limited nutrients; Soil salinization; Resource competition
	VI	Sinker root establishment of seedlings	2 years at a good site	Soil salinization; Soil compaction; Moisture stress; Root competition; Grazing
	VII	Growth of seedlings	3-4 years of vigorous height growth of a main stem	Nutrient limitations; Moisture stress; Soil salinization; Root competition; Grazing
Sapling	VIII	Growth form development of saplings	Dependent on site quality, perhaps 3-4 years	Soil and groundwater salinization; Limited nutrients; Moisture stress; Tree competition; Insect damage
Pole Stage	IX	Maturation of pole trees	Dependent on site quality	Moisture stress; Soil and groundwater salinization; Limited nutrients; Insect damage
Mature Tree	X	Reproductive maturation of adult trees	Decades to centuries	Moisture stress; Soil and groundwater salinization; Limited nutrients; Insect damage

Primary floods stimulate the earliest stages (I-V). Firstly, the flood induces flowering which provides seed production for the *following* year. Primary flooding may have a similar role to fire, by prompting seed stored in the tree canopy to fall and be dispersed by the recession of the flood waters. The primary flood also provides nursery sites for germination by disturbing the soils and depositing nutrients on the floodplain. When primary floods do not occur, the initial stages of regeneration are affected and may be reflected in the apparent 'health' of the parent trees. Reduced tree health may negatively affect flowering and seed production, limiting the reproductive potential of the population. Reduced flooding could also disrupt the timing of flowering and seed fall, so that less seed is available when appropriate conditions prevail. Stage V may be the most limited by reduced flooding. A lack of nursery sites with sufficient water, nutrients and other resources, may reduce the level of germination that can occur on floodplains. Germination could also be limited by interference from competing plants or seed predators that would normally be eliminated by the more natural flood regime.

Later stages in regeneration (VI and VII) involve the survival and growth of seedlings and their establishment to the sapling stage. These stages are dependent on secondary floods ('follow-up' floods) for water and nutrients. Like germination, stages VI-VII may also be limited by a lack of resource renewal on the floodplain. At this stage, salinisation may modify seedling establishment as reduced flushing flows and raised saline groundwater levels force salt into the shallow root zone. Further, as deep sinker roots establish and encounter saline ground water, growth is stunted. Competition for resources with surrounding vegetation and grazing by livestock and native herbivores may also inhibit establishment and survival.

The sapling and pole stages (VIII, IX) are characterized by height and crown development. Saplings have a distinct main stem with branches beginning to form and fall. Saplings develop into pole trees once the lower branches are no longer quickly shed and the main stem is further developed. While these stages also depend on secondary or follow-up floods, they are unique in that they are the first regeneration stages well developed enough to withstand perturbations experienced during earlier stages. Both saplings and pole trees exhibit the characteristic flexibility usually associated with mature trees. Root systems are well developed to access groundwater but also use rainfall, when available, to withstand dry conditions as well as flood inundation. Consequently, the impacts on stages VIII and IX result more from the limitations of the floodplain rather than directly from flooding. Salinisation is significant for these stages. It retards the growth and maturation of the trees. This inhibits development to a reproductive life stage by physiologically limiting resources allocated for reproduction.

Stage X is the maturation of pole trees into adult trees capable of producing their own flowers and seeds. Because of the longevity of eucalypts, no studies have strictly established the time necessary for trees to reach this stage of development. However, trees are generally classified into three groups regarding the age at which seed is produced in significant quantities. Early seed producers bear seed at age 10-20 years. The most common age is between 20 and 40 years, but in late seed producers seed development is delayed until age 40-60 years (Jacobs, 1955). Eucalypts are generally categorized as middle age producers bearing seed between 20 and 40 years of age. The consequence of later maturation to reproductive potential is that mature trees with reproductive capabilities are susceptible to limitations by both primary and secondary flooding. As adult trees, limited secondary flooding may impact the 'health' of the tree as discussed earlier, but also the primary floods may limit phenological events.

As Roberts and Marston (2000) point out, the critical question is not whether regeneration is occurring but whether it is sufficient to maintain populations. It is suggested that in a red gum forest a single tree may produce 100,000,000 to 150,000,000 seeds before it is replaced by a new individual growing from a single seed (Jacobs, 1955), and that one successful seedling in about 150,000,000 germinating is all that is necessary to carry on a forest. While flooding provides the opportunity for regeneration, survival depends on factors other than the initial flood. Survival implies not only preventing the destruction of some existing stands but also ensuring that the conditions to which they are subjected will permit natural regeneration as older trees die (Pryor, 1981). Arguably, germination and establishment may not strictly depend on flooding since germination can occur without flooding if there are sufficient water resources, but they may be enhanced by the right conditions (Roberts and Marston, 2000).

There is little understanding of the 'right conditions' for regeneration and reproductive processes in floodplain vegetation. While environmental flows attempt to prescribe flood regimes for riparian systems, flows for regeneration remain unclear. The current level of understanding implies that a single flood event will be sufficient to reinstate natural responses, but as outlined above different floods are required for different events. For the dominant trees on the floodplain, a single flood event may stimulate seed set, but another flood is necessary approximately 9 months later for germination to occur. And yet another flood event is required one year later to maintain seedlings for sinker roots to develop. The implication is that sequential environmental flows are needed and that ad hoc allocations are insufficient. Clearly, for environmental flows to be effective further understanding of the flooding requirements at each stage of development must be examined.

Chapter 3 Eucalypt demography*

3.1 Introduction

The recruitment and survival of woodland trees are indicated by their age-class distribution. The *stand structure* (Husch *et al.*, 1982) may include several over-lapping age classes (Kadavul and Parthasarathy, 2001), or there may be distinct *cohorts*, fostered by events that enhance the availability of resources for germination and growth (Oliver and Larson, 1996; Smith *et al.*, 1997). Stands are initiated where a flood, fire or other disturbance creates a vacant space for germinants (Smith *et al.*, 1997). Subsequent disturbances may alter the spatial and temporal distribution of trees (Woodgate *et al.*, 1996) but ultimately, if a stand is to remain viable, mortality of older trees should not exceed the growth of young trees. Viability is reflected in the frequency distribution of age classes or, in a predictable growth environment, by tree diameters (Condit *et al.*, 1998). Ideally, this distribution should approximate a smooth, 'inverse J-shaped' pattern approximating the log normal function (Figure 3-1) (Smith *et al.*, 1997). This pattern reflects the large number of small trees required to cover the space occupied by a single mature tree, and attrition due to mortality. It may be modified by environmental factors and by interactions between the age and size of trees (Guedje *et al.*, 2003; Kohira and Ninomiya, 2003).

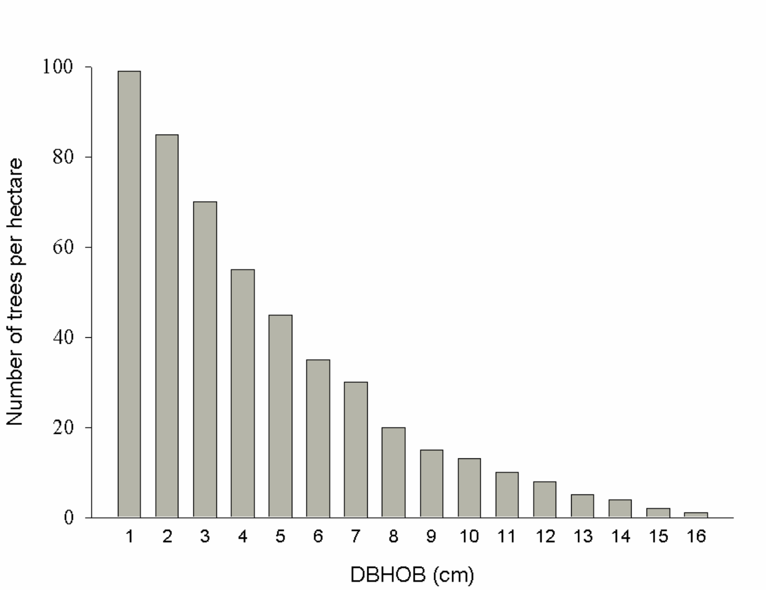

Figure 3-1 A typical Diameter at Breast Height Over Bark (DBHOB) distribution for uneven-aged stands. Such a distribution is often referred to as an "inverse J-shape" representing the proportionate density of smaller sized trees necessary to cover an equal basal area of larger, mature trees.

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*George, AK, Walker, KF, and Lewis, MM. (2005). Population status of eucalypt trees on the River Murray floodplain, South Australia. River Research and Applications 21: 271-282.

Eucalypt woodlands (Myrtaceae), characterized by widely spaced trees with <30% foliage cover, once covered most of the 1-million km^2 Murray-Darling Basin in south-eastern Australia, particularly the floodplains along the Lower River Murray. The extent of the woodlands has been greatly reduced by clearing, mainly for agriculture, and only 38-42% of the original tree numbers remain (Walker *et al.*, 1993).

On the floodplain of the Murray in South Australia, stands of river red gum (hereafter, 'red gum': *Eucalyptus camaldulensis* Dehnh.) and black box (*E. largiflorens* F. Muell.) dominate the woodland ecosystem (Figure 3-2). The trees are remnants of once more-extensive woodlands, and are under continuing threat from clearing, rising saline ground water, grazing, disease, invasive exotics and the effects of flow regulation (Walker and Thoms, 1993; Walker *et al.*, 1995; Scott *et al.*, 1997; Lunt, 1998; Johnson, 2000).

Figure 3-2 Red gum (a) and black box trees (b) at Banrock Station. These are trees in 'good condition' for the site.

Diversions from the Murray began more than 150 years ago, but regulation intensified with dam and weir construction after about 1920, and again with expansion of irrigation schemes after about 1950 (Close, 1990). Growth in diversions has resulted in an estimated 56% reduction in the mean annual discharge of the river. Approximately 90% of the diversions are used for irrigation, 6% for rural, domestic and stock supplies and 4% for urban supplies (Maheshwari *et al.*, 1995).

Comparisons between natural and regulated flows are aided by the Monthly Simulation Model developed by the Murray-Darling Basin Commission (MDBC, 2002) . The model shows that natural flows from the Murray and Darling rivers have undergone substantial changes (Walker, 2000). In 1994, discharge at the river mouth was down to 21% of the natural flow and the natural median discharge was likely to be exceeded only 8% of the time compared to 50% under natural flow conditions. The lower Murray is now, in effect, a cascading series of pools that are maintained near bankfull capacity (1100-1300 GL), except during large floods (Walker, 2000).

Floods play a vital role in maintaining floodplain vegetation. Whereas regulated, in-channel flows mimic drought conditions by limiting the exchanges between the floodplain and river, the long-term natural flow regime, including overbank flows, governs the structure, composition and dynamics of vegetation communities (Breen *et al.*, 1988). These communities are highly vulnerable to changes in the frequency, timing, and magnitude of flooding, as have occurred in the Murray (Close, 1990).

The effects of regulation are likely to be exacerbated in semi-arid regions, like the Murray-Darling Basin, where for long periods rivers may be the only source of water for trees. The effects are most obvious in terms of dieback and regional declines of tree health, but they should be apparent also in changed patterns of survival and recruitment (e.g. Cordes *et al.*, 1997; Stromberg, 1997; Hampe and Arroyo, 2002; Rooney *et al.*, 2002), even though they may be manifest over years and decades (Nilsson *et al.*, 1997).

This chapter concerns red gum and black box woodlands at one site on the River Murray floodplain. The objectives were to describe the stand structure of each species, and to infer whether the stands are viable. The study reflects wide concern over the long-term status and survival of floodplain trees, especially along the River Murray in South Australia (MDBC, 2003).

3.2 Methods

3.2.1 Study site

Banrock Station (34°10’S, 140°19E) is a 1750 ha property on the Murray floodplain 179 km NE of Adelaide, South Australia (Figure 3-3). It was heavily farmed and grazed for approximately 100 years, but livestock were removed in 1992 and 240 ha of elevated land is now used for viticulture, leaving 900 ha of floodplain and wetlands in a more natural state. The local wetlands are listed under the international Ramsar treaty (Environment, 2002), and the owners, BRL Hardy Ltd, promote ecotourism as an adjunct to wine.

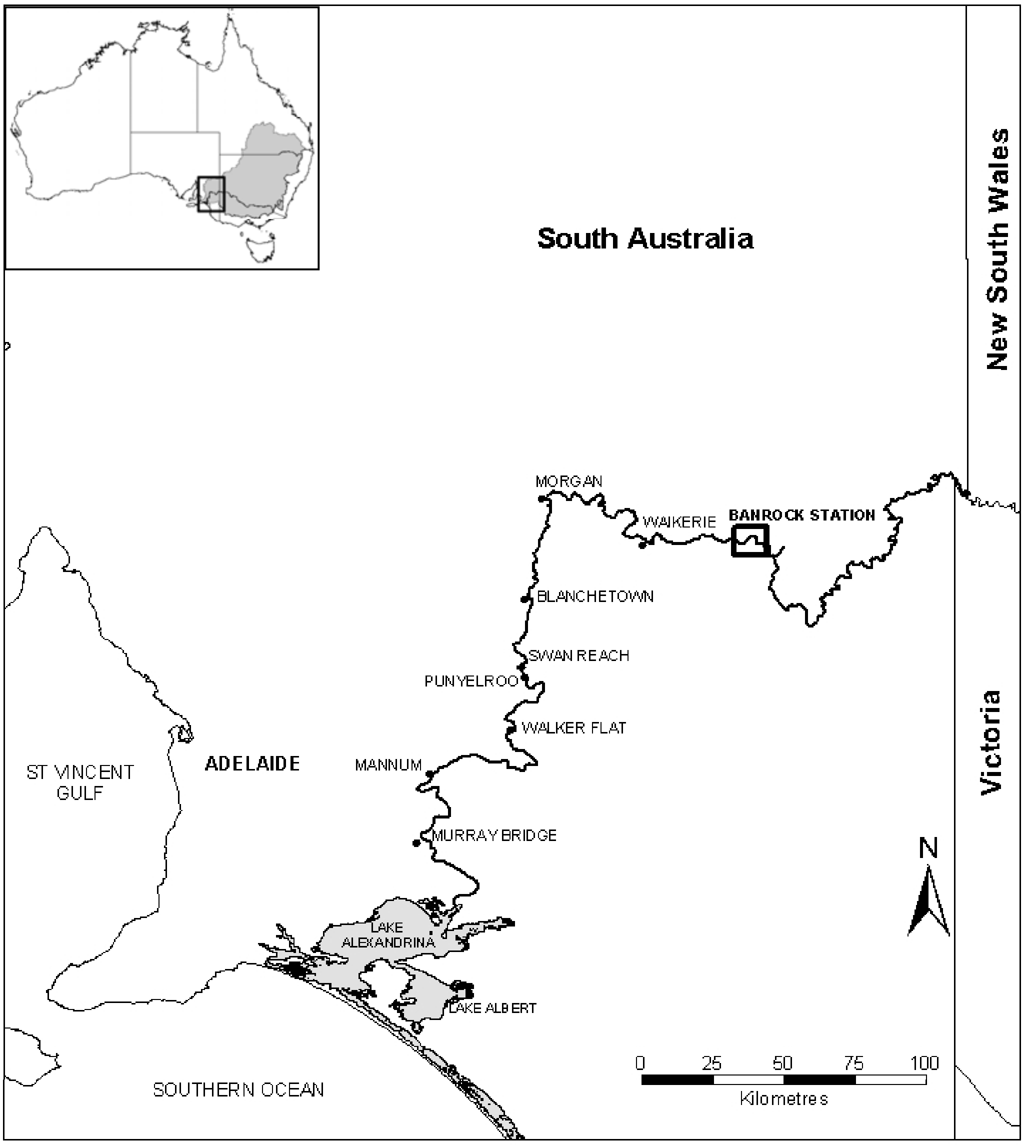


Figure 3-3 River Murray in South Australia. Banrock Station is delineated by a dark square, approximately 75 km from the border of South Australia, Victoria, and New South Wales.

The regional climate is semi-arid, with warm, dry summers and cold, wet winters (mean monthly temperatures 9-27°C, mean annual rainfall 250 mm). The floodplains are surrounded by ‘Open Scrubland’ including multi-stemmed eucalypts such as red mallee (*E. socialis*) and yorrell (*E. gracilis*), growing on harsh, limestone soils (Specht, 1972) (Figure 3-4). The floodplain itself is categorized as ‘Low, Open Woodland’ dominated by red gum and black box, with a shrub understorey (lignum: *Muehlenbeckia florulenta*) (Specht, 1972; Specht and Specht, 1999). Trees such as river cooba (*Acacia stenophylla*) and species of *Casuarina* and *Callitris* are often found associated with the eucalypts, and the understorey includes boobialla (*Myoporum platycarpum*), species of *Eremophila* and *Melaleuca*, silver saltbush (*Atriplex rhagodioides)*, ruby saltbush (*Enchylaena tomentosa*), mulga grass (*Aristida contorta*) and native millet (*Panicum decompositum*) (Boomsma and Lewis, 1980). The floodplain soils are medium to heavy clay soils at least 2 m thick. They have low infiltration rates and 'poor' physical properties (Cole, 1978), and often are saline.

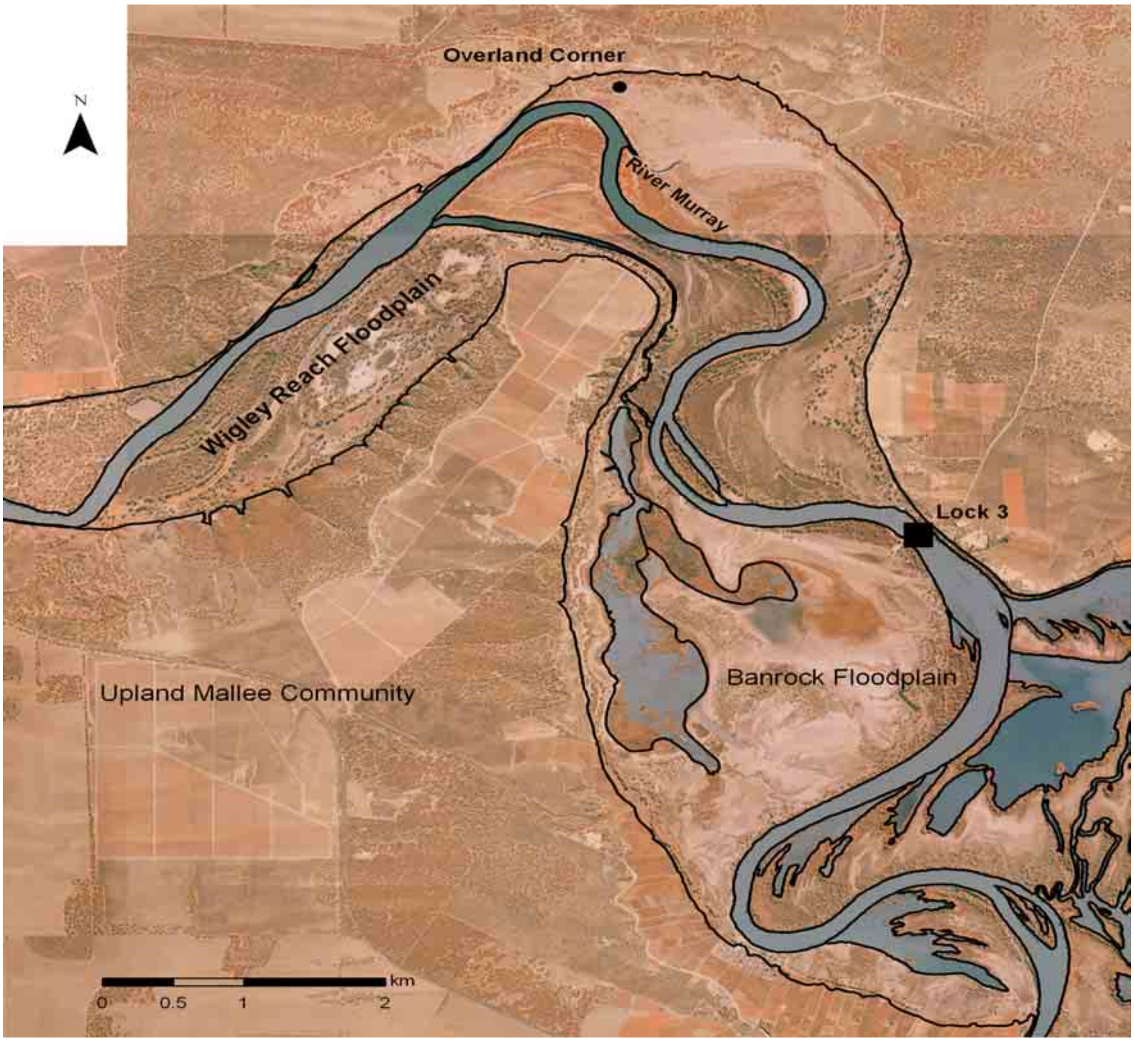


Figure 3-4 Site map for Banrock Station within the Murray-Darling Basin.

The combined effects of upstream dams and, regionally, serial weirs constructed in 1922-1937, have reduced the magnitude, duration and frequency of regional floods in the Lower Murray, although the seasonality of flows is little changed (Walker and Thoms, 1993; Maheshwari *et al.*, 1995). Under natural conditions, the floodplain at Banrock would have been flooded once in 3-4 years, but the area is now watered only once in about 12 years, with the exception of the local wetlands. Water control structures were installed in the Banrock wetlands in 1992, enabling the owners to re-instate an annual wetting and drying cycle. In early spring, water is diverted to the wetlands from upstream of Lock 3 (Figure 3-4) and released over 3 months to

Banrock Creek, where it returns to the Murray downstream of Lock 3. This cycle is accelerated relative to natural conditions, but has been effective in promoting native flora and fauna.

3.2.2 Field survey

Trees were surveyed in 127 plots on the Banrock and Wrigley Reach floodplains in November and December 2002 (Figure 3-5). Circular, 40-m diameter plots were used to offset the 'edge effects' associated with rectangular or square plots (Krebs, 1999). Smaller plots were considered, but not used because they did not accurately represent tree density, given the spacing between woodland trees. A total 16 ha was surveyed for tree density and size composition. Sampling was conducted along 21 transects across the floodplain, perpendicular to the river, and was stratified to account for the distributions of red gum, which favour low-lying areas along the river margins, and black box, which grow at higher elevations, further from the channel. Samples were taken at each point along transects where dominant tree species composition was judged to have changed noticeably. Thus, the numbers of sample plots along transects depended not on transect length but on the relative numbers of the two species. While, such sampling is partly subjective, randomised sampling during a pilot study was inconclusive and inefficient, due to the irregular, generally wide spacing characteristic between woodland trees.

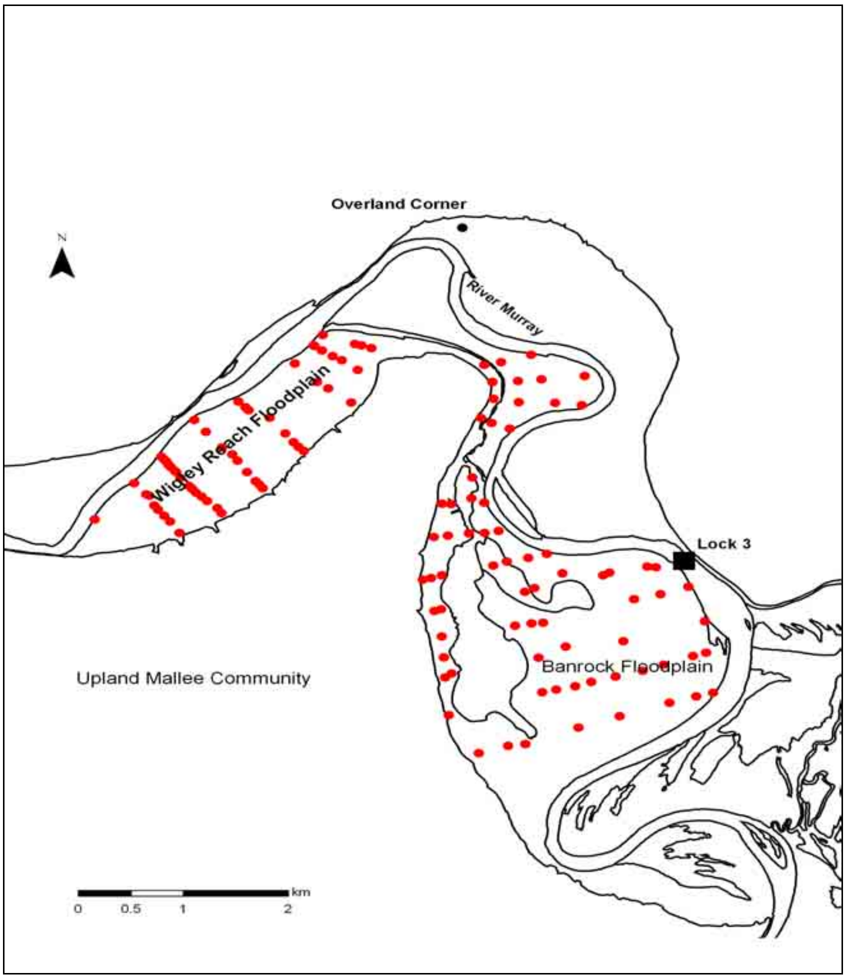


Figure 3-5 Banrock Station sample plots, along transects perpendicular to the river.

3.2.3 Population structure

Age estimation is problematic for eucalypt trees in semi-arid regions of Australia, where variable rainfall and aseasonal temperatures constrain the production of annual tree rings (Dunwiddie and LaMarche, 1980; Argent, 1995). In the absence of an appropriate method for age determination, it was necessary to use tree size as a surrogate variable. This was assessed using Diameter at Breast Height Over Bark (DBHOB), calculated from the total circumference of the bole, measured 1.3 m above the base. Thus, DBHOB was measured for all trees >1.3 m high. Corrections for multi-stemmed trees were made by summing DBHOB for each stem. No corrections were made for the irregular boles of large-diameter trees, because precise measurements are not critical for assessment of relative ages. Tree height was also determined using 'degrees of incline', measured 20 m from the base using a Suunto Inclinometer. Trees <1.3 m were tallied as 'seedlings' but not measured; their small stature implies that they may not be fully established and thus not contributing to recruitment.

While tree seedlings in temperate climates generally may be fully established within the first year after germination, seedling establishment in this environment may be severely limited by reduced connectivity between river and floodplain. This has resulted in uncharacteristically high mortality after the initial 2-3 years following germination, due to drought and soil and groundwater salinity. Therefore, seedlings on this site are not considered to be true 'recruits' until reaching greater heights.

Trees >1.3 m tall were categorised as *sapling*, *pole* or *mature* trees. Saplings generally were shorter, with a narrow, pointed crown, and pole trees were taller with fuller and rounder crowns than those of saplings, but not as wide and full as mature trees. These categories are modified after Jacobs' (1955) descriptions of eucalypt developmental stages, and are similar to those used by Woodgate *et al.* (1996) for old-growth forests. They are a means to estimate stand age relative to the size distributions measured in the field.

3.2.4 Population viability

Total abundance and density for both eucalypt species were referred to two size classes (DBHOB >10 cm, DBHOB <10 cm), following studies where the 5-10 cm class was judged most important for population maintenance (Fensham and Bowman, 1992; Guedje *et al.*, 2003). Density per hectare was then calculated for each species and size class.

To provide for estimates of viability, the initial maximum longevity of red gum and black box in the Lower Murray region was assumed to be 200 years. This is a tentative, probably conservative assumption based on Snowball (2001) estimate of 250 years for two large black box trees (65, 143 cm DBHOB) on the Murray floodplain at Overland Corner (Figure 3-4). Snowball's estimate was based on radiocarbon dating of heartwood from both trees. The samples returned an age of 'Modern', indicating an age of 200 years or less, relative to 1950, placing germination following a large flood event around 1780. Black box grow at relatively high (less-often flooded) elevations on the floodplain, or along the floodplain margins where they are believed to mark the limits of major floods. The two trees at Overland Corner are at elevations above the level of the largest recorded flood in this region (1956). The maximum recorded ages for red gum in different areas range from 100-950 years (Ogden, 1978). Given this apparent variation in longevity between the two tree species, viability estimates were expanded to include longevity ranging from 150-1000 years.

Regional tree growth is highly variable, reflecting a changeable climate, and trees that appear to be saplings may be 50 years old. For example, certain black box trees at Chowilla (South

Australia), known to have germinated in 1956 (Jack Seekamp, Renmark, pers. comm., 2001), presently are only 1.5 m high and 2-cm diameter. While trees at Chowilla (Murray floodplain near Renmark, about 176 km upstream of Banrock) are greatly impacted by salinity and reduced flooding, the stands at Banrock are less affected, particularly by saline conditions. On this basis, trees at Banrock are assumed to attain >10 cm DBHOB only after 100 years (half their maximum lifespan). The designated years of sapling 'release' are conservative; they recognize that growth rates at Banrock may be higher than at Chowilla but also allow for suppressed growth due to poor conditions. Sapling release is a consequence of self-thinning in cohorts, as weaker trees are suppressed and die (Smith and Long, 2001). It distinguishes the *chronological* age of a tree and its *effective* age, measured from the commencement of active growth. In floodplain woodlands, where young tree growth is less dependant on canopy gaps for light, sapling release is more likely initiated by other factors such as flooding and water relations.

The foregoing observations and assumptions were applied to simple calculations that estimate, for a given stand, the proportion of current saplings that needs to survive to maintain the population at its current status. Fensham and Bowman (1992) proposed the calculations as a way to combine tree density data with longevity assessments for eucalypts in tropical northern Australia (Mucha, 1979). Tree size was employed as a surrogate for age or growth stage, as in the present study. It has not been confirmed that size is correlated with age, but this remains the best available basis for assessments of stand structure, hence population viability.

3.3 Results

3.3.1 Field Survey

Calculated density and dominance values for both red gum and black box trees survey at Banrock are presented in Appendix 1. Total absolute tree density across the Banrock floodplain was determined to be 88 trees ha^{-1} and only 11 trees per plot. Trees, contributing a total of 13.7 m^2 basal area per hectare, covered <1% of the ground. While red gum and black box occurred at about equal frequency (41 and 40, respectively), basal area contribution varied between species. The relative dominance of red gum was 60%, based on density measures of 69 trees ha^{-1} and 8.2 m^2 of basal area ha^{-1}. Black box contributed 40% of the site basal area with densities of 18 trees ha^{-1} and 5.5 m^2 of basal area ha^{-1}.

3.3.2 Population structure

Figure 3-6 and Figure 3-7 show the distributions of DBHOB and height for red gum and black box trees at Banrock Station. The distributions differ between species (DBHOB: Kolmogorov-Smirnov 2-sample test $D = 0.408$, $p < 0.001$; height: $D = 0.230$, $p < 0.001$). The shape of the black box plot differs from the smooth ‘inverse J-shape distribution’ described by Smith *et al.* (1997), suggesting either episodic recruitment or increased mortality rates for smaller size classes.

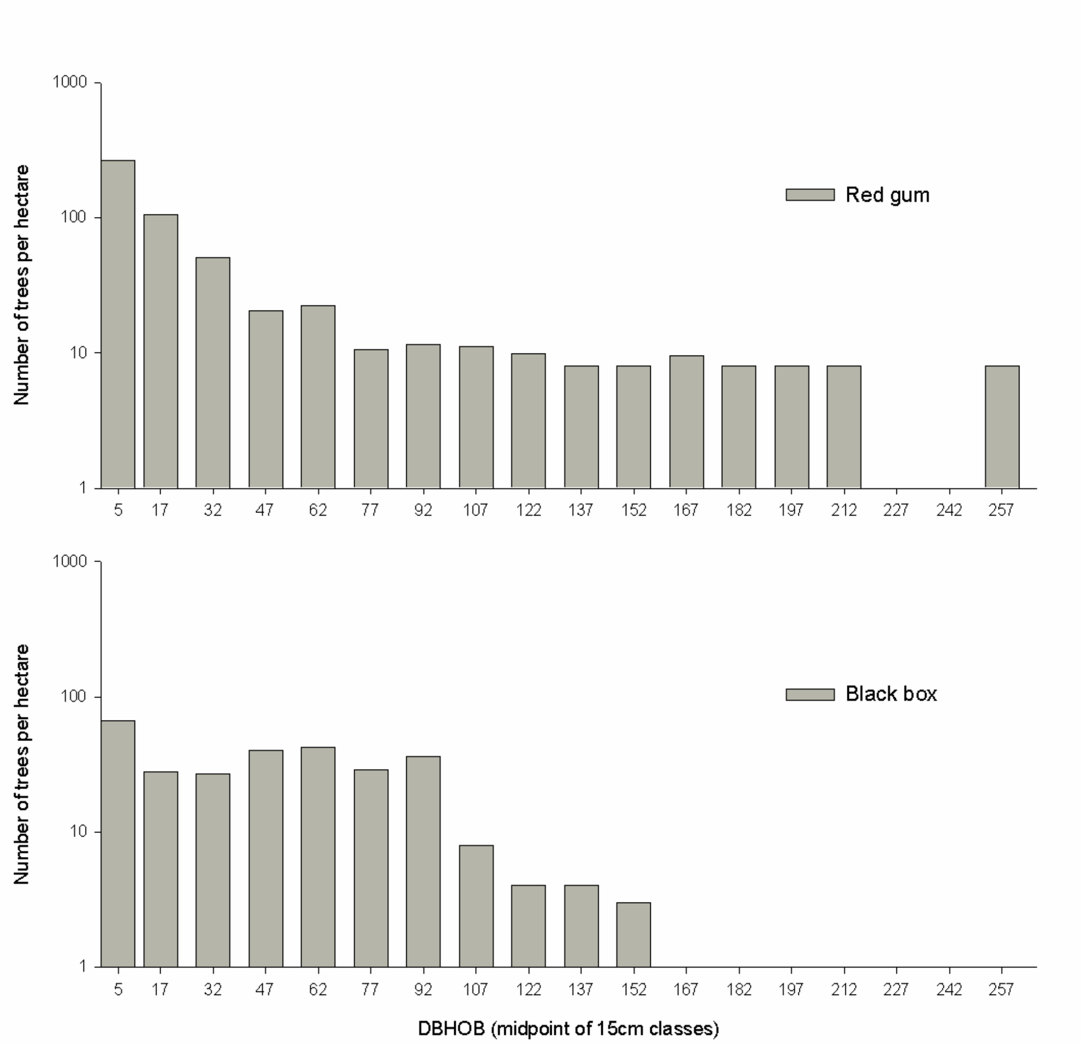


Figure 3-6 Distribution of DBHOB of river red gum and black box at Banrock Station.

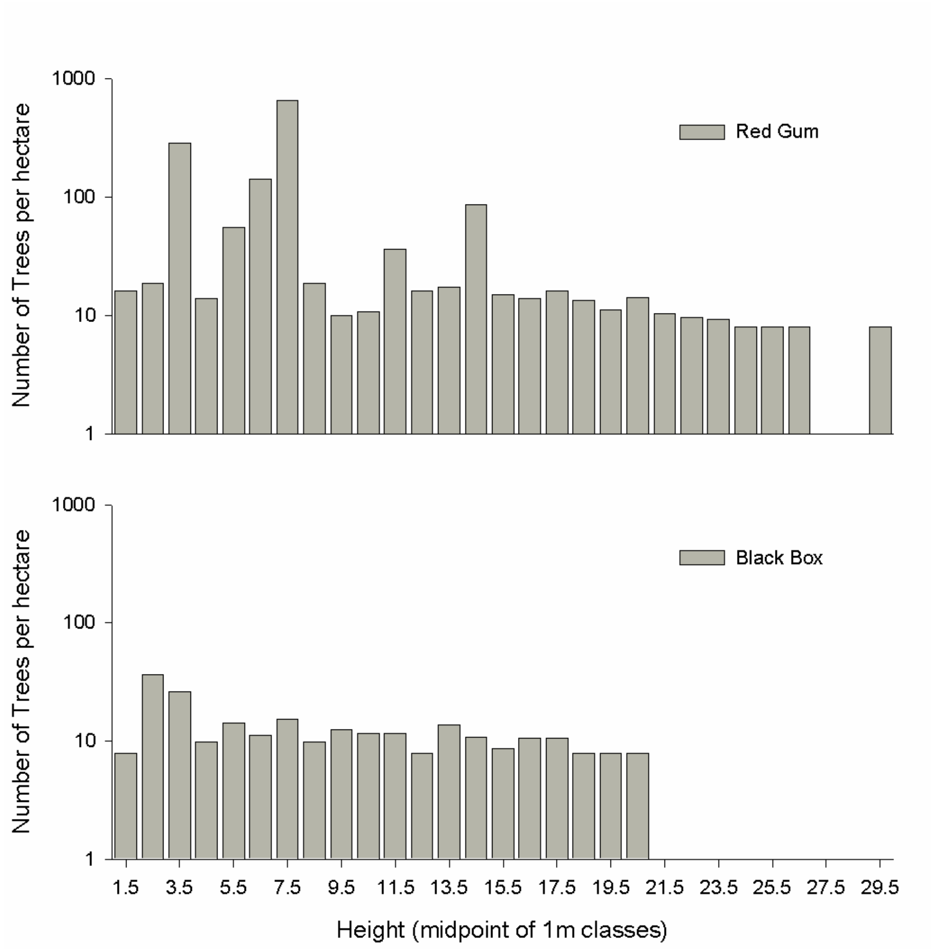


Figure 3-7 Distribution of height for river red gum and black box at Banrock Station.

Relationships between visual growth stage assessments and height and diameter were problematic because some trees had extremely large diameters or heights relative to their crown structure. Median values for each diameter and height class were used to evaluate correlations between diameter and height. Although median DBHOB and median height were correlated in both species (red gum: Spearman's rho = 0.75, n = 1108, p <0.0001; black box: 0.78, 290, <0.0001), the large range of DBHOB values recorded for any single height class made interpretation of the correlations difficult. For example, DBHOB values for the 10-m height class ranged between 15 and 139 cm. In this case, classifications based on height and DBHOB would yield quite different distributions, as DBHOB could represent eight size classes relative to one height class. The problem might be resolved by including canopy shape and structure as criteria, as they compensate for distinctions between relative growth stages within the developmental cycle, and for variation between sites.

Although red gum at Banrock Station outnumber black box by about four to one, the smallest diameter (0-10 cm) black box are nearly as common as seedlings of that species Figure 3-8, whereas the smallest diameter red gum (0-10 cm) are 10 times more abundant than seedlings.

Small trees of both species occur in localised clumps, and size-class distributions exhibit peaks and falls suggesting episodic recruitment and opportunistic survival.

Visual assessments of growth stages indicate almost equal density of mature and sapling black box trees with reduced densities of seedling and pole growth stages (Figure 3-8). Red gum densities more closely represent the population structure expected, with saplings having more than three times the density of mature trees. The lower density of red gum seedlings relative to saplings could be of concern from a population perspective.

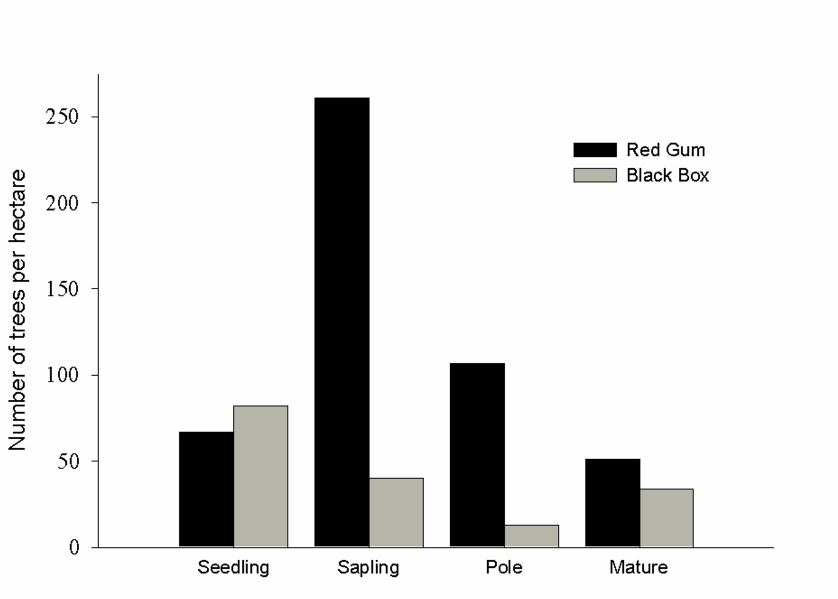


Figure 3-8 Density of growth stages for the two tree species at Banrock Station, grouped by visual canopy structure.

3.3.3 Population viability

Density for trees >10 cm DBHOB was calculated as 25.1 red gum stems ha^{-1} and 14.0 black box stems ha^{-1}. These values differ from the values represented in Figure 3-8 because of the division into two size classes relative to 10 cm DBHOB. Given the assumptions described earlier, an average 0.25 mature red gum will die each year (25.1/100, or 1 tree in 4 years). The density of saplings <10 cm DBHOB is 44.4 stems ha^{-1}. If these are assumed to be 100 years old based on suppressed growth conditions, then an average 0.44 saplings ha^{-1} is released each year (44.4/100). To maintain the red gum population at its present level, 57% ((0.25/0.44)*100) of the extant saplings must survive.

For black box there are greater constraints. For trees >10 cm DBHOB there were 14 stems ha^{-1}, and an estimated average 0.14 mature trees will die each year (14/100). The density of saplings <10 cm DBHOB is only 4.2 saplings ha^{-1}, indicating that 0.042 (4.2/100) saplings are released each year. Thus, 333% of saplings, more than three times the actual number, must survive to maintain the population ((0.14/0.042)*100).

These estimates change, of course, if the longevity and release assumptions are varied (Table 3-1). To test the sensitivity of the estimates, although in an approximate way, the assumed maximum longevity for both species was set to vary between a conservative 150 years and 1000 years, suggested by Jacobs (1955) and Ogden (1978) as maximal ages for red gum in south-eastern Australia. Similarly, sapling release was set to one-third rather than one-half of the lifespan. With longevity at 200 years, but sapling release at one-third of the lifespan, survival need not be as high as previously estimated for either species. The red gum at Banrock would require only 19% sapling survival, but the black box would still require more than 100% survival. Similar calculations with release set to half of the lifespan suggested no change from the original results: red gum required 57% and black box 333% survival. This suggests that the timing of sapling release may have a greater role in population maintenance than the longevity of individuals.

Table 3-1 Estimated percentage sapling survival required for stands of the two tree species at Banrock Station, as a function of longevity. It is assumed that sapling release occurs at one-third of the lifespan (thus, trees spend two-thirds of their lifespan as >10 cm DBHOB).

Longevity (years)	**150**	**200**	**250**	**300**	**500**	**1000**
Black Box	167	111	333	167	222	222
Red Gum	28	19	38	28	38	38

3.4 Discussion

3.4.1 Stand structure

Red gum and black box woodlands on the Lower Murray floodplain have complex stand structures. There are conspicuous gaps in one or more size classes of both species, suggesting that recruitment is episodic and possibly associated with large-scale ‘disturbances’ (Norton *et al.*, 1995). Clearly, black box do not exhibit a smooth, ‘inverse J-shaped’ distribution that would imply continuous recruitment. For both species, flooding is the primary source of moisture for germination and seedling establishment (e.g. Dexter, 1967, 1978). This is illustrated, for example, by reports of seedlings in litter at the margins of a flood (Roberts and Marston, 2000). Widespread regeneration of red gum along the middle Murray occurred only six times from 1880 until the 1970s, in tandem with big floods (Dexter, 1978). These observations, and changes induced by flow regulation in patterns of regeneration and growth of red gum forests (Bren, 1991), substantiate the presumed link between recruitment and flooding.

Black box stand structure at Banrock Station differs from that of red gum in respect to discontinuities in the height and diameter size classes. This is anticipated, as trees at higher elevations, or on the margins of the floodplain, experience less flooding. Red gum stand structure was more continuous, with many smaller trees, but the larger size classes nevertheless included distinct peaks. The prevalence of smaller trees need not imply increased survival, as young red gum often occur in dense copses of 500 or more saplings. Thus, one sample plot that happened to include a copse may skew the stand distribution toward smaller trees. Judging by the density of mature trees, self-thinning is likely to remove perhaps 40-60% of the trees in a copse.

The different size-frequency distributions for red gum and black box imply that they have different requirements for germination, growth and development, and that they respond differently to flooding. Dexter (1970) suggested that stem damage and mortality during flooding are affected by topography (*i.e.* trees at lower elevations must tolerate deeper, more prolonged flooding). Heinrich (1990) confirmed that red gum are physiologically more tolerant of flooding than black box, but less tolerant of dry conditions.

Tree size class distributions are sensitive to many environmental factors (Kohira and Ninomiya, 2003 and references therein) and they are a hazardous basis for predictions of population performance. There may be no better method, however, in environments where direct methods for age estimation do not apply. Indeed, size class distributions have been used successfully in numerous studies (e.g. Hett and Loucks, 1976; Bongers *et al.*, 1988; Fensham and Bowman, 1992; Guedje *et al.*, 2003; Webb and Sah, 2003; Williams-Linera *et al.*, 2003).

3.4.2 Stand viability

The viability of stands depends on a balance between the number of individuals removed from the population and the number entering through recruitment and regeneration, and requires a progression of individuals from smaller to larger size classes (Harper, 1977; Rooney *et al.*, 2002). The number of survivors reflects the number initially present, and high initial densities increase ‘demographic momentum’ (Rooney *et al.*, 2002). Viability is also influenced directly by the current structure of the population. This is best determined from long-term inventories, where those data exist (Condit *et al.*, 1998). In their absence, ‘snapshot’ observations of size-class distributions are a simple tool to identify populations with failing recruitment (Kohira and Ninomiya, 2003).

Regardless of the tentative assumptions made here regarding longevity, rates of sapling release and mortality and the validity of using tree size as a surrogate for age, there are sound reasons for concern over the viability of black box stands in the Banrock area. The data for red gum also warrant concern, not only because seedling density is much lower compared to saplings, but self-thinning will cause major attrition of young trees. In this case, the timing of sapling release appears to be critical.

Population maintenance at any site requires the presence of various growth stages so that as older trees die, they are replaced by younger, established trees. Applying active management techniques, simulating soil and surface disturbance by flooding, could potentially enhance not only germination and establishment but also survival of existing trees. Additionally, the relationships between flood frequency and growth stages should be examined.

Chapter 4 Flooding and Regeneration Stages

4.1 Introduction

The dependency of floodplain vegetation upon flooding is encapsulated by the Flood Pulse Concept (Junk *et al.*, 1989). The concept proposes that seasonal flooding provides regular exchanges between rivers and their floodplains, and thereby governs the dynamics of the riparian vegetation, through changes in morphology and anatomy or physiological and phenological processes. Puckridge *et al.* (1998) proposed that pulses need not be regular as in seasonal changes. Instead, suggesting ‘flow pulse’ or stage variation governs vegetation dynamics; predicting organisms will adapt to the variability of the given system.

Biotic responses can be through direct or indirect influences. Floods directly supply water and nutrients essential for maintaining and enhancing physiological functions. Indirect influences result from geomorphologic changes to the floodplain through sediment erosion and deposition (Hughes, 1994; Hupp and Osterkamp, 1996; Hughes, 1997; Thoms, 2003). Such physical processes provide suitable regeneration sites and drive successional trends (Hughes, 1994; Richter and Richter, 2000).

Floodplain species responses have been quantified in arid and semi-arid regions of North America, where declines in woodland and riparian vegetation have prompted studies to determine the requirements for successful regeneration and establishment. For example, Rood *et al.* (1998) found that extensive establishment of cottonwood (*Populus angustifolia, P. balsamifera*, and *P. deltoides*) seedlings occurred following a large-scale flood (1 in 100 recurrence; peak flow 4042 m^3s^{-1}). They determined that scouring, resulting from high floods, enabled successful recruitment and survival by creating suitable germination sites. A similar mechanism was found following a 10-year return flood (368 m^3s^{-1}) in the Hassayampa River of the Sonoran Desert (Stromberg *et al.*, 1993). Despite being of smaller magnitude, the flood deposited an average of 8 cm of sediment creating optimal conditions for extensive *Populus fremontii* and *Salix gooddingii* recruitment and establishment. These riparian species recruit episodically; thus, bare surfaces created by sediment deposition were optimal for recruitment.

The serial flood events also contribute to successful regeneration and establishment of vegetation (Stromberg, 1997). Serial flood events of equal magnitude were examined by comparing vegetation community responses following floods in 1993 and 1995 (Stromberg, 1997). While the first flood allowed recruitment, the second flood addressed different flood requirements for different growth stages in riparian and floodplain species. Comparing the differing roles of serial floods in the regeneration process emphasizes the role of hydrograph evaluation in regeneration studies. Stage hydrographs can be used to identify flood pulses that positively correlate with proportionate vegetation cover irrespective of the volume of floods (Zamora-Arroyo *et al.*, 2001). The work by Johnson (2000) supports this by determining the importance of low flows following recruitment and moderate flows during early growth stages, showing that while large magnitude floods shape the floodplain, small and moderate sized floods provide appropriate water conditions for growth and survival of vegetation.

These two flood types (one for initiating regeneration and one for sustained growth) are defined as ‘committed ecological outflows’ (Hughes *et al.*, 2001). ‘Committed ecological outflows’ refer to defined water quantity requirements for particular riparian ecosystems. These two types of flows distinguish between the physical processes contributing to floodplain sediment turnover rates that create favourable recruitment sites and the biotic maintenance of populations so that they are able to respond during favourable conditions.

Australian studies linking floods and vegetation are concentrated in the Mid-Murray where the river has a network of anabranches and many tributaries. Early studies found that flooding stimulated red gum regeneration by providing not only water for germination but also the appropriate microsite conditions (e.g. Dexter, 1967; Dexter, 1978). Germination and recruitment of eucalypts in the Barmah forest were greatest when the soil surface had been disturbed by manual site preparation or by flooding (Dexter, 1970). Bren and Gibbs (1986) built on this by illustrating a positive association between flood frequency and vegetation types and site quality in the red gum forests. Bren *et al.* (1987) refined these associations by determining the extent and duration of inundation as well as the range of flood frequencies red gums experienced during a 22 year period (Bren, 1988a). These studies combined with work conducted within the Cooper Creek system in Queensland (Capon, 2003) indicate that, despite the extreme variability found in Australian rivers, vegetation relies heavily on flows for population maintenance and expansion.

Regeneration can be limited by alterations to river hydrology characteristic of highly regulated rivers. In Canada, Cordes *et al.* (1997) determined that flood attenuation has spatially restricted regeneration to fringe areas so that expanses of large mature poplars are not likely to be replaced under the current river regulation. In Australia, Bren’s work presents similar conclusions. In the Barmah-Millewa forest, regulation has reduced the average duration of flooding by one month and also substantially increased the time between floods (Bren *et al.*, 1987; Bren, 1991). Bren (1988a) further demonstrated that regulation has caused decline in flood frequencies linked with partial flooding and has increased the occurrence of small un-seasonal floods during summer. Since flood frequency is inherently associated with eucalypt growth rates (Bacon *et al.*, 1993), such changes to river hydrology have negatively affected the growth and regeneration of river red gum forests along the middle Murray .

Sustainability of the River Murray as a resource for human, riverine and floodplain species has been closely scrutinized (Young *et al.*, 2000). River regulation, as discussed in Chapter 2, has decreased the frequency and magnitude of floods throughout the Murray River floodplains. The impacts of these changes are exacerbated by an absence of studies linking hydrology and ecology (Thoms *et al.*, 2000). Hydrological integrity is paramount for ecosystem integrity; therefore comprehensive characterization of water needs significant for different stages of the regeneration process would promote appropriate allocation of water resources for environmental or ecological uses. Thus, this chapter aims to examine the links between river hydrology and ecologically significant events for woodland trees.

The objectives here are to:

1. Relate present tree distributions to ecologically significant inundation events,
2. Identify key hydrologic parameters contributing to ecological tree response, and
3. Determine hydrologic patterns during specific time periods corresponding with tree recruitment.

4.2 Methods

4.2.1 Tree distribution and flood extent

4.2.1.1 Tree survey and mapping

As outlined in Chapter 3, red gum and black box trees were surveyed and classified by growth stage and the distributions of seedling, sapling, pole and mature trees were mapped across the Banrock Station floodplain. Growth stages corresponded to predicted growth forms based on tree height (greater or less than 1.3 meters) and canopy structure, including size and shape of the main stem and primary branches. Seedlings, excluded from analysis in Chapter 3, have been included here since the distribution of seedlings relative to flood extent may provide information regarding the magnitude and frequency required for germination. The spatial distribution of each growth stage was mapped using GIS software (ArcMap 8.1) to visualize the locations of each growth stage relative to one another.

4.2.1.2 Flood extent

Using the River Murray Flood Inundation Model III (Overton, 2001), flood extent and minimum flow magnitude required to inundate each plot were calculated. The model first derives elevation for the floodplain using backwater and flood attenuation curves from measured river flows at the South Australian border. River stage height is then compared to elevation, calculating the minimum flood magnitude required to inundate each sample plot. Output from the model includes a visual extent of flooding at defined magnitudes. Flow magnitudes represented by the model inherently define the river stage variations required to initiate tree response by representing the level at which inundation occurs. Tree growth stage distribution and flood extent maps were overlain using ArcMap 8.1. The combined maps allowed extrapolation of growth stage flooding requirements from the minimum flow magnitudes represented by the Flood Inundation Model.

4.2.1.3 Regeneration time periods

While exact ages of trees could not be determined, growth stages representing relative age classifications (discussed in Section 4.2.1.1) were used to infer time periods for germination and establishment (Table 4-1). Time periods assigned to sapling and pole stages were significantly longer than for seedling and mature trees. Based on findings in Chapter 3, these growth stages appear to be most susceptible to environmental factors such as flooding and drought. The sensitivity of these stages results in reduced sapling release rates and depressed pole stage development. To compensate for potentially high errors in age estimation resulting from visual crown structure, the time periods were subjectively extended. Seedling and mature growth stages were more easily recognized in the field, providing more confidence in relative age classification. Therefore, these time frames did not need to allow for variability in rates of growth and establishment. Growth stages and associated time periods were not assigned separately to red gum and black box species. River flows are the same for specific plots regardless of the species present, thus no additional information could be derived by splitting flows between species.

Table 4-1 Growth stages with assigned time frames to designate probable time of germination. Flows were assigned from the River Murray Flow Model.

GROWTH STAGE	YEARS OF TIME PERIOD	NUMBER OF DAYS IN TIME PERIOD	TYPE OF FLOW
Seedling	1990 - 2002	4748	Actual regulated
Sapling	1960 - 1990	10,958	Modelled regulated (1960-1968); Actual regulated (1968-1990)
Pole	1920 - 1960	14,610	Modelled regulated
Mature	1900 - 1920	7304	Simulated natural

Daily flows to South Australia, provided by the Murray-Darling Basin Commission, were assigned to each time period. Actual daily flows to South Australia are available from 1968, but simulated natural and regulated flows are modelled using the MSM_Bigmod model (MDBC, 2002). The model links the Monthly Simulation Model with the daily flow and salinity routing model, using observed flows at upstream tributaries, historical rainfall and temperature records to simulate daily flows to South Australia under natural (unregulated) and regulated conditions prior to 1968.

Flow duration, flood frequency, and flow spells analysis were calculated for each time period using the minimum flow magnitudes determined in Section 4.2.1.2. Each calculation was conducted using data for regulated (actual and modelled regulated) and modelled natural flows. These calculations were intended to determine if the effects of river regulation have varied between the defined time periods. Variation between time periods may define the hydrological limitations to different growth stages. The program AQUAPAK (Gordon *et al.*, 1992) was used for flow evaluations. Flow data were provided as megalitres per day (ML day^{-1}), but were converted to cubic meters per second (m^3s^{-1}) to accommodate the data requirements of AQUAPAK.

4.2.2 Flood evaluation

The relationship between trees and flow magnitudes was evaluated only for survey plots containing trees. It was presumed that plots absent of trees had characteristics which prevented tree recruitment and establishment such as salinisation, lack of flooding or impervious soils. Therefore, treeless plots would not provide information on the flooding requirements for tree regeneration.

A set of hydrological parameters, derived from daily flow measures at the South Australian border, was included with the number of trees (Table 4-2). The relationship of trees and flows was attempted using Non-metric Multidimensional Scaling (NMS) ordination in PC-ORD Version 4.28 (McCune and Mefford, 1999). The data were log-transformed and relativised, and converted to Sorensen (Bray-Curtis) distance measures. The NMS ordination was run with 100 runs of real data and 500 iterations for the final solution. Monte Carlo tests included 200 randomised runs. Six dimensions with a step-down rate of 0.2 were set to identify the dimensionality of the data set. NMS was run a second time, applying dimensions identified from the preliminary run. Four location outliers (two plots from Wrigley Reach and two from Banrock floodplains) were then removed from the data set to determine the effect of the outliers.

Table 4-2 Hydrological and tree parameters examining the association between trees and river flows.

PARAMETERS	ABBREVIATION FOR NMS
Number of trees	Ntrees
Maximum number of wet days	Nwet
Maximum number of dry days	Ndry
Percent time inundated during time period	Timeind
Mean duration of wet days (days)	Durwet
Mean duration of dry days (days)	Durdry
Flood frequency since expected germination	Flodgerm
Flood frequency during germination time period	Flodtime
Number of years in time period	Yrstime
Frequency of winter floods	Freqwint
Frequency of spring floods	Freqsprg
Frequency of summer floods	Freqsumm
Frequency of autumn floods	Freqautm

4.2.3 Hydrologic Characterization

4.2.3.1 Hydrologic parameter development

Hydrological parameters such as total discharge, flood frequency, drought frequency, flow duration, seasonality of peak flow, and flow sequencing (the number of times multiple flows occur during a specified time frame) have been cited as relevant for floodplain vegetation (Thoms *et al.*, 2000). While these parameters may be significant for mature or established floodplain populations, reproductive growth stages are likely to depend more on hydrograph parameters such as the rate of rise and fall of flows, mean flow duration, flow magnitudes, and seasonality (Thoms *et al.*, 2000 and references therein). To assess variable hydrologic dependency by growth stages, 63 potentially important hydrologic parameters were identified and calculated from daily flows to South Australia for a time period of 103 years (1900 to 2002) (Table 4-3). Parameters related to magnitude (annual and monthly) were included as a means of defining the extent of wetted area, which indirectly delineates the availability of habitat for regeneration (Richter *et al.*, 1996). Duration and frequency of extremes represent conditions under which regeneration is most likely to occur. Major periods of regeneration have been found to correspond with extreme flood events (Dexter, 1970; Dexter, 1978; Cordes *et al.*, 1997). Hydrologic parameters associated with the frequency, rate and timing of changes were determined to address the requirements of various life-cycle phases or growth stages in this study. The frequency of conditions and their rate of change are tied to population dynamics by influencing regeneration events (Richter *et al.*, 1996). The evaluation of such changes is required to understand the frequency of flows required to maintain existing and developing trees since the influence of flood recharge has relatively short-term effects (Bren, 1987; Richter *et al.*, 1996). Seasonal changes were included within the parameters to address the presumption that younger growth stages are more closely associated with features of the hydrograph including seasonal variation and rate of rise and fall (Thoms *et al.*, 2000). Because this component of the study aimed to identify patterns in hydrology, the parameters were evaluated by flows in each given year regardless of tree species or tree density. Therefore, the evaluation does not incorporate tree density associations.

Table 4-3 Hydrologic parameters.

Parameter Classification	Hydrologic Parameter	Abbreviation for NMS
Monthly magnitude	mean annual monthly flow	memflow
Annual magnitude and Duration of extremes	**annual 7-day max**	**sevdmax**
	annual 7-day min	sevdmin
	annual 7-day mean	sevdmean
	annual 3-day max	**thrdmax**
	annual 3-day min	**thrdmin**
	annual 3-day mean	**thrdmean**
	max annual daily flow	**dmax**
	min annual daily flow	**dmin**
	mean annual daily flow	**dmean**
	mean autumn monthly flow	meauflow
	mean winter monthly flow	mewiflow
	mean spring monthly flow	mespflow
	mean summer monthly flow	mesuflow
	annual monthly min flow	mminflow
	annual monthly max flow	mmaxflow
	Season of monthly max	**seammax**
	Season of monthly min	**seammin**
Frequency of extremes	**flood year**	**floodyr**
	flood in previous year	**pfloodyr**
	annual #days overbank	doverbk
High and low pulses	mean annual duration (days) high pulse - natural	ndurhig
	#annual high pulses - natural	**ntohig**
	total annual high pulse days - natural	ndhigh
	mean annual duration (days) high pulse - current	cdurhig
	annual #high pulses - current	ctohig
	total annual high pulse days - current	cdhigh
	total annual low pulse days - natural	ndlow
	mean annual duration (days) low pulse - natural	ndurlow
	annual #low pulse - natural	ntolow
	mean annual duration (days) low pulse - current	cdurlow
	annual # Low pulse - current	**ctolow**
	total annual low pulse days - current	**cdlow**
Rate of condition changes	annual duration (days) of rise	durris
	annual duration (days) of fall	durfal
	annual mean rate of rise	mrisrate
	annual mean rate of fall	**mfalrate**
	annual total # rises	totnoris
	annual total # falls	totnofal
Timing of changes	mean winter rate of rise	wirisrat
	mean spring rate of rise	sprisrat
	mean summer rate of rise	surisrat
	mean autumn rate of rise	aurisrat
	mean winter rate of fall	wifalrat
	mean spring rate of fall	spfalrat
	mean summer rate of fall	sufalrat
	mean autumn rate of fall	aufalrat
	mean # days in rise winter	widris
	mean # days rise spring	spdris
	mean # days rise summer	sudris
	mean # days rise autumn	audris
	mean # days fall winter	widfal
	mean # days fall spring	spdfal
	mean # days fall summer	sudfal
	mean # days fall autumn	audfal
	total # days rise winter	**dwiris**
	total # days rise spring	**dspris**
	total # days rise summer	**dsuris**
	total # days rise autumn	**dauris**
	total # days fall winter	**dwifal**
	total # days fall spring	**dspfal**
	total # days fall summer	**dsufal**
	total # days fall autumn	dsufal
	total # days fall autumn	daufal

4.2.3.2 Hydrologic parameter evaluation

One member of each pair of hydrologic parameters showing correlations between 90-100% (shown in bold in Table 4-3) was deleted from the dataset, to minimize redundancy. The final dataset included 40 parameters. The data were transformed using a generalized logarithmic transformation (McCune and Grace, 2002) to produce comparable magnitudes while preserving the relationship between zeros and other data values.

NMS was applied as for flood evaluation in Section 4.2.2. Preliminary NMS was run for the dataset comprised of 103 years using Relative Euclidean Distance measures with 100 runs with real data and 500 iterations for the final solution. Monte Carlo tests included 200 randomised runs. Six dimensions with a step-down rate of 0.2 were set to identify the dimensionality of the data set, and NMS was run again using the dimensions resulting from the preliminary assessment. Outliers in hydrologic parameters were then removed from the data set to determine their influence on the ordination.

Further, the dataset was subdivided to correspond with the growth stage time periods described in Section 4.2.1.3. NMS ordinations were run for each time period as outlined in this section. These tests reduced effects resulting from extreme values or outliers within any single time period. For example, the 100-year flood event in 1956 occurred during the pole stage time period, but the magnitude of the flood is large enough to skew results from the sapling time period where no equal magnitude flood event took place.

4.3 Results

4.3.1 Tree distribution and flood extent

4.3.1.1 Tree distribution

For both species, mature trees are more widespread than the younger stages (pole, saplings and seedlings) (Figure 4-1).

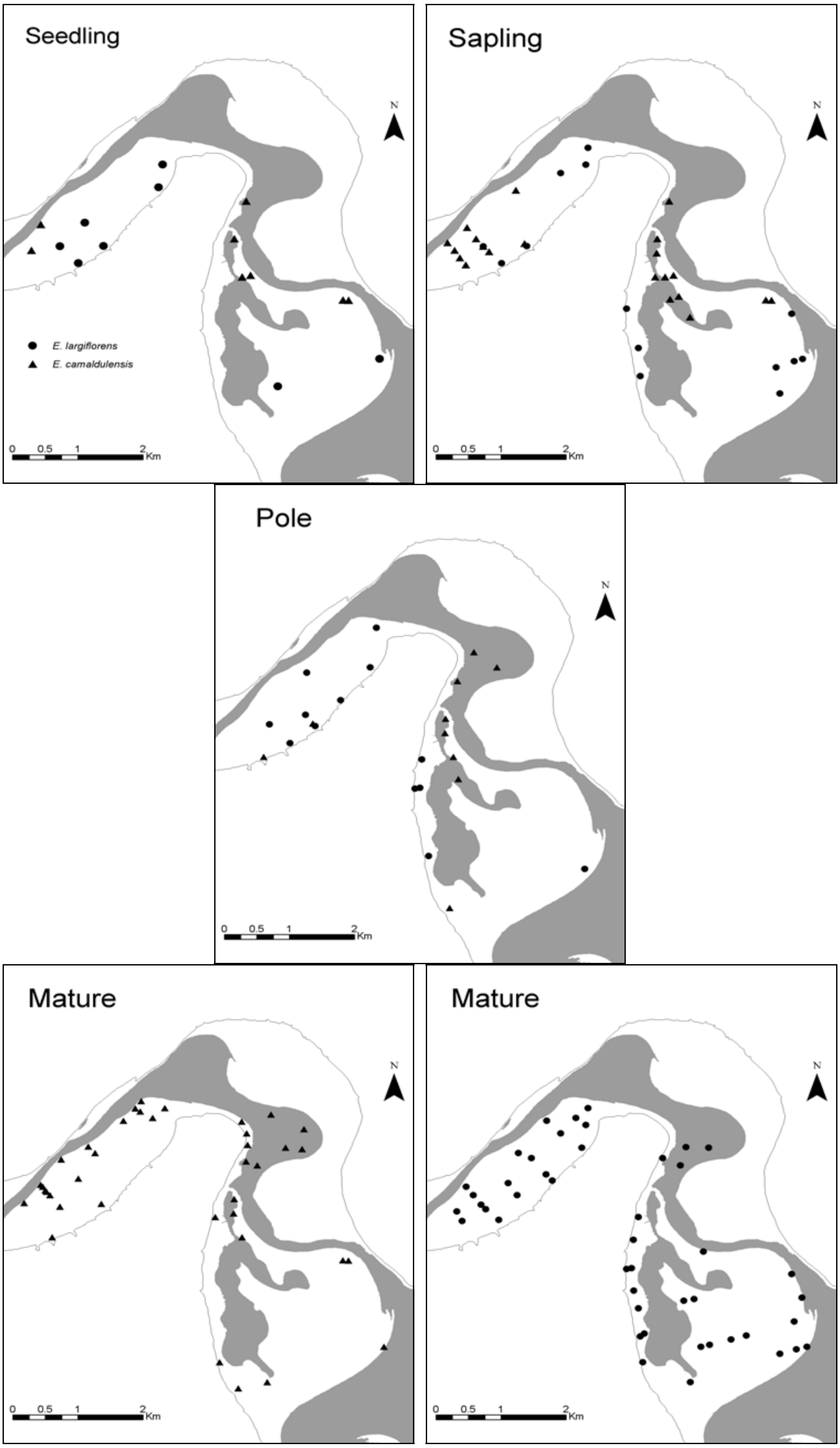


Figure 4-1 Growth stage distribution for (•) black box and (▲) red gum across Banrock Station. Note that maps for mature trees are divided by species, while early growth stage distributions are combined. Each dot marks the presence of the growth stage across the site.

Seedlings have the most restricted distribution. Seedlings for both species are located where water is most readily available, on the margins of the floodplain and along the main channels of the river and lagoon. Sapling and pole trees appear to have less distinct associations with water. Saplings are distributed both around the edges of the floodplain as well as across the less-frequently inundated middle areas. The distribution of pole trees more closely resembles that of seedlings, occurring along the edges of the floodplain where inundation from river flows or run-off from surrounding cliff faces and irrigation areas may accumulate. Mature red gums clearly illustrate the variable dependency on available water with distributions predominating in areas with direct links to river water. Mature black boxes occur across the expanse of the floodplain with no clear delineation within less frequently flooded areas. Despite the greater density and cover provided by *E. camaldulensis* (see Chapter 3), the spatial distribution of this species is limited compared to that of *E. largiflorens*, particularly when individual growth stages are examined.

4.3.1.2 Flood extent

The range of flows at the South Australian border required to inundate sample plots are shown in Table 4-4. The limitations of the flood model are illustrated by the representation of flows equalling zero and the exclusion of flows beyond 1181 cubic metres per second (m^3s^{-1}) (102,000 ML day^{-1}). Flows beyond 1181 m^3s^{-1} are represented by the arbitrary value 9999. These represent areas that theoretically have an elevation high enough to prevent inundation except during extremely large-scale flood events, such as the 1956 flood where maximum flows exceeded 3472 m^3s^{-1} (300,000 ML day^{-1}). However, when using the flood model to visualise flood extent, flows of this magnitude are of little concern since the limits of the 1956 flood are used to define the extent of the floodplain. Historically, flows of this magnitude have only occurred approximately 115 days during the last century.

A flow of zero indicates that the plot is continuously flooded and thus less affected by river flow variation. No corrections for sample plots characterised by flows equal to zero were made since during the sampling period no sites were inundated. Thus, these areas were presumed to be inundated by the smallest flow magnitude represented (58 m^3s^{-1}) since they are likely to be closely related to a backwater reach or river trigger point allowing these areas to retain water with minimal hydrological input.

Table 4-4 Range of flows required to inundate sample plots measured in Chapter 3 and area of floodplain inundated by each flow. Flows are shown as both ML day^{-1} and m^{3}s^{-1} to provide comparable units during later sections.

Flow (ML day^{-1})	Flow (m^{3}s^{-1})	Area Inundated (ha)
0	0	*
5000	58	7699
31000	359	8099
38000	440	8724
46000	532	9207
48000	556	9522
51000	590	10298
52000	602	10366
54000	625	10430
59000	683	11858
61000	706	12173
63000	729	12976
64000	741	13208
65000	752	13322
66000	764	13621
70000	810	15281
71000	822	16305
72000	833	16782
75000	868	17634
76000	880	17799
77000	891	18320
89000	1030	22469
95000	1100	22782
97000	1123	23023
98000	1134	23051
102000	1181	23320
500000	5787	*

Examination of the extent of various magnitudes illustrates the spatially discontinuous nature of flows (Figure 4-2) Thus, tree lines along the river's edge do not necessarily benefit from increased river flows before trees along the outer edge of the floodplain. Flow will follow trigger points or areas of low elevation where water can flow inland by backwater streams and flood runners.

Each flow magnitude represented in Figure 4-2 was found during at least one year of each time period (Figure 4-3). Flows in 1915, 1945, 1983, and 1995 failed to exceed the lowest represented flows of 58 m^{3}s^{-1}.

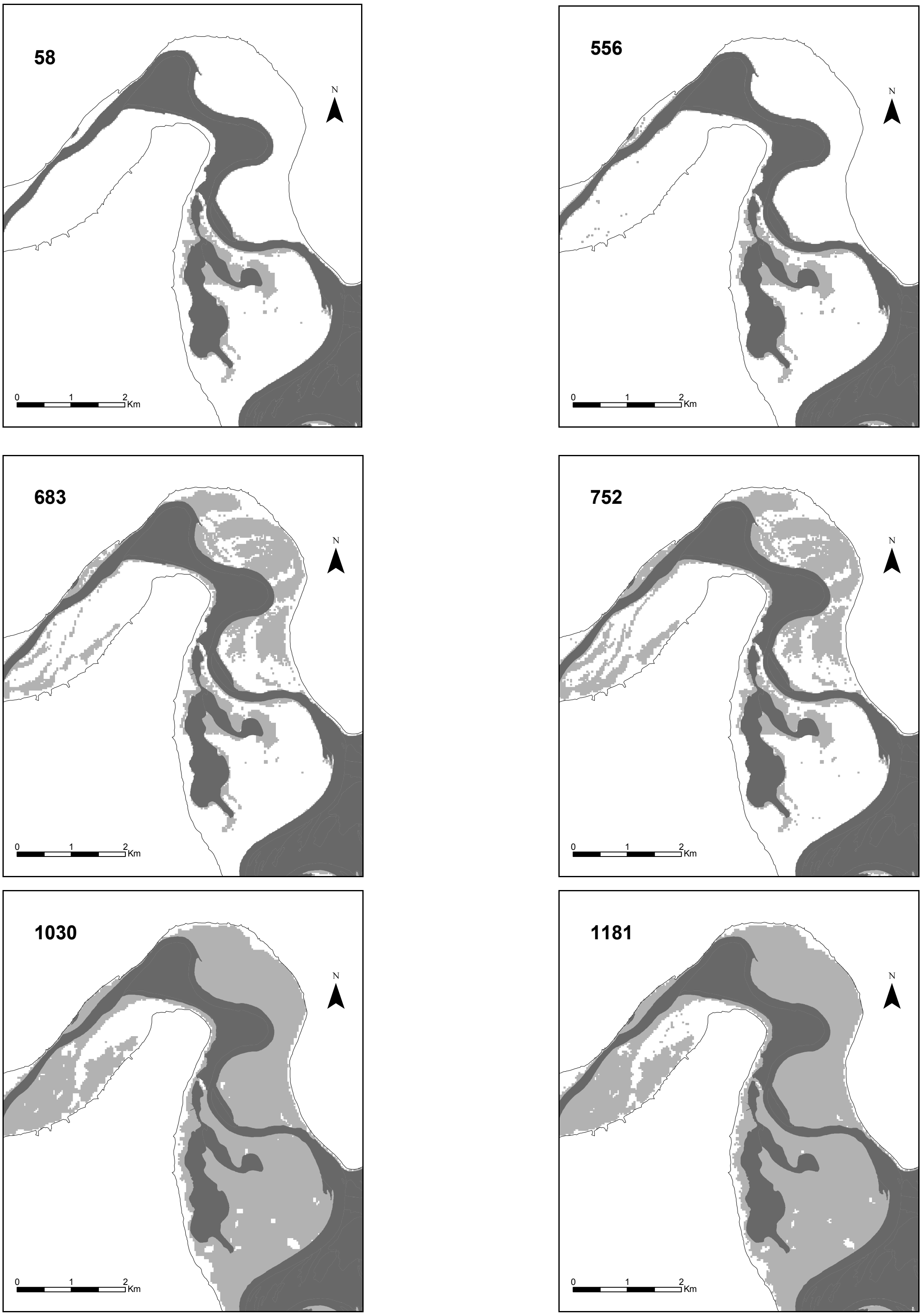


Figure 4-2 Spatial extent of various flow magnitudes measured in the River Murray at the South Australian border. Flows represent small, moderate, and large magnitudes as m^3s^{-1}. Dark gray indicates permanent water; light grey is extent of given magnitude.

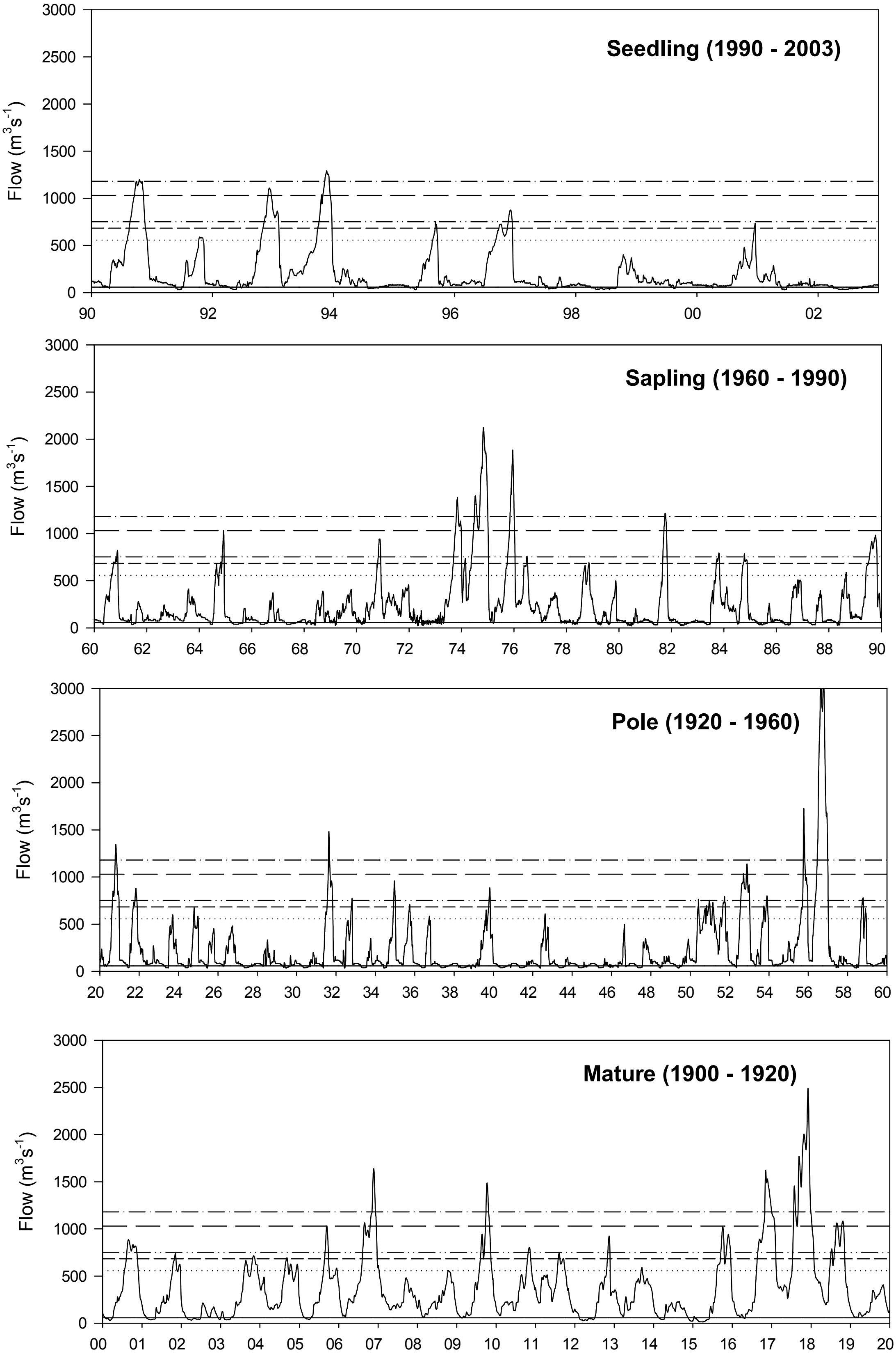


Figure 4-3 Flow magnitudes and hydrographs for each growth stage time period. The abscissae axes are the years corresponding to each time period (00 = 1900; 20 = 1920; 60 = 1960;90 = 1990). Horizontal lines demark flow magnitudes shown in Figure 4-2.

The range of flows required to inundate trees across the floodplain shows associations relative to species and growth stages (Table 4-5). All growth stages for *E. camaldulensis* are inundated at 58 m^3s^{-1} while the smallest flow event required by *E. largiflorens* growth stages is 440 m^3s^{-1}. This flow magnitude is required only by the mature growth stages (younger stages are inundated at much larger magnitudes of 729 m^3s^{-1}). The maximum flows required for *E. camaldulensis* are also much less than for *E. largiflorens*. Each of the *E. largiflorens* growth stages requires flows of 1181 m^3s^{-1} or greater, but younger growth stages of *E. camaldulensis* require only 810 – 891 m^3s^{-1}.

Table 4-5 River flow magnitudes required to inundate sample plots containing black box (BB) and red gum (RG) trees.

GROWTH STAGE	INUNDATING FLOWS (m^3s^{-1})
BB seedlings	729 - 1181
BB saplings	729 - 1181
BB pole	810 - 1181
BB mature	440 - 1181
RG seedlings	58 - 891
RG saplings	58 - 891
RG pole	58 - 810
RG mature	58 - 1181

4.3.1.3 Regeneration time periods

4.3.1.3.1 Flow duration

Comparing the ratio of time inundated between natural and regulated flows for each time period indicates a severe decline in time inundated for both red gum and black box (Figure 4-4). Under natural flow conditions, black box would be inundated between 5 and 20% during each time period. Regulation has reduced inundation within all time periods to 1-5% of the time. A similar trend is found for red gum where natural conditions would inundate growth stages from 10-95% of the time but with regulation inundation declines to only 1-85% of the time. The larger range of flows and the higher ratios of time inundated found for red gum under both natural and regulated conditions reflects the higher dependency on inundation frequency compared to black box.

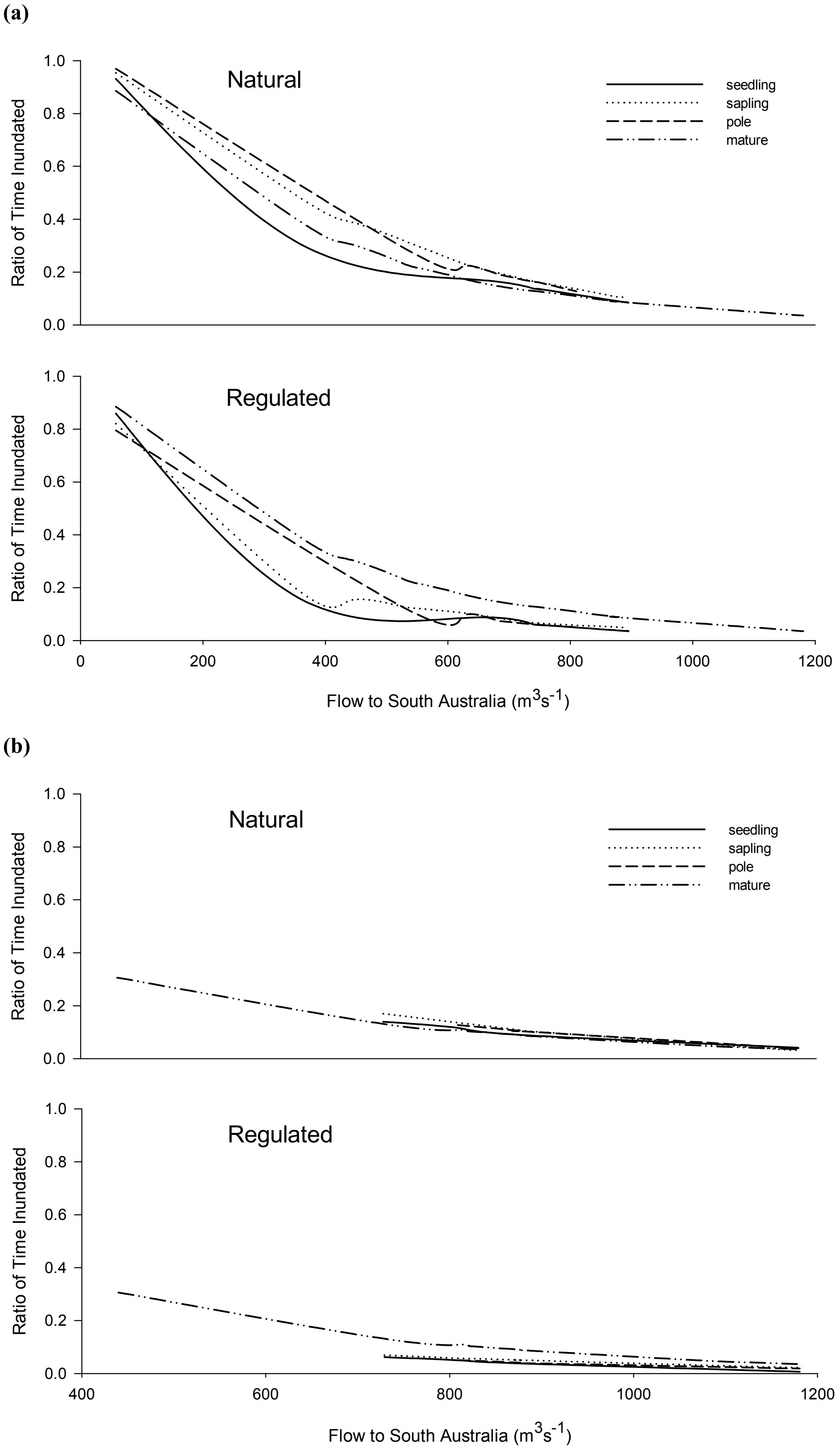


Figure 4-4 Flow duration curves for (a) red gum and (b) black box growth stages under natural and regulated flows. Varying abscissae for each species was necessary to distinguish the differences between species and flow conditions.

4.3.1.3.2 Flow frequency

Flow frequency curves for regulated and natural flows (Appendix 2) were used to derive exceedance probabilities and recurrence intervals of selected flow magnitudes for each growth stage time period. Because flow frequencies are calculated from flows measured at the South Australian border, which do not incorporate tree presence or absence, frequencies are not calculated for individual species. Rather, flow frequencies apply to time periods relative to both species.

Annual exceedance probabilities were greatly reduced under regulated flow conditions in each growth stage time period. A flow magnitude of 700 m^3s^{-1} was examined for differences between regulated and natural conditions during the various time periods. A flow magnitude of 700 m^3s^{-1} was the closest discernable value on the frequency curves to the minimum magnitude (694 $m^3 s^{-1}$) necessary to initiate flooding by overbank flows in elevated areas of the floodplain (I. Overton, pers com.). Under natural conditions exceedance was 62-78%, but decreased with regulation to 23-34% (Table 4-6). A similar trend was found for the recurrence intervals at the same flow magnitude, with recurrence intervals more thant doubling with regulation.

Table 4-6 Exceedance probabilities and recurrence intervals (years) for a moderate magnitude flow event under regulated and natural flow conditions. Values are derived from the flow frequency curves shown in Appendix 2. A flow of 700 m^3s^{-1} was the closest discernable value to the minimum value of moderate to large flows.

	Exceedance Probability *700 m^3s^{-1}*		**Recurrence Interval** *700 m^3s^{-1}*	
	Regulated	*Natural*	*Regulated*	*Natural*
Seedling	34	67	20.6	10.4
Sapling	34	78	20.6	8.9
Pole	28	71	25.0	9.8
Mature	23	62	30.4	11.2

To ensure these trends were not relevant only for moderate to large flow events, flows of 350 m^3s^{-1} were also examined (30000 ML day^{-1}) (Table 4-7). A flow magnitude of 350 m^3s^{-1} was chosen to represent small or low flows that deliver water to floodplains without overbank flooding. Declines in exceedance and recurrence intervals were present but not as pronounced as for moderate to large flows. Exceedance under regulation was between 50-70% but 85-97% under natural conditions. Recurrence intervals dropped approximately one year, except for the time period associated with mature trees, which decreased by 3.1 years.

Table 4-7 Exceedance probabilities and recurrence intervals (years) for 'small' flow events under regulated and natural conditions.

	Exceedance Probability $350\ m^3s^{-1}$		Recurrence Interval $350\ m^3s^{-1}$	
	Regulated	*Natural*	*Regulated*	*Natural*
Seedling	65	85	5.3	4.1
Sapling	70	96	5.0	3.6
Pole	62	97	5.6	3.6
Mature	50	90	7.0	3.9

4.3.1.3.3 Flow-spell analysis

Flow-spell analysis provides information regarding the distribution of low-flow days and thus the sequencing of flows, which is not apparent from flow duration curves alone (Gordon *et al.*, 1992). The graphical output of Flow-spell analysis in AQUAPAK occurs as two graphs. The first is the duration of low flow spells, which considers the length of time flows are maintained below threshold levels represented as a percentage of the mean daily flow. The duration of low flow spells represents an extended dry period. An extended period of low-flow days mimics drought conditions, which can disrupt the regeneration process by limiting the germination of seeds and reducing seedling and sapling development. To represent this reduced tolerance of younger, establishing floodplain trees to dry conditions, a spell duration of 200 days (6 months) was evaluated. The spell duration curves derived using AQUAPAK are located in Appendix 3. Longer periods, such as 1 year (365.2 day) were not well represented on the graphical outputs because even under natural flow conditions, such periods are common.

The spell duration curves for regulated and natural flow conditions illustrate the greatest changes in the 40 and 60% threshold exceedance values, particularly within the sapling and pole growth stages (Table 4-8). Seedling and mature growth stage spell durations were much less impacted at the 40 and 60% thresholds. For each growth stage, values at the 20% threshold appear to be the least impacted by regulation, and values at the 80% threshold only moderately impacted.

Table 4-8 Percent of years within each time period that a spell duration of 200 days was exceeded. Threshold values represent the percentage of mean daily flow. Values are derived from spell duration curves presented in Appendix 3.

	20% Threshold		40% Threshold		60% Threshold		80% Threshold	
	Regulated	*Natural*	*Regulated*	*Natural*	*Regulated*	*Natural*	*Regulated*	*Natural*
Seedling	--	--	2.5	12	14	14	58	40
Sapling	4	4	22	8	35	25	45	38
Pole	3	2	25	6	52	19	52	35
Mature	5	5	8	12	17	22	38	50

The second output provided by AQUAPAK is flow 'deficits' represented as the percentage of mean annual flow for each growth stage. Spell deficiency curves can be found in Appendix 4. Deficiency volumes at 10% of the mean annual flow were examined to compare changes between natural and regulated flows (Table 4-9). As with spell duration, volumes at the 80% threshold seem to be slightly impacted by regulation. Values at the 20% threshold show little impact, but that could be because deficiency volumes under natural conditions were generally not exceeded any more than under regulated conditions. Also, as with duration values, sapling and pole growth stages show most divergence from volumes under natural conditions.

Table 4-9 Flow spell analysis deficiency volumes at 10% of the mean annual flow. Threshold values are calculated from spell deficiency volumes shown in Appendix 4.

	20% Threshold		40% Threshold		60% Threshold		80% Threshold	
	Regulated	*Natural*	*Regulated*	*Natural*	*Regulated*	*Natural*	*Regulated*	*Natural*
Seedling	--	--	0.4	14	41	31	--	74
Sapling	0.4	--	15	12	70	52	85	75
Pole	--	--	10	10	70	40	88	72
Mature	4	3	17	18	50	50	80	80

4.3.2 Flood evaluation

A representation of the proportion of plots with trees related to flow is presented in Table 4-10. Growth stages for each species appear to occur in similar proportions of the sample plots, but red gum show higher proportions relating to flows. According to the flood model and tree distributions, more black box trees are within continuously flooded or dry plots. A benchmark of 579 m^3s^{-1} (50,000 ML day^{-1}) was used to assess the relative dependency on large or small flood magnitudes. This value was chosen because the majority of the floodplain does not become inundated until flows of approximately 694 m^3s^{-1} (60,000 ML day^{-1}) occur. A smaller value was chosen to compensate for inflows to backwater and flood runners that may retain water for longer periods than sheet flows at higher magnitudes. Based on this, both species occur more frequently in areas inundated by larger magnitude flows. Red gums also show some relationship with smaller flows, particularly during the sapling and pole growth stages.

Table 4-10 Comparisons of flooding characteristics for growth stages of both species. (BB: *E. largiflorens*, RG: *E. camaldulensis*)

Growth stage	% Plots with trees	% Plots related to flow	% Plots flooded continuously	% Plots dry continuously	% Plots flooded by > 579 m^3s^{-1}	% Plots flooded by < 579 m^3s^{-1}
BB seedlings	6	50	38	13	50	0
BB saplings	11	57	36	7	57	0
BB pole	10	54	46	0	54	0
BB mature	36	67	28	4	63	4
RG seedlings	6	100	0	0	75	25
RG saplings	17	100	0	0	68	32
RG pole	8	62	20	0	50	30
RG mature	31	87	13	0	72	15

The final ordination attempting to define the relationship between tree growth stages and flows resulted in a final stress of 11% and instability of 0.02. Ordination results show a relationship between advanced growth stages and flooding (Figure 4-5). The explained variance, described by r^2 (coefficient of determination), was 83% with Axis 2 accounting for 73% and Axis 1 contributing 10%. Time inundated, number of wet and dry days, and the duration of wet and dry days are the strongest vectors. These vectors appear to be more applicable to advanced growth stages of pole and mature trees for both species since these stages tend to be clustered along Axis 2. Seedlings and saplings spread more along Axis 1 where the vectors are seasonal flow frequencies.

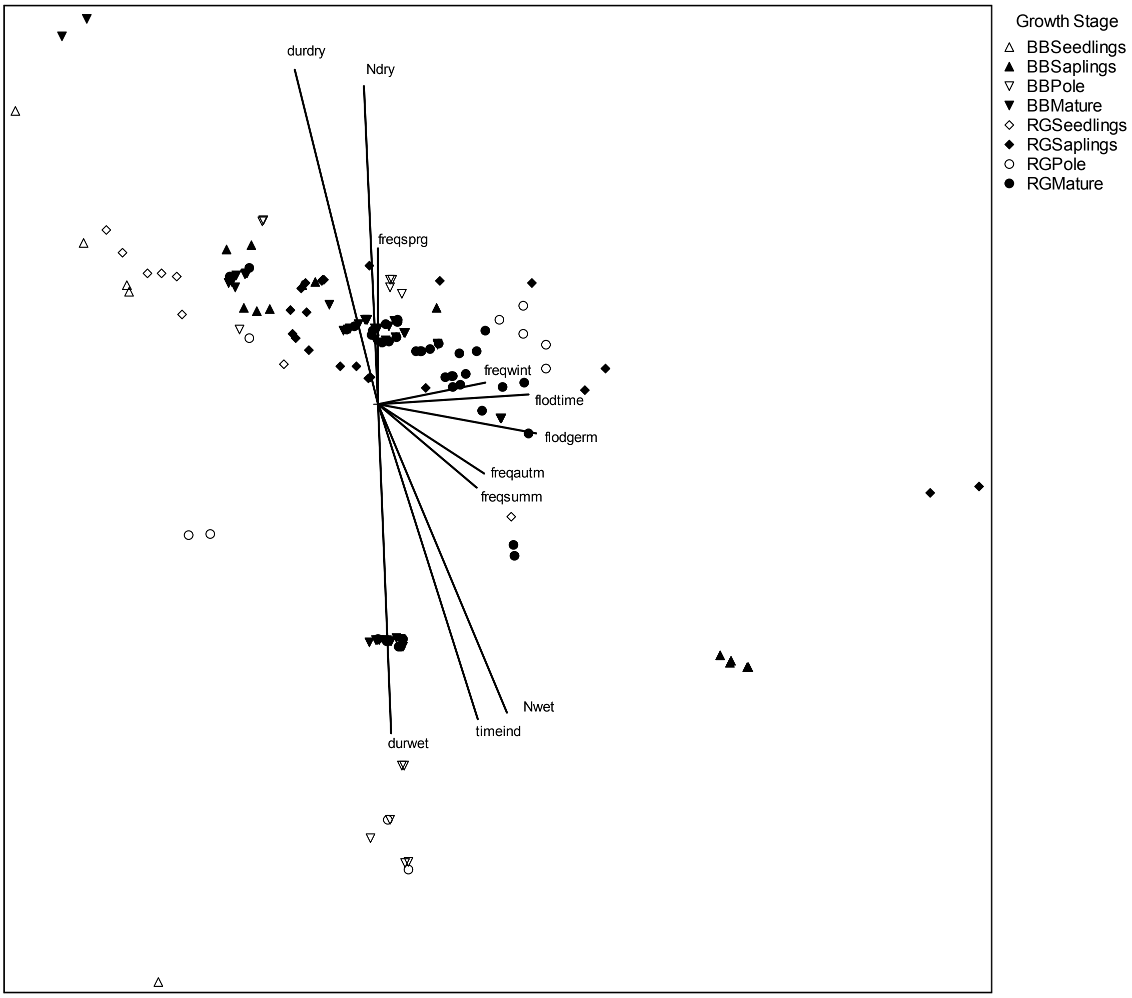


Figure 4-5 Ordination results for growth stage and flow parameters. (BB: *E. largiflorens*, RG: *E. camaldulensis*).

4.3.3 Hydrologic Characterization

4.3.3.1 Hydrologic parameters

A 2-dimensional solution resulted from the NMS ordination for the dataset of 103 years. The final stress for the ordination was <20% and axis 2 contributed most variance (Table 4-11). Overall, the ordination explained 91% of the variation within the dataset.

Table 4-11 NMS results for combined years for all red gum and black box growth stages.

Dataset	Total r^2	r^2 axis 1	r^2 axis 2	Outliers	Final Stress	Final Instability	Cutoff r^2 value
103 Years	0.915	0.675	0.240	Cdurlow Doverbk Ndurhig	11.12	0.004	0.500

The ordination shows that flow years associated with seedling and sapling growth stages are grouped in the upper portion of the graph by low pulse days and number and duration of high pulses (Figure 4-6). Pole and mature growth stages show grouping associated with each of the strong parameters, indicating no definable relation with some parameters over others. The years associated with pole trees show the greatest spread across the ordination graph. The increased numbers of years for this time period as well as the number of occurrences of extremes during this time most likely contribute to this inconsistency. Further extrapolations of tree density and flows were not feasible given the regional characterisation of the data.

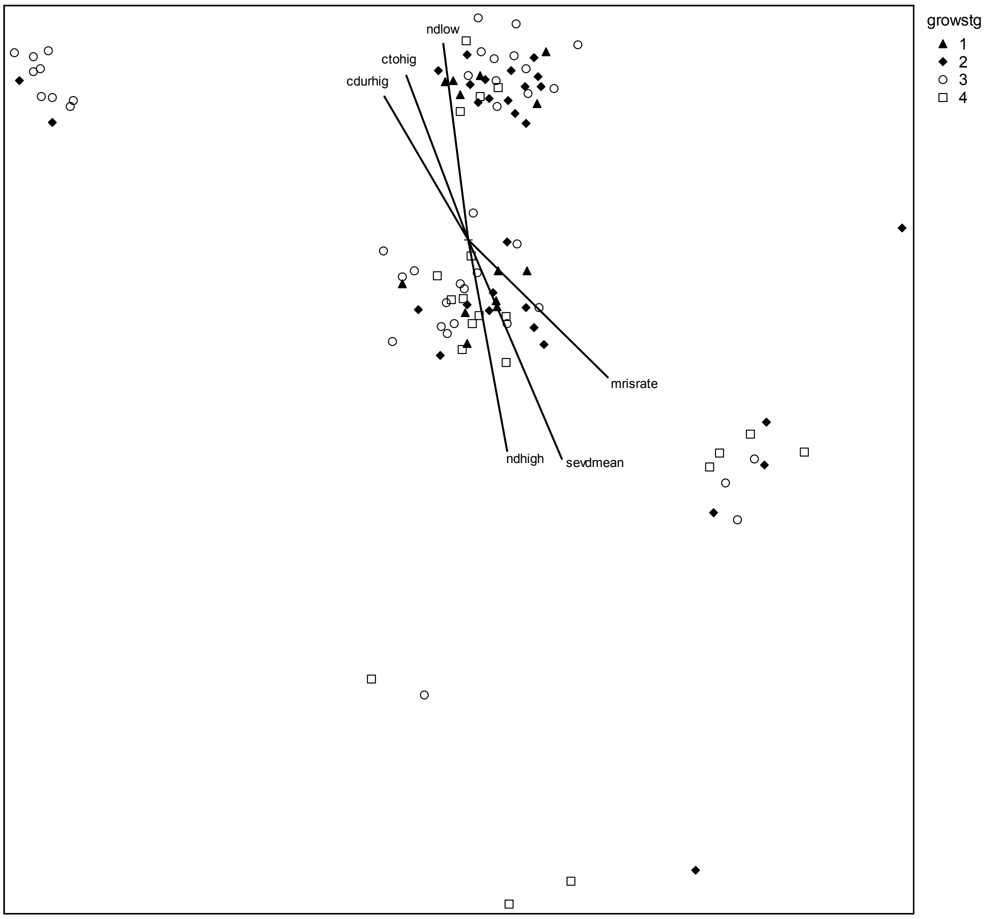


Figure 4-6 Ordination results for dataset representing all growth stages combined. (▲ = seedling, ♦ = sapling, ○ = pole, □ = mature).

4.3.3.2 Hydrologic time periods for growth stages

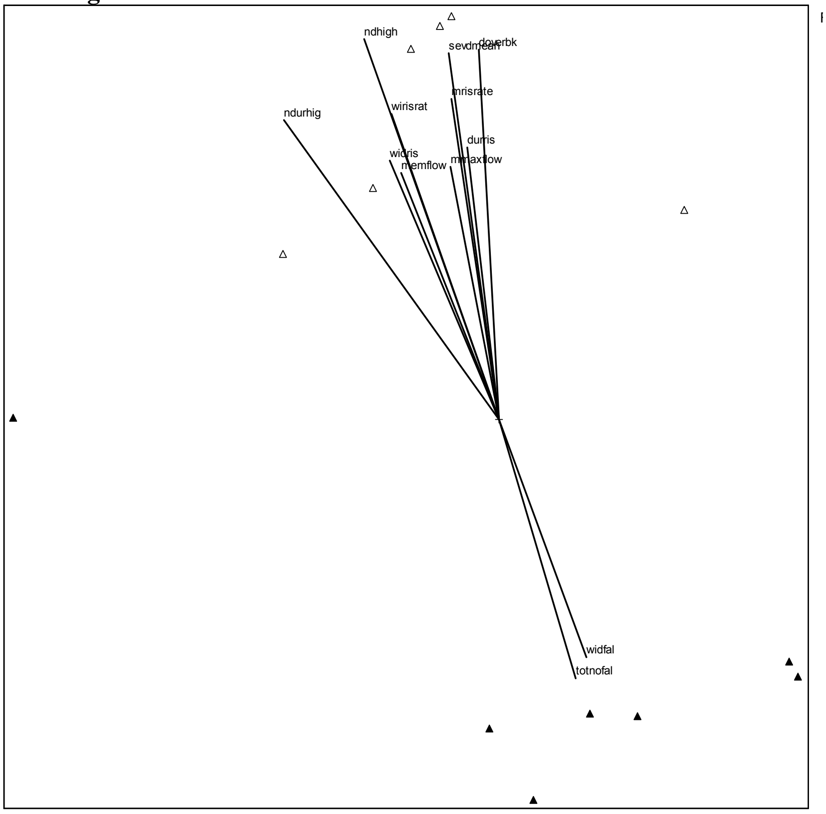
The complete 103 year dataset was divided into four groups associated with potential growth stages to determine if various hydrological components or patterns were apparent in each group that were not present when the data were evaluated as a single dataset. Ordination results for the time periods corresponding with growth stages are presented in Table 4-12. Final stress values for each period are below 10% with a large percentage of the variation (r^2) explained by the ordination. Axis 1 accounts for more than 80% of the variation for all but the sapling time period. No varimax rotations were applied since rotations did not improve the grouping. The sapling time period, driven by axis 2, has the least amount of explained variation represented by a total r^2 value less than 90%. It was the only time period where years did not emerge as outliers in the dataset.

Table 4-12 NMS results for growth stage ordination.

Growth Stage	Total r^2	r^2 axis 1	r^2 axis 2	Outliers	Final Stress	Final Instability	Cutoff r^2 value
Seedling	0.901	0.836	0.065	Cdurlow Doverbk Ndurhig Ndhigh 1991	5.47	0.005	0.500
Sapling	0.841	0.130	0.711	Doverbk Ndurhig Ndhigh	7.76	0.0005	0.500
Pole	0.932	0.901	0.031	Cdurlow Doverbk Ndurhig Ndhigh 1956 1951	7.01	0.0003	0.500
Mature	0.943	0.828	0.116	Cdurlow 1918	5.74	0.005	0.500

There was little variation between ordinations for different time periods. Each time period was most clearly grouped by high and low flows (Figure 4-7 and Figure 4-8). The division of years for each time period was most clearly explained by each year categorized as flood year or non-flood year. Within those categories fewer groups were apparent. Each time period being dominated by vectors such as duration of high and low flow pulses, number of high and low pulses the and number of days with overbank flows. The time period associated with pole growth stages was the only period to exhibit different vectors (Figure 4-8). These included an influence from the annual seven day mean and the mean rate of rise in winter and spring.

Seedling



Sapling

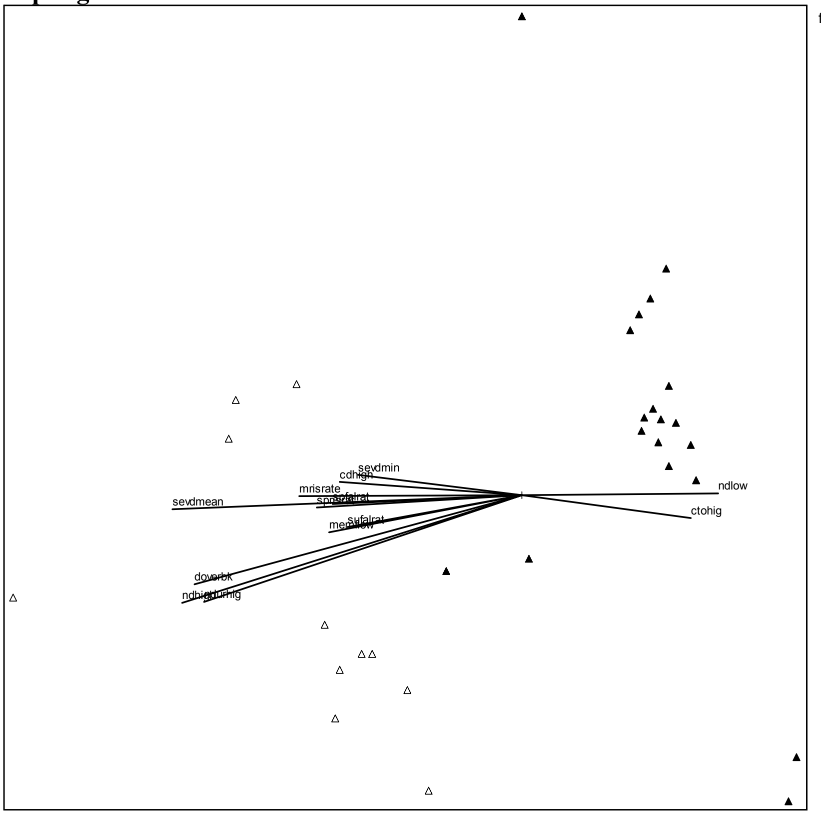
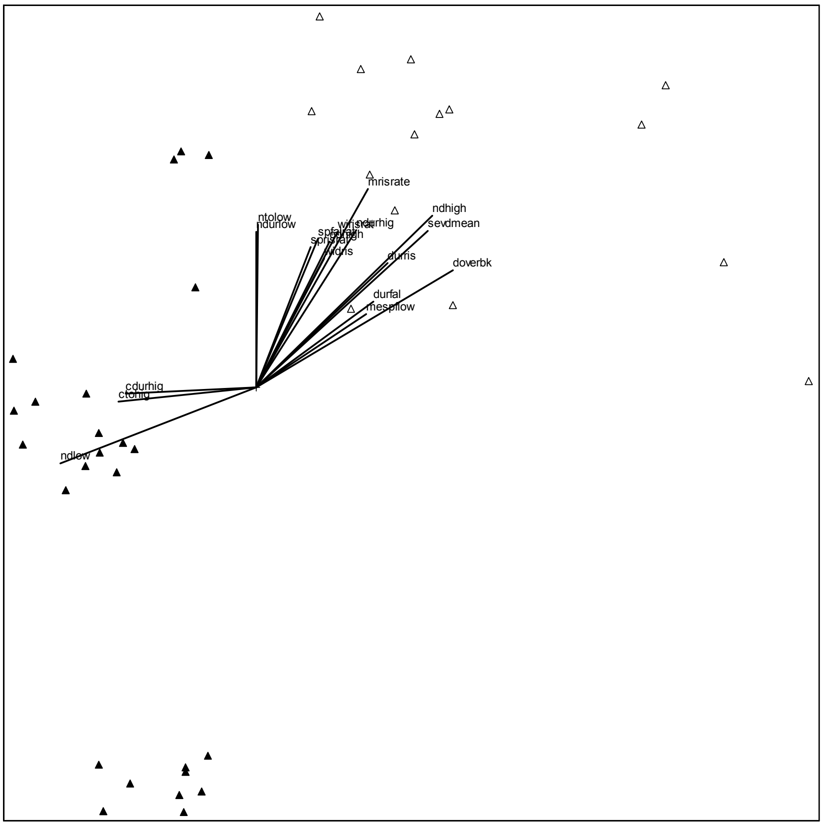


Figure 4-7 Seedling and sapling growth stage ordinations including hydrological outliers. (▲: Not flood year; Δ: flood year). A flood year is defined as a year with flows exceeding 694 m^3s^{-1} (60,000 ML day^{-1}), the minimum flow required to initiate flooding by overbank flows.

Pole



Mature

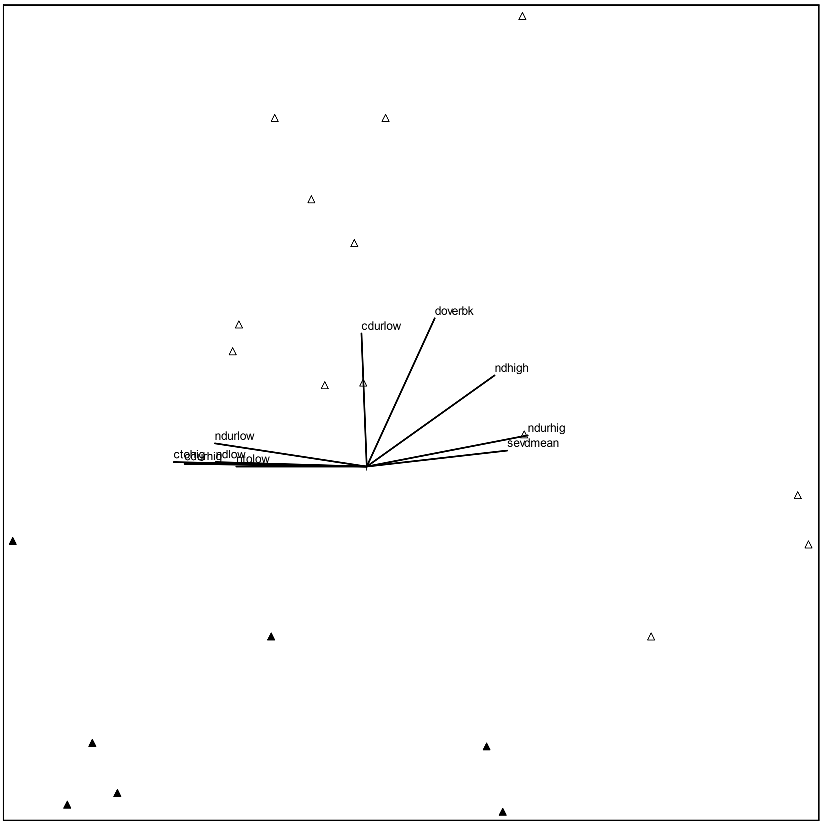


Figure 4-8 Pole and mature growth stage ordinations. Hydrological outliers are included. (▲: Not flood year; Δ: flood year). A flood year is defined as a year with flows exceeding 694 m^{3}s^{-1} (60,000 ML day^{-1}), the minimum flow required to initiate flooding by overbank flows.

The ordinations did show a distinct difference in seasonal representation of maximum and minimum flows between time periods. During the mature growth stage time period, represented by simulated natural flow conditions, minimum flows occurred more frequently during spring with maximum flows prevailing during summer and autumn. During subsequent time periods, minimum flows occurred predominately during spring and summer with some minimum flows occurring in winter during the sapling time period. These shifts distinctly illustrate the seasonal shift of flows resulting from river regulation that were shown by Maheshwari *et al.* (1995).

Maximum flows also shifted from summer/autumn during the pole growth stage time period to winter and autumn flows. No pattern was evident for the seedling or sapling time periods where all seasons were represented for maximum flows during various years.

4.4 Discussion

4.4.1 Tree distribution and flooding

The distribution of growth stages clearly shows the association between trees and flow magnitudes. Trees are absent from regions of the floodplain where flooding is rare or absent and run-off is limited. Most important is the apparent shift in localized regeneration patterns illustrated by the decrease in growth stage dispersion across the floodplain. Since advanced growth stages are more widely distributed, a wider range of germination and recruitment conditions must have been present during the period prior to full regulation of the River Murray. The younger growth stages show distinct clumping in areas where flooding is more frequent and run-off provides a more consistent water resource. Localization of growth stages may reflect changes in river hydrology resulting from regulation. For example, saplings occur more frequently than pole trees, based on distribution, but this could reflect nearly a decade of moderate flows during the 1970’s. Similarly, fewer pole trees could illustrate the impacts of a predominance of extreme flows (both high and low) during the 1950’s. Fewer pole trees germinating and establishing during this time period could reflect depressed germination and growth response to both small and large events or, equally feasible, the absence of moderate sized flows.

As outlined in Chapter 2, flow studies of the River Murray have shown a clear reduction in the frequency of moderate flows, but larger magnitude flow events are less affected by regulation. When considering that large magnitude flows provide microsite variation for germination and recruitment, and moderate flows provide necessary requirements for establishment and continued growth, such changes to the flow regime are reflected in the growth stage distribution of both species. Growth stages for both species occur in areas where moderate flow events still provide water for opportunistic germination and recruitment, but trees are absent in areas where moderate flows no longer provide surface flows for establishment.

The distribution of both tree species concurs with previous studies regarding the dependency of these trees on flooding events (MPPL, 1990; Cunningham *et al.*, 1992). Red gums are located primarily within areas that are more frequently flooded, and black box dominate along the outer edges of flooded areas and in areas less frequently flooded. The scattered younger black box on the inland regions of Wrigley Reach floodplain could be used as evidence to refute this point, except that they clearly benefit from upland irrigation of the vineyards through seepage and direct run-off. It may be that tree populations forced to rely on run-off and seepage as primary water sources will be limited in their ability to tolerate further periods of stress.

The established flow magnitudes necessary for inundation also clearly support the range of flow recurrence intervals proposed by earlier studies. Work by MDBC, (1995) and Thoms *et al.* (2000) suggests that small and moderate flows are necessary for tree maintenance. The changes in flow frequency, duration, and flow-spells all support the reliance of floodplain trees on moderate flows. Pole and sapling stages show again the high decadal flows during the 1950's and 1970's. The present work shows that red gums rely on a more diverse flooding regime and can benefit from the smallest flow event, provided that the water reaches the floodplain. Distributions suggest that red gum require flow magnitudes of 58 – 891 m^3s^{-1} and should be inundated between 1 and 4 of every 5 years for sustained population viability and expansion. These values imply moderate flows are the maximum magnitudes useful to red gum. However, Dexter (1978) references six periods during which high rates of localized regeneration occurred. Each of these periods is during, or following, a year with flows at least 683 m^3s^{-1} or greater. These periods suggest that red gums may have a stronger reliance on moderate and large magnitude flows than their distribution reflects at this site.

According to the results of this work, black box require less frequent flooding, relying on more moderate sized magnitudes (440 – 1100 m^3s^{-1}), which are the most impacted and reduced by regulation (Maheshwari *et al.*, 1995). The results also suggest that optimal inundation should occur about 10 – 15% of the time to retain viability for this species. Reliance on moderate flows may allow for an increased tolerance of stress but as flooding frequency continues to decline the trees may reach a level of decline from which they are unable to recover. Robertson *et al.* (2001) speculated that many smaller floods during a given period could simulate the effects of a single large-scale flow event. But since large scale flow events relative to black box flood requirements are relatively unaffected by regulation, the smaller scale flow events would need to be moderate sized events. If moderate sized flow events were reinstated, even at half their frequency under natural flow conditions, it could benefit not only black box but also red gums. Younger stage red gums could expand their distribution beyond simply the edge of the river and backwater inlets.

4.4.2 Key hydrologic parameters

Identifying key hydrological parameters contributing to specific growth stage responses was inconclusive. However, general patterns of growth stage response could be discerned which reiterated the conclusions based upon tree distribution. Early growth stages in red gum depend on smaller flows and older red gum and black box require moderate and large flows. Also parameters pertaining to duration and quantity of wet and dry years were most relevant for advanced growth stages. This suggests that advanced growth stages depend on the fluctuation between wet and dry periods rather than a response to continuous wet or dry conditions. Younger growth stages appear to be linked with the timing of flows or seasonal variation. While this was a weaker association it could be a consequence of the shorter time period particularly for seedlings. Thoms *et al.* (2000) suggest that advanced growth stages rely on parameters related to flood frequency, flow sequencing and flow seasonality, while the transition to seedlings relies more on duration and magnitude, but also seasonality. Findings from this study concur with the importance of flow frequency in adult stages, but also found that frequency was equally important for younger growth stages. Flow magnitude and timing also appeared to relate to growth stages. As presented in the previous section, small and moderate flows may contribute to differentiation of growth stages during eucalypt life cycles. These results may have differed if hydrological data at a smaller spatial scale had been applied. Given the distance of the site from the border, flow attenuation could be significant enough to alter the tree response to localized flows so that possibly local hydrological data (if available) could have revealed stronger correlations.

4.4.3 Hydrologic patterns

It appears that no distinct pattern in hydrological parameters can be found for each time period that could illustrate variable regeneration. Thus, most likely regeneration and recruitment are simply dependent on wet conditions. One of the few parameters that suggested a pattern was the number and duration of high and low pulses relative to younger growth stages. This implies that seedlings and saplings may require more extreme flow variation. Richter and Richter (2000) make a similar point for trees in North America, and propose that variable flow behaviour is a stronger measure of response than simply frequency and magnitudes. Variability in flows further supports the assessment of decadal scale in hydrological analysis. Analysis at this scale could locate patterns representing tree associations with extended wet and dry periods. Bren (1988a), Maheshwari *et al.* (1995) and Jolly (1996) all cite a decrease in the number of wet years since regulation, so that explanations for variable rates of recruitment and regeneration between different time periods based solely on hydrology may still be useful if different time scales are applied.

4.5 Conclusions

Growth stage distributions positively correspond with flood extents, with both *E. camaldulensis* and *E. largiflorens* dependent on moderate-sized flood events, which are the most impacted by regulation. While this study failed to identify specific hydrological parameters contributing to recruitment and regeneration, parameters relating to flow duration and frequency appear to be significant for every time period examined. This implies that neither recruitment nor regeneration should be limited for any given time period, but should be occurring equally during the time period described. These data reinforce earlier studies indicating more frequent occurrences of low flows compared to natural flow conditions.

A key finding is that advanced growth stages (pole and mature) do have differing flow requirements compared to younger growth stages (seedling and sapling). This is significant for defining environmental flow allocations. The cumulative effects of moderate sized flow events clearly indicate that allocations based solely on maintenance flow for advanced growth stages will ultimately result in population fragmentation and a further loss of intra-specific population structure.

Chapter 5 Reproductive Potential

5.1 Introduction

Surveys of floodplain eucalypts on the Murray, especially in South Australia, indicate large-scale declines in tree vigour, presumably from ‘drought-like’ conditions caused by a reduction in river-floodplain connectivity. Floodplain eucalypts throughout the Lower Murray region exhibit symptoms consistent with prolonged water stress, which causes health decline and dieback (Landsberg and Wylie, 1983; Eldridge *et al.*, 1993; MDBC, 2003). Lichtenthaler (1996) illustrated the relationship between stress and permanent physiological damage. Physiological functions like photosynthesis and translocation are maintained under normal conditions, but as stress increases these functions are reduced. Plants can recover if the stress abates before the threshold of tolerance is exceeded, otherwise the plant can no longer compensate by leaf senescence, fruit shedding, canopy reduction or other mechanisms, and permanent physiological damage occurs. This will result in outwardly visible signs of reduced health. Lichtenthaler (1996) emphasised that, under continuous stress, a plant’s ability to respond to favourable conditions decreases, and prolonged stress leads to a decline from which plants may not recover.

Grimes (1987) demonstrated that the effects of stress high enough to limit growth would be exhibited most dramatically within the canopy of trees. Water stress may produce a reduction of leaf area (Kozlowski *et al.*, 1991) reducing photosynthesis and the photosynthate available for reproductive growth, which is more vulnerable to damage than vegetative growth. Translocation of carbon to reproductive structures can be a stress-response mechanism, but rapid turnover of reproductive structures, associated with damage by drought, high temperatures, insects or disease (Kozlowski *et al.*, 1991), may drain resources needed for stress recovery (Chaves *et al.*, 2003). When carbon allocations are depleted to a critical level, vegetative and reproductive growths are reduced, affecting phenology and seed fall. The stress responses of individuals are then extended to population processes, including regeneration.

Reproductive structures, particularly seed supply, are ‘rarely limiting’ in eucalypts (Boomsma, 1950; House, 1997), due to their high reproductive capacity maintained by frequent production of large numbers of flowers, fruits and seeds. Although it is acknowledged that phenological events reflect carbon-allocation strategies (Montenegro, 1987; House, 1997), this may understate the role of parent trees in the regeneration process by presuming that reproduction is consistent regardless of health. Are the parents exhibiting critical levels of stress and, if so, is this affecting reproductive potential? Also, are the responses similar for co-occurring river red gum and black box? There are potential indicators of stress and responses to stress in different reproductive phases, including seed fall (canopy to soil), seed viability and the phenology of budding, flowering, and fruiting.

The health of parent trees is the most visible expression of population decline but other, less apparent effects may be involved. In the present chapter, the implications of reduced vigour for the production and viability of seeds are considered. The focus is on regeneration stages I, II and III (flowering, seed storage, seed fall) of the parent trees, and Stage X in the mature growth stage, including the maturation of adult trees as an expression of bud development (Chapter 2). This chapter examines the relationships between observable tree health and reproductive potential in the two Murray floodplain species. Three potential indicators, namely seed fall and viability and the phenology of budding, flowering and fruiting, are used to address four hypotheses:

(1) Seed fall and seed viability should increase with parent health status (*i.e.* lower in unhealthy trees than in healthy trees);
(2) The magnitude and frequency of flowering should be less in unhealthy trees than in healthy trees;
(3) Rates of bud initiation and development should be reduced in unhealthy trees; and
(4) Black box reproduction will be more robust than river red gum because of their decreased reliance on continuous water (Chapters 3 and 4).

5.2 Methods

5.2.1 Tree vigour

Ten vigorous, healthy trees and ten unhealthy trees of each target species were located at Banrock Station (Figure 5-1). The original plan was to select half of the *Eucalyptus camaldulensis* and half of *Eucalyptus largiflorens* trees from the Wrigley Reach floodplain and half from the Banrock floodplain, but neither species was evenly distributed across both areas of the site. Instead, an equal number of ***trees***, regardless of species, were selected from the Banrock and Wrigley Reach floodplains. Selections were based on pre-defined criteria, explained below.

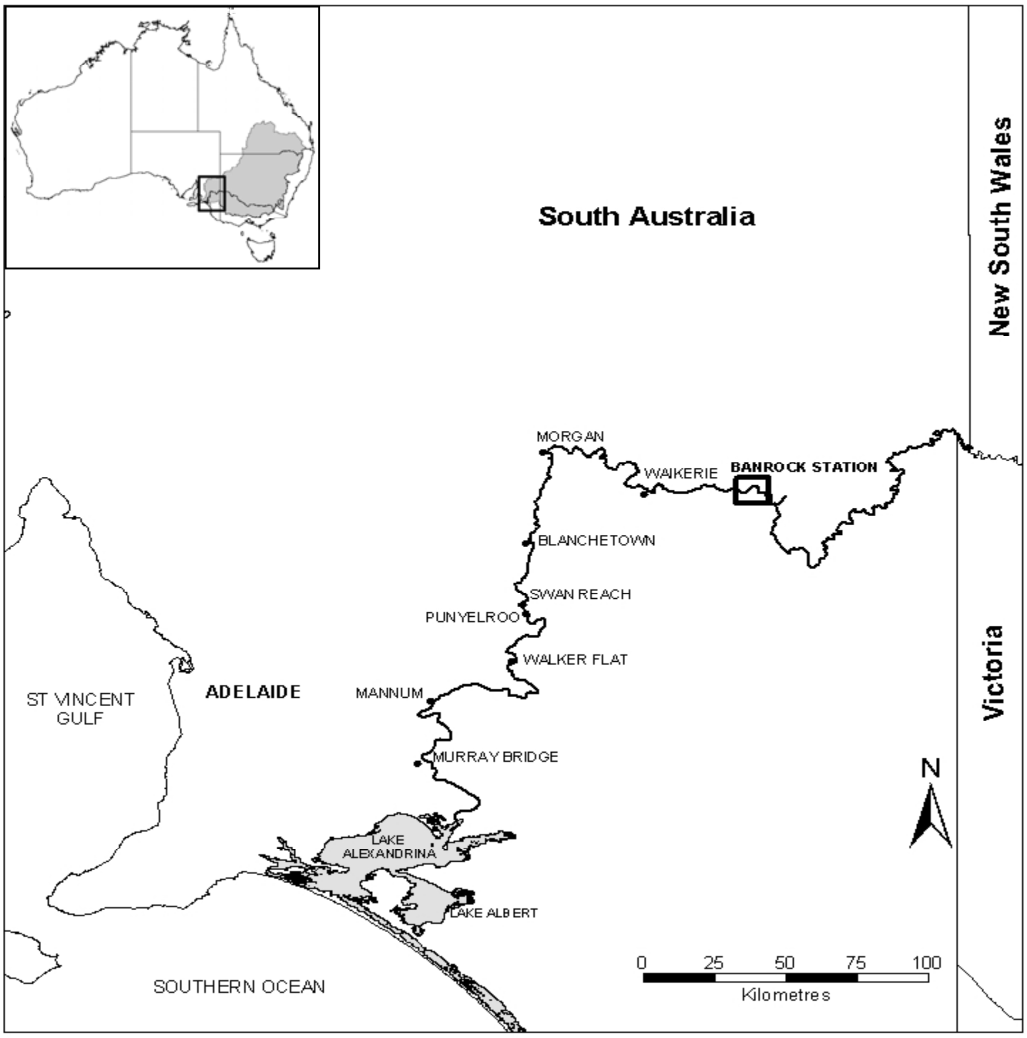


Figure 5-1 Banrock Station (square outline) is located in South Australia within the Murray-Darling Basin.

1. Relatively isolated and dominant

Isolation and dominance within the population structure were primary factors for selection. Because seeds may be widely dispersed by wind, this criterion attempts to reduce the possible influence of seeds from neighbouring trees of different health status.

2. Mature, but not senescent, age classification

Most eucalypts do not flower until approximately 20-30 years' age, and so do not produce seeds during early growth (Cremer *et al.*, 1978). Once flowering and seed production begin, they increase until senescence (Jacobs, 1955). Thus, peak seed production and flowering are from mature but not senescent trees.

3. *Flower buds or fruit capsules present in the canopy*

The presence of flower buds or fruit capsules within the canopy indicates that an individual tree has recently been vigorous enough to expend energy stores to produce reproductive structures. Even for unhealthy trees, some evidence of reproductive capacity was necessary for selection.

4. *A size accessible for collecting from the canopy (DBH and height)*

Diameter at Breast Height (DBH) and height were measured for all trees, as in Chapter 3. Because flower buds and fruit capsules were to be monitored, the tree canopy had to be accessible either from ground level or through use of a ladder.

5. *Year round accessibility*

Annual flooding at Banrock (Chapter 3) limits access to parts of the floodplain. Trees within the inundated area were excluded from selection, as monthly monitoring would be impossible. Isolated areas of the floodplain were also excluded, to facilitate rapid sample collection each month. To reduce possible bias resulting from such exclusions, effort was taken to include trees bordering the inundated areas.

6. *Fitting vigour/health description.*

Tree health was categorized as ‘Good’ or ‘Poor’, based on a visual evaluation of five tree-crown factors. Trees of ‘Moderate’ health were excluded. An evaluation of the extremes was deemed sufficient to indicate the impacts of reduced vigour. Following Grimes (1987), the crown factors included crown position, crown size, crown density, proportion of dead branches, and degree of epicormic growth. While Grimes’ Index was developed originally as a means to classify the relative growth potential of stems for silvicultural treatments, it has been modified as a health index for eucalypts (Eldridge *et al.*, 1993; Barrett, 1999). In both the original growth index and the modified index, ‘healthy’ trees have full, open crowns, robust crown sizes, high leaf density, few dead branches and little or no epicormic growth (Figure 5-2a and b). ‘Unhealthy’ trees are alive (not near death), with thinning crown size and leaf density, more dead branches and a high proportion of epicormic growth (Figure 5-2c and d). No attempt was made to diagnose the reasons for poor health. The index was applied specifically as outlined in Grimes (1987), and diameter mean annual increment values were calculated for each tree (Appendix 5). The range of values represents the relative growth potential based on canopy factors.

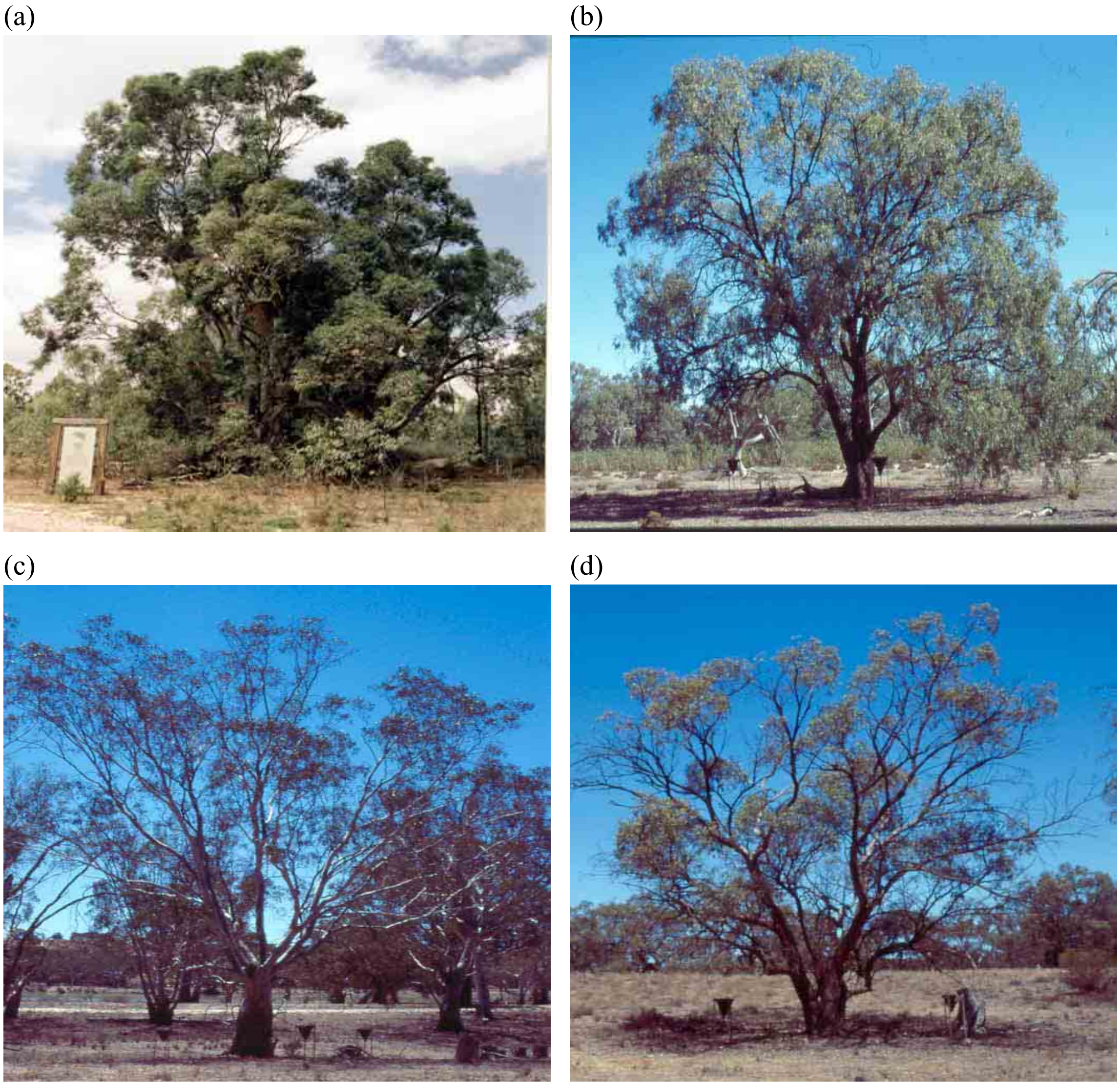


Figure 5-2 Examples of 'healthy' red gum (a) and black box (b) at Banrock Station.

Forty trees were selected. Following assessment of the size variations within species, and health categories and the time needed to complete observations, the number of trees within each category was reduced. To standardize trees sizes within each category, and prevent bias in seed-fall from larger trees, trees with extreme values of height and diameter were excluded. The final complement included six 'good' and six 'poor' trees of each species.

5.2.2 Seed fall and viability

Because of the small sizes of the seeds from both species, seed fall and viability were assessed by germinating seeds collected in elevated seed traps. Three traps were placed under the active canopy to capture the highest proportion of seed fall. Pudney (1998) found that while nearly 75% of seeds dispersed within a distance of 1.5 times the parent tree height, the highest proportion of seed fall occurs directly beneath and at the edge of the canopy. Seed predation can strongly affect the capture rates in dry environments (Yates *et al.*, 1995). Elevated traps were therefore chosen to restrict seed predation. Traps were constructed of weed mat cones (45 cm diameter x 65 cm deep) supported by a ring suspended approximately 1 m above ground level on three hardwood garden posts. This design was similar to a funnel trap tested by Page *et al.* (2002) shown to have good capture rates while being easy to construct and service. The weed mat used for the traps had a tight weave, allowing water to drain from the trap without losing seeds. Throughout the study, a number of traps close to the river were exchanged with cones constructed from broadcloth, because of damage sustained by high winds.

Contents of the traps were collected monthly between June 2002 and June 2004. The contents (seeds and debris) of all three traps were combined, as a single sample for each tree every month. Samples were returned to the laboratory and air-dried for 24 hours. The samples were then sieved using progressively smaller apertures between 1.18 mm and 300 µm to remove large debris and isolate seeds and chaff (unfertilized ovules) as much as possible. The final data were for 22 samples, because June samples for both years were excluded from analysis (June 2002 samples were damaged by faulty laboratory equipment, and in June 2003 rainfall prevented collection of samples).

Seeds were germinated using the emergence technique following guidelines established by Gunn (2001) which are similar to methods for soil seed banks (Brown, 1992). The sieved samples were placed on filter paper (Whatmans No.1) over wet vermiculite in 9 cm diameter petri dishes. Distilled water was added to keep samples moist. Variations in temperature and light promote high levels of germination for eucalypts in semi- and arid areas of South Australia (Grose, 1962; Bonney, 1994). To accommodate stratification, petri dishes were placed in a controlled temperature room with 12 hours of light where temperatures were manually fluctuated between 15 and 35°C at 12 hour intervals (see Grose and Zimmer, 1957; Grose and Zimmer, 1958). Dishes were checked daily, and eucalypts with fully emerged radicles were tallied and removed. Germination continued for three weeks or until no germinates emerged for three consecutive days. Upon completion, non-germinated seeds were tallied and squash tested for viability (Gunn, 2001). Squashed seeds were categorized as viable or non-viable depending on the firmness of the endosperm. The number of viable, non-germinated seeds was added to the total number of germinates for each sample. This value was used to assess the seed fall of each tree within the defined health categories. Germination values (including viable seed counts) were compared with the tally of non-viable seeds and calculated the percentage of viable seeds relative to non-viable seed under favourable germination conditions. These data provide some indication of potential regenerative capacity based on seeds within tree canopies.

5.2.3 Flowering phenology and fruit formation

Flower bud and fruit capsules were monitored concurrently to determine the timing and rates of formation. At the first initiation of buds, 50 buds were flagged within the canopy of each sample tree. Buds were chosen from at least three different locations within the canopy to reduce the influence of developmental changes relevant to aspect and prevailing winds or sun exposure. The developing flower buds were measured monthly across the widest portion of the hypanthium. This represented the rate of bud development prior to flowering and was intended to define the relative size that buds much reach before flowering is initiated.

Bud measurement continued through flowering and fruit maturation. Post-flowering measurements represented the rate of fruit capsule development and seed maturation. Fruit capsules were measured until seed shed occurred or fruit capsules disappeared from the tree. Throughout the 2-year study, as new bud crops initiated they were included in the monitoring in an attempt to define the sequence of budding, flowering, and fruiting.

Flowering abundance was also monitored and compared for both tree species. Flower abundance was recorded as the percentage of the canopy in flower during each sampling month. Flowering means for each health category were calculated at monthly intervals to represent season and duration of peak flowering.

5.3 Results

5.3.1 Vigour

Because of the changes to include an equal number of trees rather than an equal number of species on both sides of the floodplain, *E. largiflorens* trees chosen for this study were predominantly located on the Banrock floodplain while *E. camaldulensis* trees tended to be on the Wrigley Reach floodplain (Figure 5-3). This resulted from a lack of healthy red gum trees on the Banrock floodplain, except around the perimeter of the annually flooded wetland. Black box trees of both health categories were found on both sides of the floodplain, but were divided so that Wrigley Reach and Banrock were equally represented. Healthy black box were generally located near the river in close proximity to red gums, while those in poorest health occurred inland. As illustrated by Chapter 4, this is attributable to a combination of reduced frequency and magnitudes of inundating floods and the absence of substantial run-off within these areas.

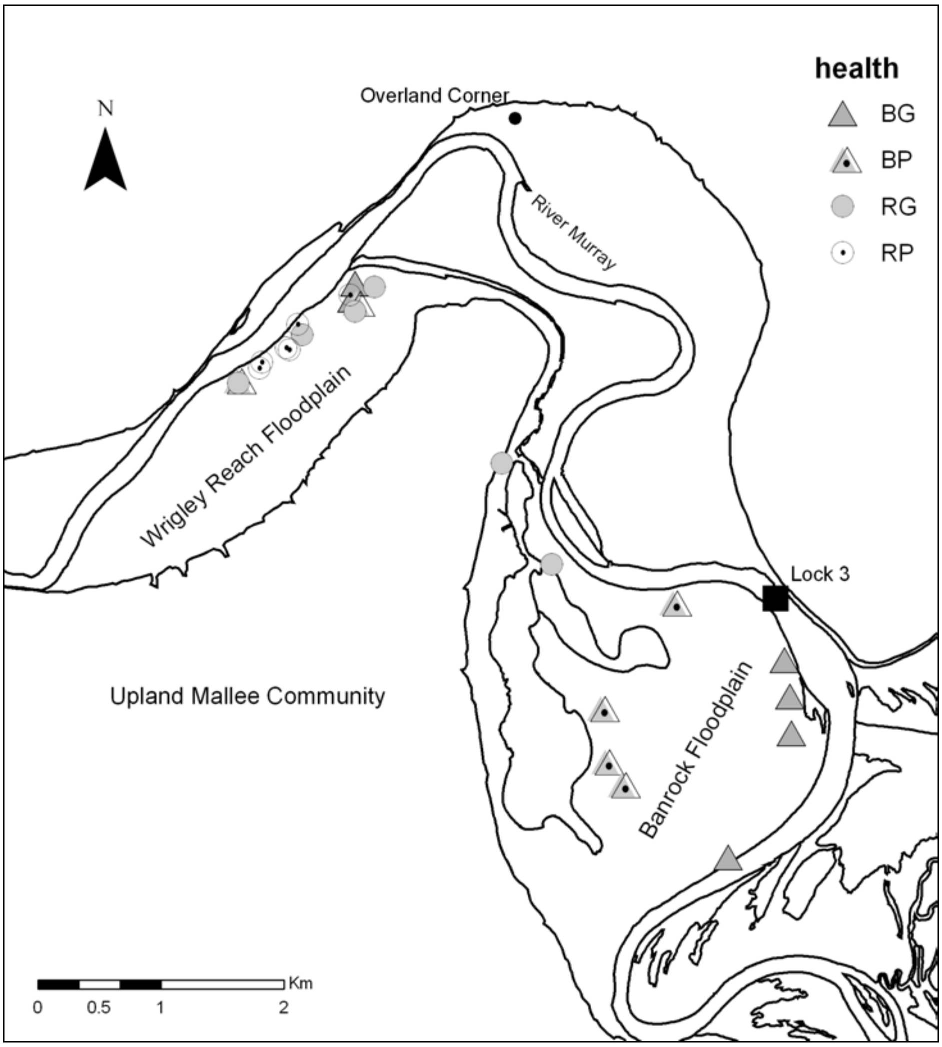


Figure 5-3 Distribution of *E. largiflorens* and *E. camaldulensis* trees categorized by vigour (BG = black box healthy; BP = black box poor; RG = red gum healthy; RP = red gum poor).

Crown assessment values representing tree health categories within each species indicate that trees included in this study fit the modifications of the health index (Table 5-1). The strict application of Grimes' Index showed that 'health' values for the sample trees were within the range of values representing diameter increments or growth. Healthy trees received 'good' ratings while poor trees received 'very poor' ratings. Of 12 healthy trees evaluated, three black box and one red gum received 'excellent' ratings. However, one visually healthy red gum received a 'poor' index rating. Of the expected 'poor' trees, both species were easily rated as 'poor' or 'very poor'. Again, red gums were rated differently than expected using Grimes' Index with two 'poor' trees receiving an 'average' rating rather than 'poor' or 'very poor'. All deviations from the expected ratings were within the outer boundaries of the defined class.

Thus, a slightly different rating in any of the canopy characteristics could have altered the initial rating to correspond with expectations.

Table 5-1 Mean tree health category values calculated using crown assessment conditions (RG = red gum; BB = black box). *dmai: mean annual diameter breast height increment. Taken from Grimes (1987) to represent the expected amount of incremental diameter growth reflected in crown condition factors.

Tree category	Mean crown assessment value	Health rating	dmai*
RG Healthy	21.67	Good	0.617
RG Poor	15.42	Very Poor	0.179
BB Healthy	23.25	Good	0.751
BB Poor	10.25	Very Poor	0.139

Height and diameter values differed between species (Figure 5-4), illustrating again the wide variation in size classes for the dominant tree species encountered from Chapter 3. Black box exhibited a greater degree of height and diameter difference between health categories than red gum. But, height and diameter tended to be smaller in poor trees for both species. An exception was red gum DBH where poor trees had slightly higher mean values than good trees.

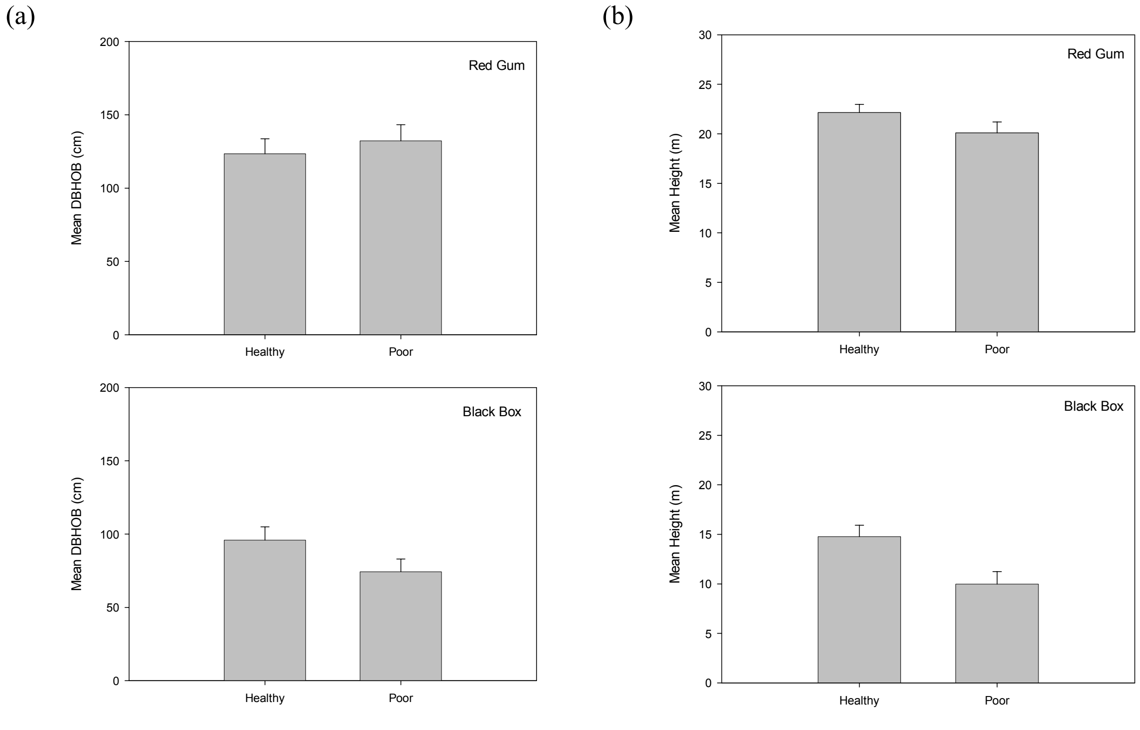


Figure 5-4 Mean DBH (a) and Height (b) values for health categories of each species. Error bars represent + 1 standard error.

5.3.2 Seed fall

5.3.2.1 Quantity and quality of seeds

Seed fall and viability were compared using two-way ANOVA. Data were log- and arcsine-transformed, respectively, and normality and homoscedasticity were confirmed using the Shapiro-Wilk and O'Brien Tests ($\alpha = 0.05$). Results are presented in Table 5-2 and Table 5-3. No significant interactions were detected. There were no significant differences between germination or viability in the two species, but significant differences were apparent between health classes, for both variables.

Table 5-2 Two-way ANOVA results for Log (germination) between species of different health categorization.

SOURCE	df	SS	MS	*F*	*P*
Model	3	16.86	5.62	29.23	
Species	1	0.60	0.60	3.14	0.08
Health	1	16.25	16.25	84.51	<0.0001***
*Health*Species*	1	0.007	0.007	0.04	0.84
Error	84	16.15	0.19		
Total	87	33.01			

Table 5-3 Two-way ANOVA results for seed viability between species and health classes.

SOURCE	df	SS	MS	*F*	*P*
Model	3	0.34	0.12	4.63	
Species	1	0.02	0.02	0.86	0.36
Health	1	0.33	0.33	12.87	0.0006***
*Health*Species*	1	0.005	0.005	0.18	0.67
Error	84	2.17	0.03		
Total	87	2.53			

The evident differences between health categories could be reflecting variation between individual trees rather than health categories. To examine this point, nested ANOVA was conducted on trees within health categories. As shown in Table 5-4 and Table 5-5, significant differences ($p < 0.001$) in germination counts and seed viability were evident between trees. F ratios were re-calculated to determine the variance of health categories exclusive of individual trees. Health categories for seed viability were found not to significantly contribute to the overall variance ($p = 0.33$, $F = 1.01$, df = 1, 22), but health categories did significantly contribute to the variance for germination counts ($p = 0.0002$, $F = 19.04$, df = 1, 22). Thus, seed viability appears to be determined by the health of the individual trees rather than a more broadly applied mean visual health within species. Differences in germination counts appear to be equally impacted by the mean health of the species and individual tree health.

Table 5-4 Nested ANOVA results for germination between trees within health categories.

SOURCE	df	SS	MS	*F*	*p*
Health	1	72.92	72.92	282.47	<0.0001***
Trees[Health]	22	84.29	3.83	14.84	<0.0001***
Error	504	130.10	0.26		

Table 5-5 Nested ANOVA results for seed viability between trees within health categories.

SOURCE	df	SS	MS	*F*	*p*
Health	1	1.08	1.08	7.22	0.0075**
Trees[Health]	22	23.55	1.07	7.15	<0.0001***
Error	504	75.44	0.15		

5.3.2.2 Timing of seed fall

The timing of seed fall for red gum and black box health categories was assessed using the monthly germination counts. Box whisker plots were initially used to identify the variation in distribution of counts between sampling months (Figure 5-5). Healthy black box was the only group clearly illustrating differences in the distribution of germination counts, with little overlap of the whiskers showing the outermost values of the data. Healthy black box illustrated a peak in seed fall in March for the first year of the study. Lowest seed fall occurred in winter of the first year but shifted to autumn during the second year. For healthy and poor red gum and poor black box, the distributions were relatively similar. Therefore, distinct peaks and falls in the timing of seed fall were not easily detected.

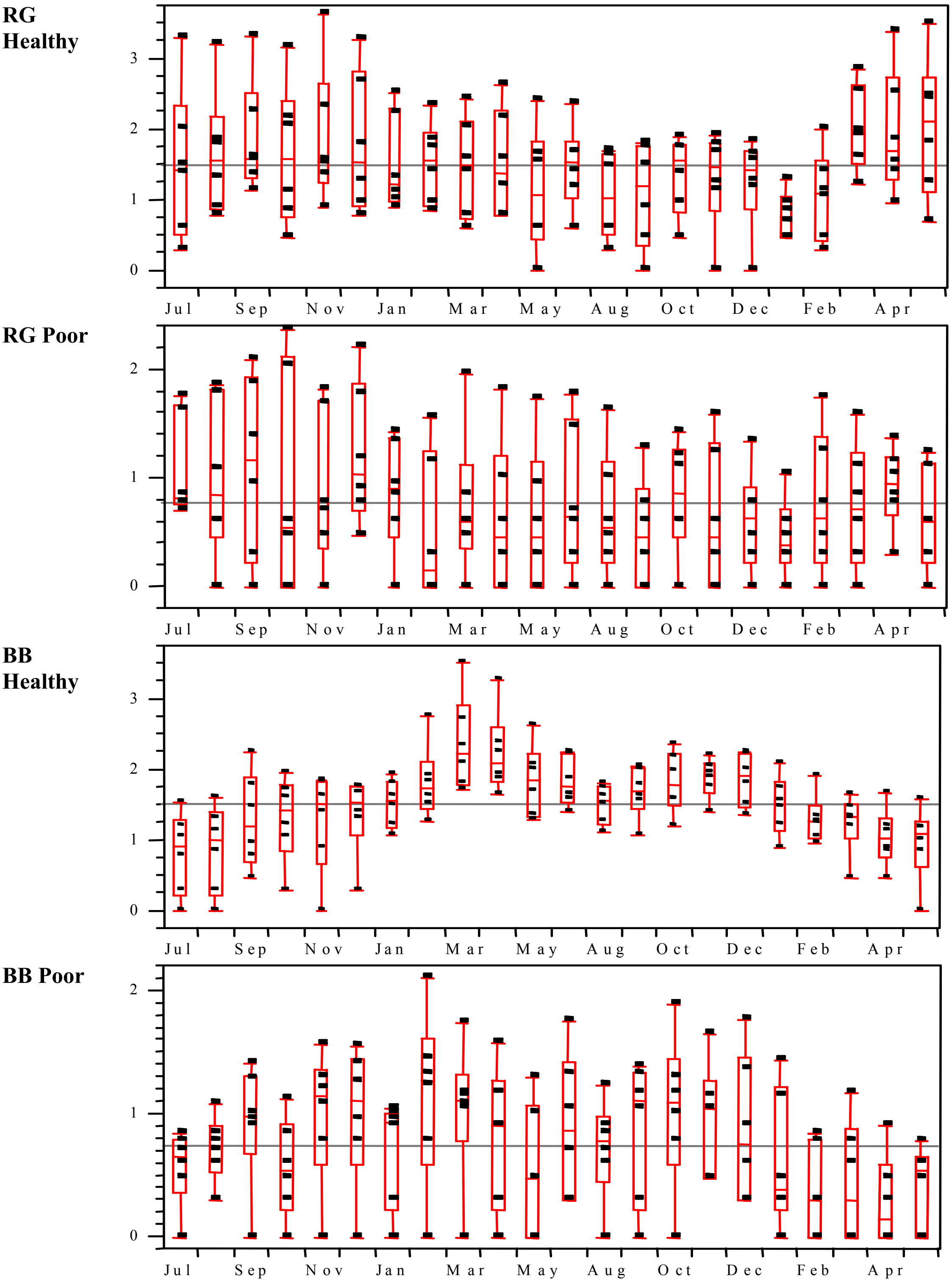


Figure 5-5 Box whisker plots indicating the distribution of germination counts relative to tree health categories. The ordinate axis for all plots is Log(germination count). The scale differs for healthy and poor trees because counts between health categories and species varied by magnitudes. The box represents the 25% and 75% quartiles of the data and the whickers extend to the outermost value within the calculated quartile. Given the difficulties in illustrating variation in health using these plots, additional methods for comparing differences are presented in the following sections.

Histograms representing timing of seed fall for both species and health categories were then created using mean seed counts (Figure 5-6). In accordance with the results from the previous section, the magnitude of difference between seed fall for health categories was obvious.

As derived from the Box-whisker plots, seed fall in healthy black box trees peaked in late summer and early autumn (February, March and April) during the first year of monitoring, and changed to mid spring, early summer during the second year (October, November and December). The second year peak was not as great as the first and the Box whisker plots show that there was relatively little change in seed fall between the initial peak in March and the following spring. Figure 5-6 shows seed fall for poor black box was more variable, with only a minor peak during February in the first year (one month before the highest value of healthy trees). During the second year, fluctuations were more like those of healthy trees, with minor peaks in October and December.

In healthy red gums, peak seed fall occurred in November of the first year and then was just beginning to peak during mid to late autumn (April and May) of the second year. The timing of this second increase differed from all other groups indicating some process initiating seed fall that possibly did not affect other tree groups. As in the black box groups, poor red gums had only minor seed fall peaks compared to healthy trees along with much more variation in monthly seed fall. Poor red gums peaked in October during the first year with minor peaks in July and February of the second year. Similar to poor black box, poor red gum peaks during both sampling years occurred one month *before* those of healthy trees. The decline in seed fall during the final months of monitoring was similar to both black box groups.

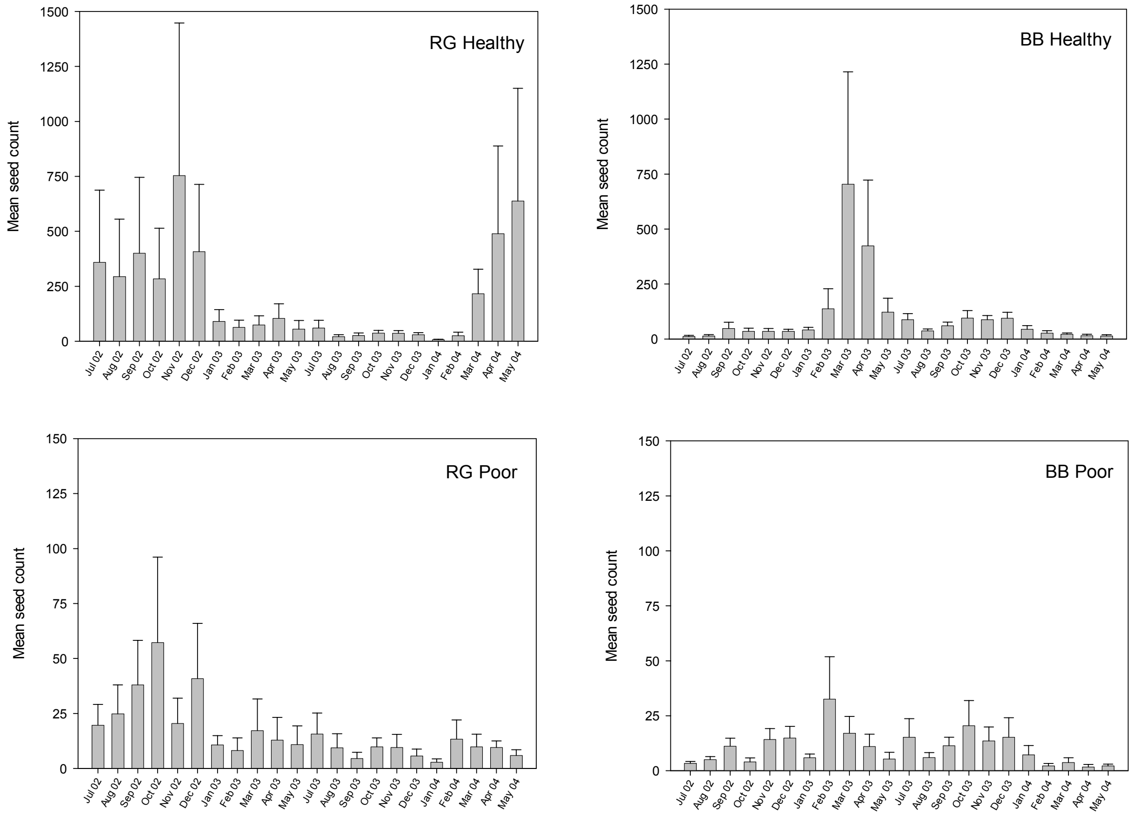


Figure 5-6 Mean monthly seed fall for red gum and black box trees during 22 month sampling period. Note the difference in scale of the ordinate axis between healthy and poor tree groups. Error bars represent + 1 standard error.

5.3.2.3 Association of seed fall and rainfall

Rainfall during the two-year study was erratic, typically so for semi-arid regions (Molles *et al.*, 1992). The first year of monitoring followed one with high rainfall, and the second followed one of the driest years on record. Figure 5-6 shows the distinction between wet and dry years as seed fall for all categories was greater during the first year of the study compared to the second. Comparing monthly rainfall at Banrock Station (Figure 5-7) to the seed fall histograms indicates a strong association between localized rain patterns and seed fall events in the absence of alternate sources of available water. The comparisons yield an approximate 1-2 month delay between higher rainfall and increases in seed fall. This delay is not as evident for poor trees of either species. The pattern of seed fall in poor trees follows that of rainfall, particularly during the first year of the study. Delay between rainfall and seedfall in healthy red gums showed both trends. During the first and last months of the study no lag was evident, but the intermediate times show the monthly delay.

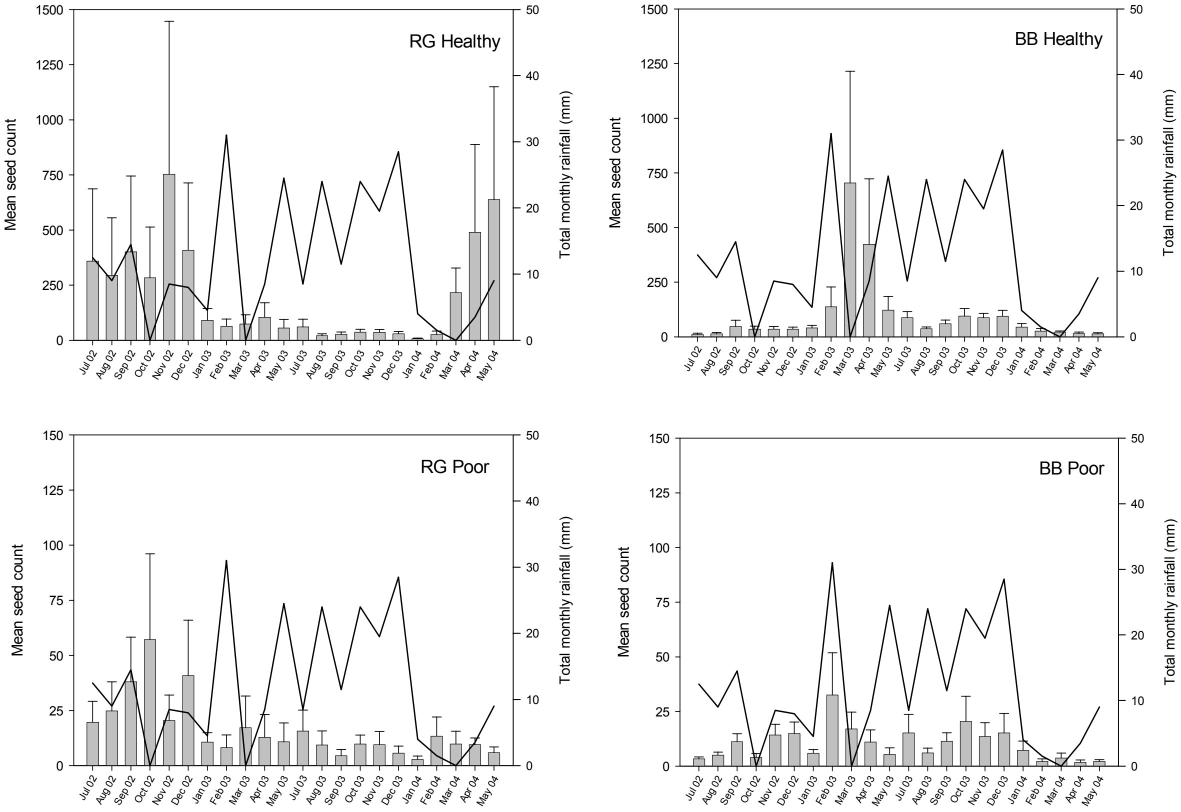


Figure 5-7 Rainfall (solid line) combined with seed counts for health categories of red gum and black box trees. Error bars represent + 1 standard error.

5.3.3 Flowering phenology

5.3.3.1 Flower abundance and frequency

Flowering abundance was reduced in poor black box trees. Figure 5-8 illustrates healthy black box flowering abundance was 50-80%, while flowering in poor trees averaged 10-40%. Similar to seed fall, flowering in both categories during the first year exceeded flowering measured during the second year. Healthy black box was the only category to begin a third flowering event towards the end of the sampling period.

Poor red gums also had reduced flowering abundance compared to healthy red gums, but only during the first year of the study. Healthy red gums had 30% flowering while poor trees had 25% flowering. The second flowering event differed because both health categories had a mean flower abundance of 50%. These values during the second year exceeded values obtained during the first year and were similar to flowering abundance measured in healthy black box for the same time period.

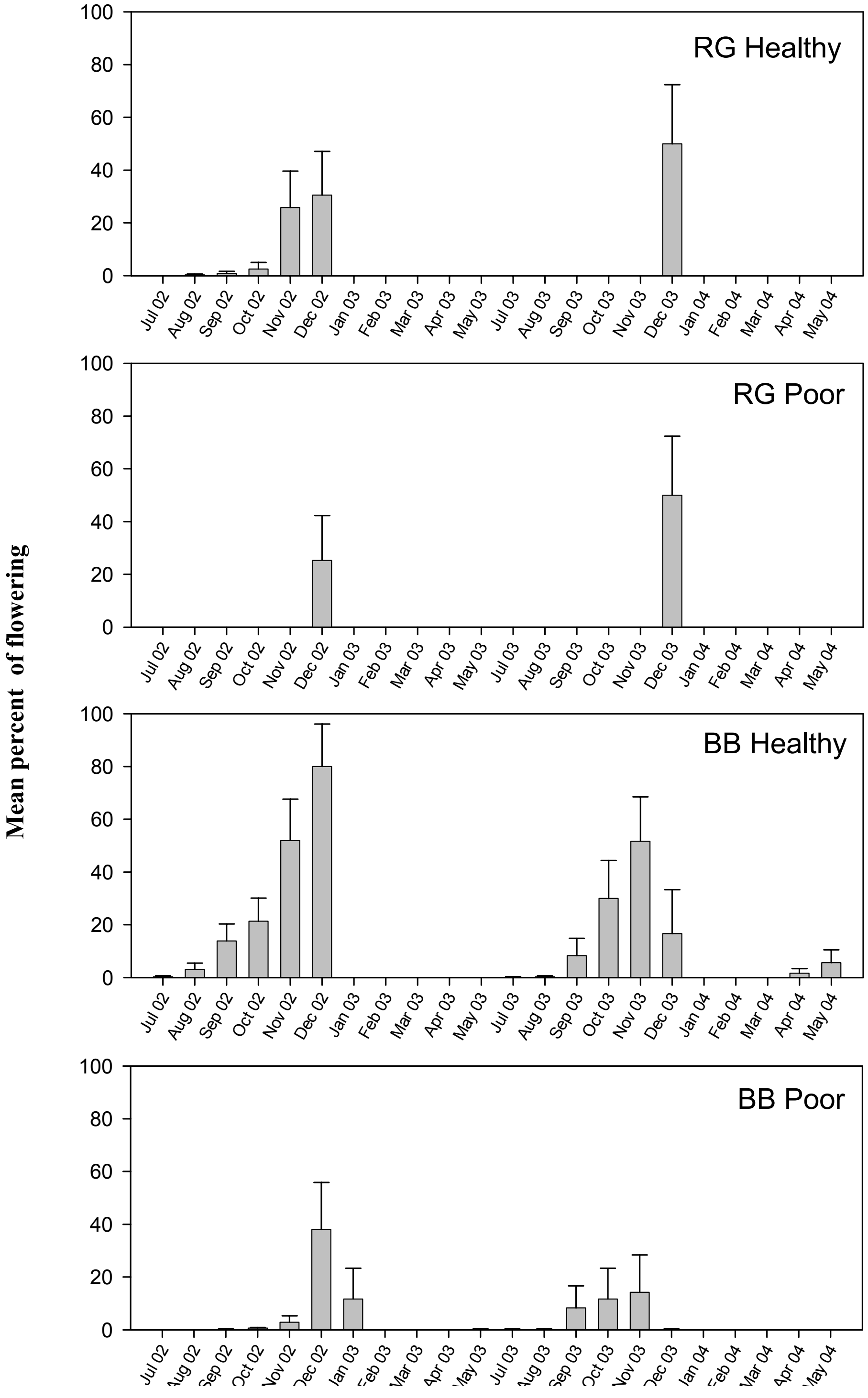


Figure 5-8 Flowering times for health categories of red gum and black box trees (n=6 for each category). Error bars represent + 1 standard error.

The variation in flowering abundance implies no detectable pattern between species, but the absence of patterns may result from variation within species and the small number of trees examined. Table 5-6 shows that both categories of red gum had few trees contributing to the mean flowering abundance. Flowering occurred in only half of the poor red gums during both years and during Year 2 half of the healthy trees failed to flower. Five of six healthy red gums flowered during Year 1 of the study.

Black box also had different numbers of trees flowering between years. All trees flowered during Year 1, but substantially fewer trees contributed to mean flowering during the second year. The most dramatic decrease was only two of six poor black boxes flowering compared with four healthy trees.

Table 5-6 Number of trees contributing to mean flowering within health categories (n = 6). Note that during Year 1 flowering occurred in all Black Box trees evaluated. Differences between health categories were in the percent of the canopy in flower.

	FLOWERS PRESENT	
	Year 1	**Year 2**
RG Healthy	5	3
RG Poor	3	3
BB Healthy	6	4
BB Poor	6	2

5.3.3.2 Timing of flowering events

All but one health category exhibited two primary flowering events (Figure 5-8). As pointed out, healthy black box began a third flowering towards the end of the sampling period, but these measurements were collected from a single tree. Therefore, only the two primary flowering events will be examined. The first flowering event peaked during December for all groups. The second flowering event for red gums also peaked in December, but shifted to November for black box.

The duration of flowering differed dramatically between species but not between health categories. Black box flowering began as early as July during both years and was completed by the end of January. Thus flowering spanned nearly seven months regardless of health. Flowering in red gum health categories spanned 4 to 6 weeks. Again, a single red gum varied during the first flowering event, flowering over four months instead of weeks. The differences between weeks and months of flowering duration altered the time between events. Black box trees had a six month time between flowering and red gum delayed almost ten months until the next flowering event.

5.3.3.3 Association of flowering and rainfall

Contrary to seed fall results, no distinct association was found between flowering and rainfall for either tree species (Figure 5-9). Flowering did not consistently lag behind rainfall at the time scale represented in the study nor did rainfall exhibit extreme peaks that could have initiated abundant flowering during either year. Peak flowering in both red gum categories during Year 2 coincided with a higher monthly rainfall, but a similar association was absent during Year 1.

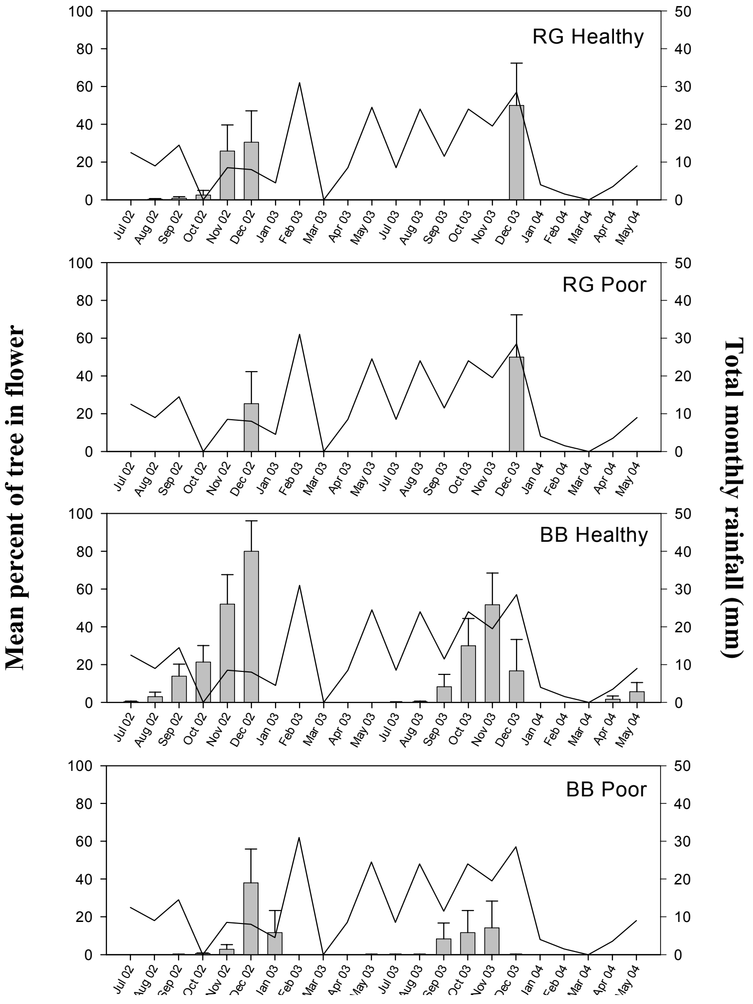


Figure 5-9 Association between localized rainfall (solid line) and flowering for black box and red gum. Error bars represent + 1 standard error.

5.3.4 Bud and fruit development

5.3.4.1 Crop frequency and rate of development

Three bud and fruit crops were monitored for both species (Figure 5-10). Each curve represents a single bud group monitored from initiation to loss from the canopy. Development spanned over one year in most categories and nearly two years in healthy black box trees. At this point capsules disappeared from the canopy. It is unknown if seed fall occurred prior to capsule loss since capsules were not recovered. The length of the bud group curves shows that poor trees of both species lost capsules more quickly than healthy trees. The first bud crop in poor red gums lasted 8 months but 17 months in healthy trees. A similar trend was present for black box trees with capsule duration of 16 months in poor trees compared to 22 months in healthy trees. The second crop monitored lasted an approximately equal amount of time (14 - 15 months) in both species and health categories, but the slope of the curve indicates a reduced rate of development in poor trees despite the length of time within the canopy.

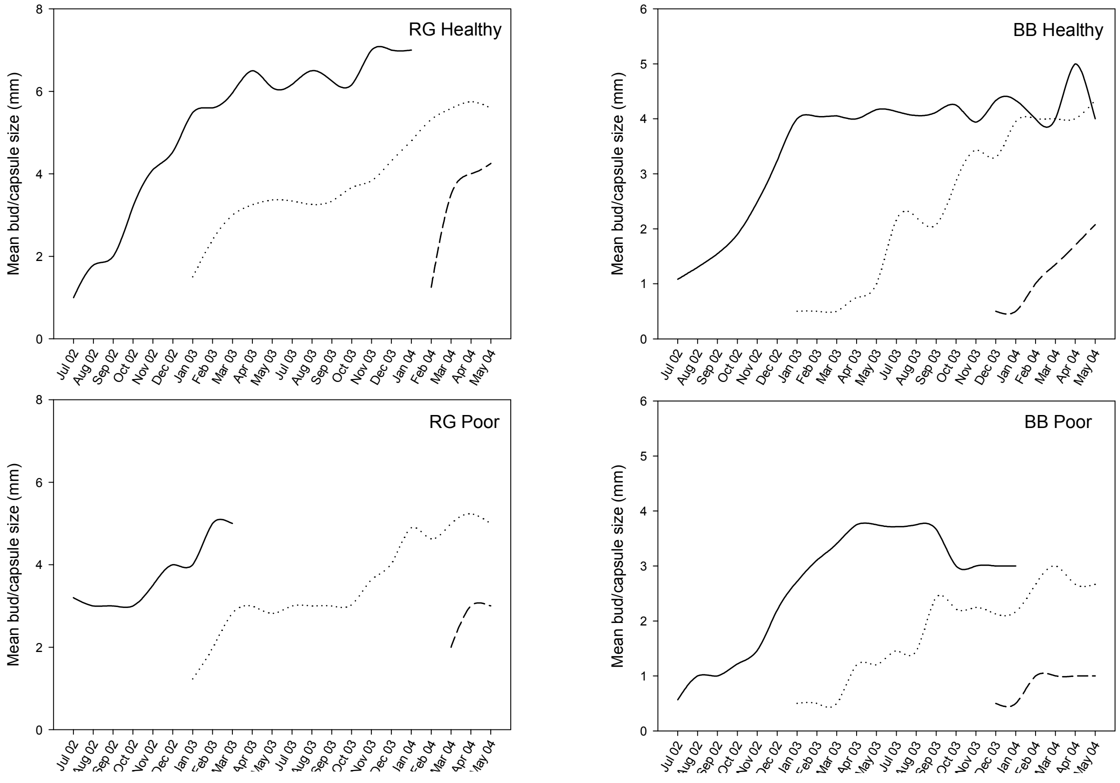


Figure 5-10 Three groups of developing buds from bud initiation to fruiting for both tree species and health categories. Each line represents a single bud group.

Development is represented by the maximum size of buds and capsules. The maximum bud size prior to flowering was 4 mm for black box and 4-5 mm for red gum (Figure 5-11). After flowering, red gum capsules continued to increase in size to 6-7 mm, but black box capsules tended to remain at 4 mm. As with other factors, poor trees of both species deviated from these measures. Capsules from poor red gums reached 4 mm prior to flowering but did not increase substantially after flowering generally obtaining a maximum size of 5 mm. Capsules in poor black box trees did not reach 4 mm prior to flowering, as in healthy trees. Instead, these buds flowered at just over 2 mm and reached a maximum diameter of only 3 mm.

The rate of development between health categories is also illustrated by the maximum capsule sizes. Poor trees of both species required a longer time for capsule development compared with healthy trees, but comparisons show red gums required more time than black box. Healthy red gum buds reached their maximum size in 9 - 12 months; poor buds were lost from the canopy after eight months with the second crop requiring 14 months for development. The same trend was found for black box. Healthy buds reached 4 mm after 6 – 10 months while the first crop of poor buds required ten months to develop and the second crop taking nearly 13 months to obtain only 3 mm.

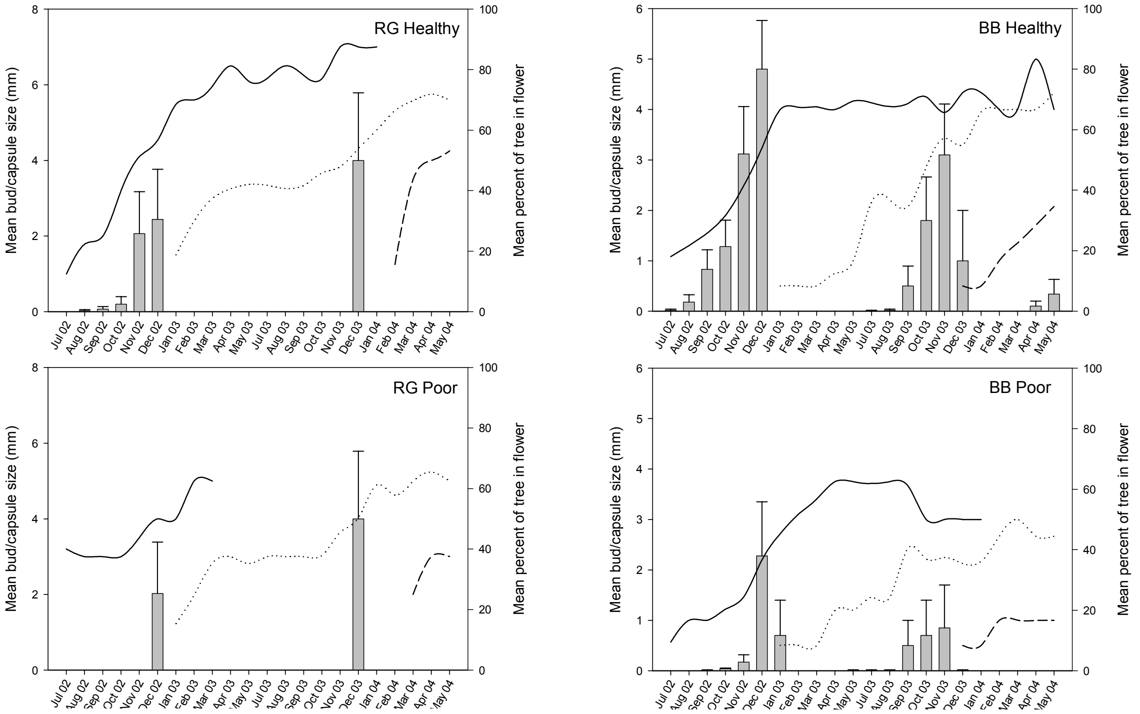


Figure 5-11 Flowering (histograms) and bud development (curves) in healthy and poor trees of both species. Note that the scale for capsule size varies between red gum and black box.

5.3.4.2 Patterns of bud initiation

Figure 5-10 illustrates an equal number of bud groups for all health categories and species. Such a trend could suggest that bud initiation is independent of species or health. Because this figure represents mean values for each month, it fails to emphasize the proportional contribution of individual trees. As with flowering, the number of trees contributing to the mean values of bud initiation and development were tallied and showed differences between health categories, species and bud groups (Table 5-7). Both healthy and poor black box trees showed a capacity to initiate new buds and carry multiple capsule groups with almost all sample trees contributing to each bud/capsule group. Healthy red gums showed similar characteristics, particularly for budding. Bud initiation and developing capsules were distinctly absent from the majority of poor red gum trees, with only a single bud group consisting of more than half of the sample trees.

Table 5-7 Number of sample trees contributing to mean bud formation within each health category (n = 6). Groups correspond with curves shown in Figure 5-10.

	BUDS PRESENT		
	Group 1	**Group 2**	**Group 3**
RG Healthy	5	6	1
RG Poor	2	4	1
BB Healthy	6	5	6
BB Poor	6	4	4

Bud crop curves, illustrated in Figure 5-10, show greater overlap in black box health categories, compared to curves from red gum categories. Overlap indicates opportunistic bud initiation in black box and cyclic initiation in red gum. Even though multiple crops were measured for both species, the proportion of tree canopy carrying buds and capsules was not assessed. The first crop examined in red gums represented only about 10% of the canopy but the second crop was found throughout the entire canopy. Conversely, bud crops in both categories of black box generally incorporated 100% of the canopy. Poor red gums were more likely to carry multiple crops by keeping over-mature capsules stored in the canopy. Because these were not initiated during this study, their development could not be monitored, thus they are not included in the development figures.

5.4 Discussion

5.4.1 Vigour

Visual assessment of tree vigour proved useful for these floodplain trees. The application of Grimes' technique is generally applicable for relative assessment within a population, and should be considered carefully if applying to two or more populations. The outward and visible signs of health decline offer only a snap-shot of health, and therefore can be altered by the manner in which particular populations or species respond to stress. The duration of the stressor could also alter the visible state of a species. This could partially explain the occurrence of anomalous ratings for red gums. As discussed earlier, any visual evaluation of health could simply indicate the immediate response of red gum to current growth conditions. For example, red gums will drop a large proportion of canopy leaves in response to short-term drought. If health is assessed during this time, it could be concluded that red gum are showing extreme signs of stress.

Conversely, trees that appear healthy may quickly decline and exhibit signs of long-term stress. One such tree was monitored during this study. Initially classified as 'good' using Grimes' technique, the canopy changed approximately four months into the study to resemble trees with 'very poor' ratings. Most leaves within the canopy fell and there was significant branch dieback. The tree was not removed from the study because it was thought that this could be a short-term response. After approximately one year, the tree began to recover, but no buds were initiated and no flowering was found at any time during the study. Seed fall within this tree resembled the figures obtained for other healthy red gum trees but these were most likely seed stored within the canopy and released as a response to the decline. An important point not represented by the data is that red gum trees in excellent or very good condition tended not to store large amounts of fruit capsules in the canopy. This contradicts reports in the literature citing the tendency of red gum to store seeds within the canopy (see Dexter, 1970; Turnbull and Doran, 1987; Cunningham *et al.*, 1992). Canopy seed storage instead appeared to be a consequence of a decline in vigour.

The differences in height and diameter between health categories were not unexpected, as stress suppresses vegetative growth and associated physiological functions (Kozlowski *et al.*, 1991). Divergence from this expected association between healthy and poor red gums was more surprising. The longevity of this species coupled with characteristic changes in physiological functions with advanced age implies that the differences could be symptomatic of age-related decline rather than simply a reflection of the current health. It is also possible that stress related health decline and age-related decline work together to expedite senescence in older trees. As discussed in Section 5.2.1, advanced growth stages are the primary seed producers within stands (Florence, 1996). Rapid losses of individual trees or the suppression of mature trees could limit the potential of stands to recover from long-term stress.

5.4.2 Seed fall and seed viability

This study shows that parent tree health primarily affects the amount of seed produced. The total seed fall for individual trees was much less than expected, especially for red gum which have been estimated to produce approximately 600,000 seeds for a single tree (Jacobs, 1955). The number of seeds captured could have been altered by any number of factors including seed predators, wind (dispersing seeds beyond the canopy boundaries), or in accordance with the study objectives, reproductive loss due to health decline. Seed capture was much less than what may be considered a 'fair yield' for these trees.

Seed viability was less impacted by health differences. Differences were related to individual trees rather than health as a categorical value. Therefore generalizations about health decline resulting in decreased viability are unwarranted at this time. Further examination of individual capsules and seeds from various health categories could yield different results. Such an examination was attempted during this study, but sample sizes were insufficient to detect variation between health categories.

Significant differences in seed fall between *E. camaldulensis* and *E. largiflorens* were expected from this study because of the high number of seeds produced by *E. camaldulensis* (Boland *et al.*, 1981; Gunn, 2001). These differences were not substantiated by the data. This implies that seed fall responses are similar for closely associated species within an area and that triggers for reproductive processes are the same regardless of the average number of seeds produced in the canopy. Any difference between species could have been altered by factors potentially impacting seed number either before or after seed fall.

Seed predation by insects is often cited as a problem for seed-fall estimations (Wellington and Noble, 1985; Andersen, 1989; Yates *et al.*, 1995). Most authors reference seed predation from the ground and cite 65-100% seed removal, but few studies discuss predation from the tree canopy itself. Few seed predators were found within the traps used for this study, but it was obvious that tree canopies, especially black box, teemed with ants. This implies that at this site seed predation from the ground is much less common than directly from the canopy. The frequent loss of capsules from the canopy of poor trees could be symptomatic of predation rather than stress.

The timing of seed fall in this study differed between species and was dependant on the condition of the tree. Timing of events seems to loosely agree with some references found in the literature (Table 5-8). Most authors cite a group of months during which seed fall was shown to be greatest, but this study shows that trees may be able to adjust seed fall timing in response to favourable conditions. Red gum, in particular, illustrates this point since seed fall peaks were at completely different times during each year of the study. Health appears to alter this ability to respond. Poor trees of both species showed indistinct patterns in seed fall compared to healthy trees which suggests that as health declines natural reproductive patterns may be disrupted.

Table 5-8 References to flowering and seed fall in red gum and black box populations. Months highlighted agree with the results found in this study; (--) indicates no data available.

Species	Time of Seed fall	Time of Flowering	Source
E. camaldulensis	Sep – Nov	Nov – Jan	(Dexter, 1967; Dexter, 1978)
	Mar – Aug	Dec – Feb	(Boland *et al.*, 1981)
	--	Nov – Jan	(Roberts and Marston, 2000)
	--	Nov – Feb	(Paton *et al.*, 2003)
	Jun – Sep	--	(Pudney, 1998)
	Feb.	--	(Boomsma, 1950)
	Feb - May	--	(Grose, 1962)
	--	Sep. – Dec.	(Friedel *et al.*, 1993)
E. largiflorens	Feb – Apr	Aug – Jan	(Boland *et al.*, 1981)
	--	May – Oct	(Roberts and Marston, 2000)

The timing or pattern of natural seed fall is dependent on climatological factors, but can be accelerated by drought or fire (Boomsma and Lewis, 1980; Florence, 1996). Given this, it could be that seed fall in areas where fire is absent or extremely limited; another dominant factor such as flooding may trigger a similar seed fall response. During the first year of this study, flooding of the wetland at Banrock Station initiated an extensive seed fall in healthy red gums where standing water was sustained for even just a few days (personal observation). This observation suggests that at this site water may be more important than temperature for initiating seed fall. Findings from Section 5.3.2.3, support this suggestion. Healthy trees positively responded to rainfall but with a two month delay. Poor tree response was almost immediate, further suggesting that health impacts environmental response patterns. The absence of time lags between rainfall and poor tree response suggests that poor trees may over-respond to even mildly improved conditions attempting to opportunistically reproduce rather than in a seasonal or cyclic manner.

5.4.3 Flowering phenology

The timing of flowering appears to be more similar to referenced literature for these floodplain trees (Table 5-8). Thus if reproductive limitations from flowering are prevalent they are likely to be associated with duration of flowering rather than season. Peak flowering occurred regularly and within the same season for both species indicating day length, rather than moisture, triggered flowering. But, this does not correspond with the obvious differences in flowering *duration* between red gum and black box. If flowering is stimulated by day length and temperature as suggested in the literature, why do black box trees begin flowering during winter when day length is shortest and temperatures are low? This implies a different mechanism is in place in black box which directs phenological responses to span over 4-6 months. Floral phenology in red gum trees seems to follow the prescribed relationship of day length and temperature by flowering very quickly during a 4-6 week time period. These findings suggest that peak flowering may not be the most appropriate measure for assessing phenological timing. Because of the rapid flowering in red gum, monthly sampling did not typically identify the exact time of peak flowering. Consequently, this study assessed relative flowering, which while influenced by bud volume (Keatley and Hudson, 1998), may not best represent the relationship between tree health and reproductive potential.

Despite the similarities in phenological events, reduced flowering in poor trees as well as the fewer number of trees exhibiting flowering illustrates that health can potentially negatively impact flower production and success. Poor trees in this area may be approaching the level Lichtenthaler (1996) refers to as the ‘Stage of Exhaustion’, where long-term stress has caused permanent damage and the plants are unable to recover, resulting in imminent death.

Information concerning water stress inhibiting flower bud initiation and flowering is contradictory in trees and results from the problems of relating phenological events to moisture patterns ranging over numerous years (Kozlowski *et al.*, 1991). These types of problems were found for this site. Flowering appeared to be relatively independent of local rainfall during the short term. This differs from the findings of Friedel *et al.* (1993) who reported that flowering was primarily influenced by recent rainfall in the current or previous season. Based on findings of this study, higher rainfall values nine months prior to flowering events is a more likely association that concurs with other studies in New South Wales (Law *et al.*, 2000). The conflicting results imply that the duration and time frame relative to rainfall were insufficient to properly characterise obvious associations. Because of the irregular rainfall typical in semi-arid climates, longer term rainfall records should be used to identify significant rainfall and flowering patterns for this area.

5.4.4 Bud development

Bud development appeared to be greatly impacted by health in both species. Not only were bud sizes stunted, the rate of development was much slower in poor trees. In addition, the number of trees exhibiting buds was lower in poor health categories. Differences were found in bud initiation between species. The opportunistic bud initiation in black box corresponds with the patterns found in seed fall. These may be used to illustrate the prevalence of this species away from direct association with the river. Conversely, the cyclic nature of red gum bud initiation also reflects a similar pattern to seed fall and its reliance on a constant water supply.

One of the most significant findings for bud development is the lack of multiple crops found in healthy red gums compared to poor red gums. Red gums are believed to store seed in the canopy, avoiding seed predation from insects and retaining seed viability independent from ground conditions. This study indicates that retention of multiple capsule groups may be a response to stress rather than a typical seed conservation measure (Pryor, 1976; House, 1997; Pudney, 1998). The limited number of poor trees showing bud initiation and the relatively low proportions of canopy holding new buds illustrates potential problems related to health. Successful seed fall in poor trees that failed to initiate buds or flowers during the entire study implies some type of seed source was available. Observations of the canopies showed a prevalence of over-mature capsules in poor trees. While over-mature capsules may hinder seed fall because of excessive woody growth (Cremer, 1965), they may be a means by which trees in poor health can sustain reproduction despite reduced physiological capacities.

5.5 Conclusions

Each process included in this study has been identified as a regeneration stage dealing with the role of the parent tree in the regeneration cycle. Outwardly visible stress in trees reflects the current physiological state that maintains a plant’s growth, expansion, and ability to contribute to the next generation. This chapter directly examined the effects that visible health decline can have on the total reproductive potential of trees. The results strongly indicate that the early stages of the regeneration cycle including seed production, budding, flowering, and fruit formation are all substantially altered by reduced parent tree health.

The quantity of regenerative investment appears to be more impacted than the timing of regeneration events. The findings of the study do suggest that there is potential for disruption in the timing if the duration of unfavourable conditions exceeds physiological tolerances maintained by each tree species.

The combination of factors considered in this study identifies eucalypts in poor health as possibly stressed to the point of reproductive limitation. This has significant implications for floodplain tree populations since reductions in reproductive effort have cumulative effects. As reproductive investments decrease, seeds available for recruitment of new individuals also decrease. Consequently, a loss in early growth stages further depresses the population; reiterating the point from previous chapters that losses in regeneration result in population losses across the floodplain as reproductive trees die because of stress.

Chapter 6 Dendroecological assessment

6.1 Introduction

The science of dendrochronology began as a means of dating wood by analysing growth rings, but has been expanded to include *dendroecology*. Dendroecology includes all disciplines that strive to obtain environmental information from tree ring sequences (Banks, 2000). Sequences result from radial growth, which is determined by the vascular cambium producing new xylem and phloem cells (Kozlowski, 1971). Variation in cell sizes, governed partly by the local climate, forms distinct growth rings that ostensibly are annual (Kozlowski *et al.*, 1991).

In favourable climates where growth is not seasonally limited, ring formation is 'complacent' or uniform (Harlow and Harrar, 1968). Tropical regions typically exhibit complacent growth because of constant climatic conditions (Schweingruber, 1988) resulting in no clear annual rings (Kozlowski *et al.*, 1991). Seasonal rainfall and temperatures in temperate regions generally result in the formation of one growth ring per year. Lower temperatures during winter induce dormancy, causing cell size variability to reflect seasons of high and low growth (Fritts, 1976; Schweingruber, 1988). 'Sensitive' ring series are typical of areas where some climatic factor hinders continuous growth, as in arid and semi-arid zones (Schweingruber, 1988; Schweingruber, 1993). Indicator or 'pointer' years from discontinuous rainfall cause corresponding variability in growth ring deposition (narrow growth bands that can be cross-dated to other trees in the same area) (Fritts, 1976; Schweingruber, 1993); these serve as a gauge of seasonal water availability (Morey, 1973).

The correlation between water and plant growth is well established (Kramer, 1962; Zahner, 1968). Water drives physiological and biochemical processes that determine the quantity and quality of cambial growth (Kozlowski, 1971; Kozlowski *et al.*, 1991). When water conditions are favourable, cambial activity may be continuous and general, but can become localized as water deficits cause physiological stress (Kozlowski, 1971). Localized growth results in characteristically narrow tree rings that are the basis for dendrochronology. For this reason, most dendrochronological studies concentrate on the negative effects of water deficits. The relationship between water deficits and tree rings has been used to re-construct climatic conditions as well as river flows and flood history. For example, Lough and Fritts (1985) applied dendroclimatic methods to trees in order to determine historical changes in the

Southern Oscillation, an atmospheric circulation pattern. They found strong correlations with winter surface climates over North America and the northern Pacific, evident in tree-ring chronologies from western North America. Jones and Briffa (1984) used oak ring-width chronologies to re-construct river flow regimes, and Cook and Jacoby (1983) reconstructed a 248 year low-flow chronology using tree-ring chronologies from hemlock (*Tsuga canadensis* Carr.), chestnut oak (*Quercus prinus* L.), white oak (*Q. alba* L.) and pitch pine (*Pinus rigida* Mill) within the Potomac River basin.

Few such studies have been conducted in Australia. Whilst the link between hydrology and trees is well-established, typical Australian trees are less amenable to dendroecological assessment than those from the Northern Hemisphere (Ogden, 1978; Ogden, 1981). Ogden (1978) argued that Australian trees have comparatively short life-spans, living for less than 1000 years. Life spans of this magnitude are insufficient for *long-term* climatological chronologies. Ogden also argued that the less clearly-defined growing seasons in Australia incur an increased number of missing or false rings, or multiple rings from opportunistic growth within a single growth period, limiting the application of dendrochronology for long-term sequences. Most success in using Australian trees has been attained using Tasmanian conifers (Norton, 1990 and references therein). However, Banks (2000) suggested that there is some potential for applications using Australian eucalypts, particularly riparian species, because of synchronised growth habits with flooding.

Schweingruber (1992) attempted to characterize growth features in southern Australian shrub taxa, and to relate growth zones to climatological areas based on macroscopic wood features (see Ilic, 1990). Schweingruber (1992) distinguished between *growth rings* (distinct boundaries between latewood and earlywood growth that extend around the circumference of the stem) and *growth zones* (growth areas where distinct boundaries between early and latewood rarely or never occur, or rings fail to go around the entire circumference), which likely represent annual growth. He concluded that the southern part of Australia is suited for dendrochronological studies, but that growth zones rather than rings may be more applicable for age estimation.

The work by Argent *et al.* (2004) illustrates this point, showing that demarcation of ring-like structures representing growth increments is possible. As previously discussed, if distinct boundaries are not present, age may be approximated by examining growth zones (Schweingruber, 1992), showing that even minor delineations allow for age approximation (Mucha, 1979). Annual growth chronologies are desired for precise dating, but in dendroecological studies annual patterns may not be essential when the focus is on the relative frequency of events rather than specific dates (Rayner, 1992). Age was successfully determined in eucalypts of the Karri forest in south-western Western Australia, where Rayner (1992) found a strong correlation between age in dominant trees and DBH.

Notwithstanding the studies using tree rings to reconstruct past climates and hydrological parameters, few attempts has been made to examine tree rings as a record of favourable growth conditions. Given that narrow rings can result from harsh conditions or stress, wide rings may provide a record of climatic or environmental conditions favouring cambial activity and diameter expansion. Only one study in Australia has explored this relationship. Martens (1992) transformed ring-width chronologies into indices that allowed flood frequency interpretation. The study relied on non-native trees such as species of *Populus*, *Quercus* and *Salix*. While Martens' approach is novel and does provide flood-history sequences, its application to native riparian vegetation is limited because it is likely that the responses of native trees to flooding differ significantly from those of exotic species.

Previous chapters linking flooding and eucalypts showed that determining the age structure of woodlands may be problematic. A dendroecological assessment could provide a better evaluation of tree ages relative to diameter, and illustrate the moisture requirements for growth in floodplain eucalypts. Wider rings may represent 'pointer' years of high water availability similar to the way that narrow rings represent water deficits. To assess this relationship, this chapter presents an examination of the growth rings of *E. camaldulensis* and *E. largiflorens* trees from the Murray floodplain in South Australia. The objectives were to examine the relationship between tree age and growth rings, and to determine if growth reflects water availability. The following hypotheses arise:

(1) Trees of similar ages will have similar diameters, validating the use of DBH as a surrogate for age (cf. Chapter 3),
(2) Tree age is correlated to the number of tree rings, representing annual growth,
(3) Ring width sequences are similar between individual trees of the same age, reflecting identifiable growth responses, and
(4) Identifiable growth responses are correlated with water availability through rainfall and river flows, reflecting the moisture requirements of the trees.

6.2 Methods

6.2.1 Tree selection

Successful cross-dating (relating rings within and between trees from different locations (Stokes and Smiley, 1968) requires dateable material. Therefore, the selection of appropriate trees was more important than the site from which they are selected. Smaller, younger trees of known age were required (20-30 cm diameter) to reduce the probability of heartwood damage from insects, disease or physical damage. Younger trees should also have more distinct rings than older trees (Fritts, 1976). Trees from times of prolific germination, following flooding (Dexter, 1978), were preferred since they would be easiest to verify and locate.

With the assistance of local landowners, three sites containing trees satisfying the selection criteria were found near Swan Reach (34^{o}34'S, 139^{o}36'E), 100 km NE of Adelaide, South Australia (Figure 6-1). *E. camaldulensis* trees were located at two adjoining properties dominated by *E. camaldulensis* with infrequent river cooba (*Acacia stenophylla*) (Figure 6-2a). These sites are in close proximity to the river and are divided by an inlet. *E. largiflorens* trees were selected from a site 3 km upstream, where the floodplain is wider and not constrained by cliffs (Figure 6-2b). Trees were scattered up-slope from a billabong directly connected to the river.

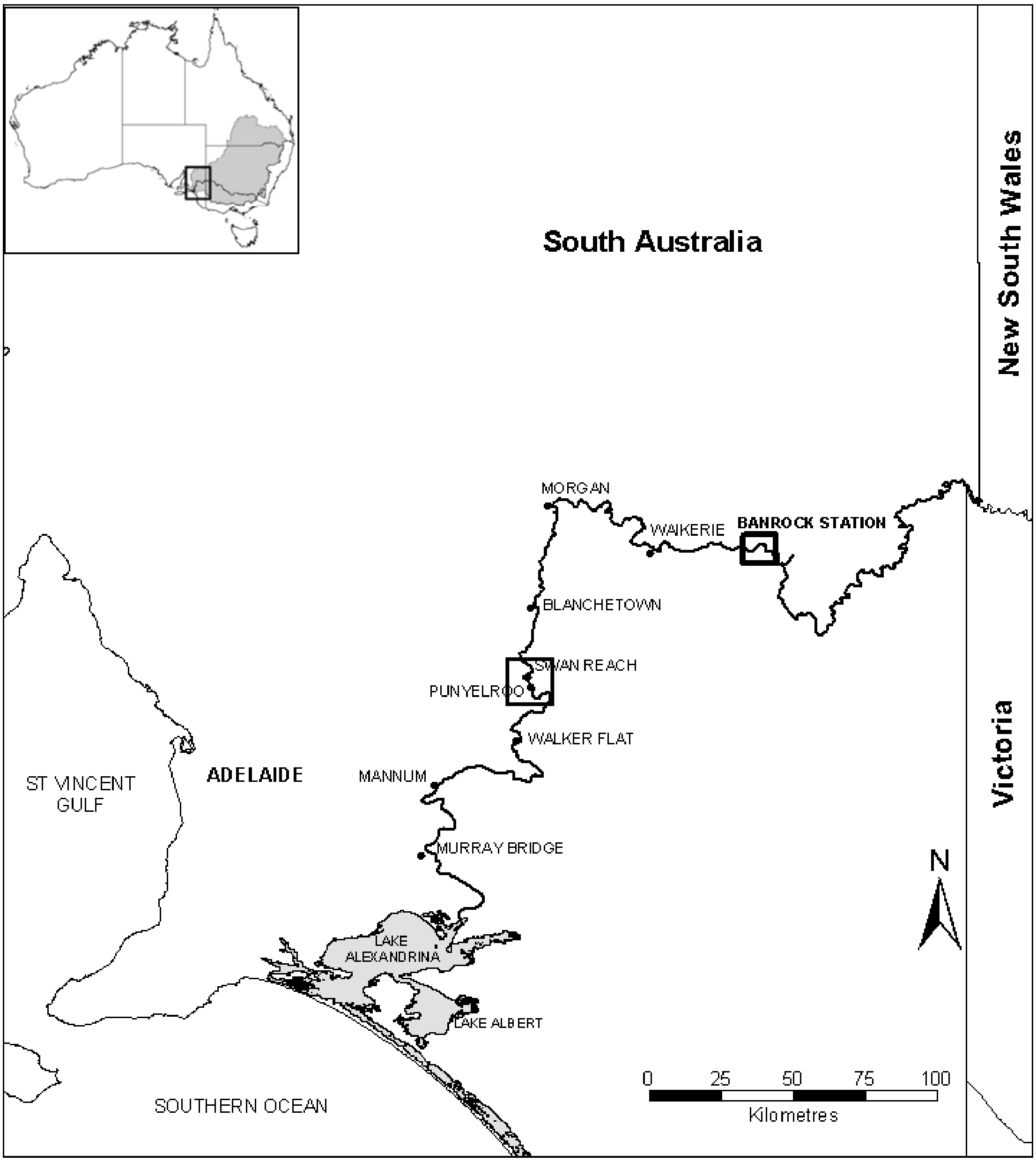


Figure 6-1 Localities along the River Murray in South Australia. Red gum and black box trees were selected from three sites between Swan Reach and Punyelroo delineated by a light square. In text, the site near Swan Reach is compared to Banrock Station, which has been outlined with a dark square.

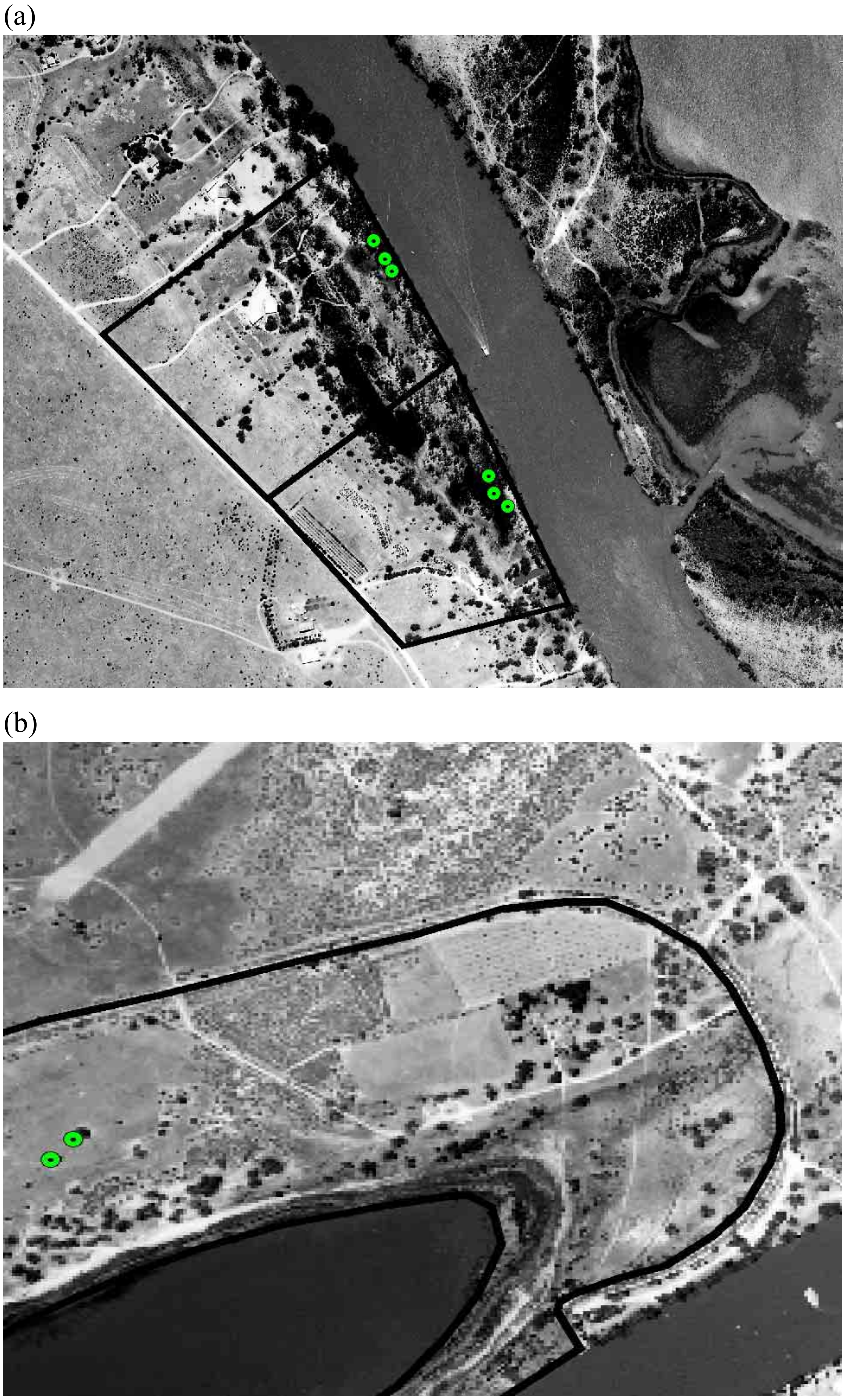


Figure 6-2 Location of red gum (a) and black box (b) trees harvested for ring analysis.

The regional climate near Swan Reach is similar to Banrock Station (Chapter 3): semi-arid, with warm, dry summers and cold, wet winters. Swan Reach is located within the Gorge region of the Lower Murray, characterized by low terrace soils with poor physical properties and a narrow floodplain (1 – 2 km wide) (Cole, 1978). The floodplain sites are ‘Low, Open Woodland’ dominated by red gum (Specht, 1972; Specht and Specht, 1999). Black box are less frequent in this area because of the constrained floodplain. A sparse shrub understorey (lignum:

Muehlenbeckia florulenta) is present. The river channel is deeply incised and infilled with Monoman and Coonambidgal Formation sediments, setting the floodplain approximately 30 m below the surrounding land. The river and floodplain are separated from the surrounding land by steep cliffs on the western side of the river.

Red gum and black box trees germinated on the recession of the 1956 flood were located, and ages were verified using aerial photographs in 10-year intervals beginning with the closest year prior to the 1956 flood. Individual trees were located by comparing temporal canopy expansion through successive photographs. Trees appearing as small patches in early images that could also be identified as dominant trees in recent images were chosen. Selecting trees from images after the 1956 flood permitted age to be attributed to flooding. Dominant trees (larger trees with well-developed crowns forming the uppermost canopies of the stand) will reflect the most active growth response to climatic factors. Co-dominant or suppressed trees will have less distinct ring structures reflecting growth response to competition rather than climate (Rayner, 1992).

Trees germinated just after 1956 were larger in diameter than originally anticipated. To verify growth rates and allow comparisons between cohorts, red gum trees germinated during a 1978/1979 high flow event were also selected using the same aerial photographs. No black box trees from other dates could be found at any of the sites, so only trees from 1956 were used.

6.2.2 Sample Preparation

Six red gum and two black boxes were harvested in March 2004. The number of trees was necessarily limited because they are protected by the *Native Vegetation Clearance Act*, 1990. This forbids the removal of native vegetation in South Australia without permission from the Native Vegetation Clearance Council. To reduce the requirements of the landowners to replace harvested trees, a limited number of trees were chosen. All red gums had a single bole, but the black boxes had double boles. Only the dominant bole was harvested in an attempt to maintain the survival of the tree. Tree diameters were measured at breast height prior to felling the tree. Logs (50 cm in length) were collected from each tree so that breast height (1.3 m from the base) was located in the middle of the log. The logs were taken to a sawmill where cross-sectional disks (5 cm in width) were cut from breast height and planed for a flat surface. Whole disks were necessary rather than core samples because dating may be problematic given the variable climate in South Australia. Further no chronology has been previously developed for South Australia therefore there is no source of comparison for tree cores. The samples were air dried for 6 weeks to reduce warping, and then polished by sanding. Aluminium oxide dry sanding sheets (60 - 180 grits) were used to remove chainsaw marks followed by progressively finer grades of silicon carbide waterproof abrasive paper (240 - 400 grit) for polishing. Polishing enhances the colour within the sample disks, assisting in identification of vessel characteristics.

6.2.3 Aging using ring characteristics

Each of the eight polished tree disks was examined for annual growth rings. Two radii were selected on each prepared disc, avoiding areas with prolific kino deposits and growth abnormalities distorting ring deposition and arrangement. Bands of paper were taped along the edge of the radius being measured, and ring boundaries were marked on the band with a pencil (Figure 6-3). These marks not only accommodated ring counts but also allowed for ring width evaluation. Traditional skeleton plotting methods were not applied because wide rather than narrow bands were of interest. Rings were counted along each radius and mean counts were calculated for each tree. Student's *t*-tests compared actual ring counts between trees of presumably similar age (1956 red gum vs 1956 black box) and between the two cohorts (1956 vs 1978). Student's *t*-tests were applied to compare the mean number of counted rings and the expected number of rings. Expected ring numbers were derived for each cohort by subtracting the probable germination year from the year of harvest. The value was then corrected for the estimated number of years required for seedling establishment. Establishment, in this sense, is defined as the required number of years between germination and attaining breast height (1.3 meters from the base of the tree). As explained in previous chapters, seedlings will grow in height before girth, therefore breast height is the minimum height obtained before growth rings are visible. Given the semi-arid climate, establishment was set at two years following germination allowing for decreased growth rates from hot, dry environments where water deficits often prevail.

Figure 6-3 Red gum tree disks from 1978 (left) and 1956 (right). The white bands show the ring markings along one radius of each disk.

6.2.4 Ring widths as growth response

Tree ring composites were compiled for individual trees by matching wide and narrow rings on both radii (Figure 6-4). This technique is a manner of cross-dating (systematic comparison of patterns of wide and narrow rings common to all radii and individual trees (Ferguson, 1970)). After identifying rings similar to both radii (‘pointer’ rings), the two ring sequences were combined to form a single sequence for each tree. The composite sequence resulted from adding rings from one radius to the other relative to the closest matched rings. Composite ring width sequences were compared within the 1956 and 1978 tree cohorts. The primary interest of this section was in locating *patterns* of growth for comparison rather than comparing absolute number of growth rings.

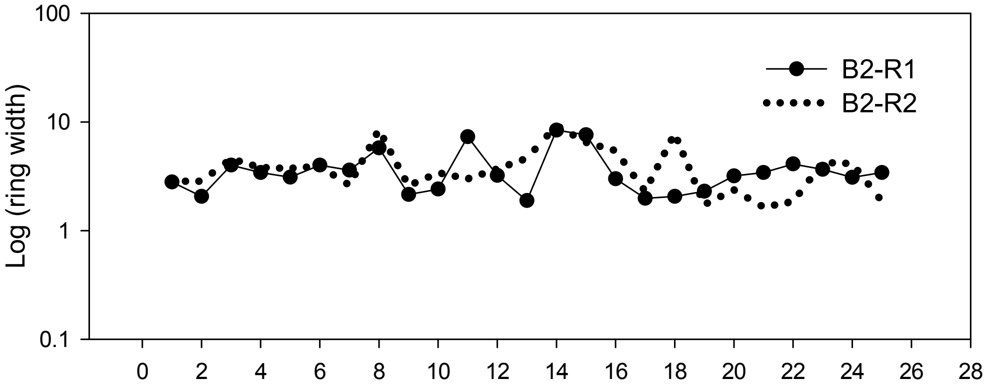


Figure 6-4 Comparison of ring widths for two radii of and individual tree. Peaks and troughs were compared to determine 'pointer'type rings.

6.2.5 Hydrological growth requirements

Water availability specific to the harvested trees was unavailable. Therefore, hydrological associations were based on the regional flow data used in Chapter 4 and local rainfall measures at Swan Reach, supplied by the Bureau of Meteorology. Total annual rainfall and mean annual rainfall from Swan Reach with peak annual flow and mean annual flow measured at the South Australian border were examined for the time periods associated with the harvested trees. Composite ring sequences from the previous section were compared with flow and rainfall data to evaluate growth trends relative to water availability regardless of the water source.

6.3 Results

6.3.1 Tree diameter and age

The tree diameters for each germination year and species are presented in Table 6-1. Student's *t*-tests comparing DBH values of red gum and black box within the 1956 tree cohort yielded no statistically significant difference ($t = 2.49$, df = 3, $p = 0.09$). Conversely, DBH values between red gums from 1978 and 1956 were significantly different ($t = 5.96$, df = 4, $p = 0.004$). Comparisons between 1956 black box and 1978 red gums were not conducted because of the unequal number of trees and the absence of comparative 1978 black box trees.

Table 6-1 Trees sampled from sites near Swan Reach, South Australia. Tree diameters are at breast height (1.3 m from the base of the tree).

	GERMINATION YEAR	SAMPLES	TREE DIAMETERS (cm)
Red Gum	1956	3	39.8; 39.5; 44.9
	1978	3	29.6; 30.2; 31.5
Black Box	1956	2	36.3; 29.3

6.3.2 Age and ring enumeration

Radii ring counts within cohorts were very similar for most trees (Table 6-2). The 1956 tree ring counts ranged between 32 and 45 rings, reflecting the older ages. Tree O2 varied most with a 30% difference in counts between radii. Other 1956 trees differed by approximately 15%. Tree B3 had the smallest variation with only 8% difference between radii. Variation in the 1978 trees was minimal with tree B2 showing no difference and trees O3 and B1 varying by only 4%. Each of the counts within the 1978 cohort reflected the proposed age of the tree.

Table 6-2 Ring counts for individual radii of each sample tree.

	GERMINATION YEAR	TREE ID	RING COUNT RADIUS 1	RING COUNT RADIUS 2
E. camaldulensis	1956	**O1**	38	45
		O2	34	21
		B3	33	36
E. camaldulensis	1978	**O3**	24	25
		B1	25	26
		B2	25	25
E. largiflorens	1956	**G1**	32	38
		G2	38	44

Expected ring counts (Table 6-3) were compared with total ring counts for each radius. Means testing failed to detect any deviation between actual and expected counts for any of the sample trees ($\alpha = 0.05$) (see Appendix 6 for calculated means test values).

Table 6-3 Number of rings expected based on estimated year of germination allowing two years for attaining 1.3 m height.

	1956 Trees	1978 Trees
Expected Ring Count	46	24

Mean ring counts were for each tree were calculated from the number of rings enumerated on the radii (Table 6-4). Each cohort exhibited a similar range of ring counts with a single exception (highlighted in Table 6-4). The mean ring count for tree O2 reflected the extreme variation between the radii counts, as suggested. Despite having a similar DBH value to other trees of the cohort, the numbers of growth rings were comparably less and more closely related to actual ring counts of the 1978 trees. Mean ring counts were statistically examined using Student's *t*-tests. Similar to the results for DBH, no significant difference was detected between the 1956 black box and red gum mean ring counts (*t* = 0.62, df = 3, *p* = 0.58) but mean ring counts differed significantly between 1978 and 1956 red gums (*t* = 3.24, df = 6, *p* = 0.02).

Table 6-4 Mean number of rings counted for tree samples collected from Swan Reach. Sample trees are grouped by estimated year of germination. The highlight indicates a sample tree in which the mean ring count did not correspond with other trees in the cohort.

E. camaldulensis		*E. largiflorens*
1956	**1978**	**1956**
41.5	24.5	35
27.5	25	41
34.5	25	--

6.3.3 Growth responses

Attempts to characterize growth rings by vessel size and density were unsuccessful. There was little variation in vessel size, and there were few rings with distinguishable vessel density changes. When vessel density visibly differed from surrounding rings, ring boundaries were often obscured by surrounding vessels limiting the usefulness of boundary delineation. Consequently, assessments were based solely on ring widths. Appendix 7 includes ring width data for radii of all sample trees. Ring widths were graphed logarithmically to characterize patterns of growth over time. Logarithmic representation ensures that ring width characteristics can be clearly seen when using short ring series (Schweingruber, 1988).

Individual radii used to generate the composite ring sequences for each tree are in Appendix 8. Composite ring sequences were grouped by cohort and the sequences matched numerically originating from the centre of the trees. Matching resulted in 11 clear matches between the 1956 germinated red gums (Figure 6-5). The patterns within the three red gums are broadly similar for wide rings. The most easily identified matches were in the middle of the sequences with more difficult matches within the most recent ring sequences. For all three trees the earliest rings were the most complicated and there were no clear matches within the initial 2 to 6 rings. There was also a visible variation in the magnitude of the growth so that while ring patterns visibly matched, the total widths differed.

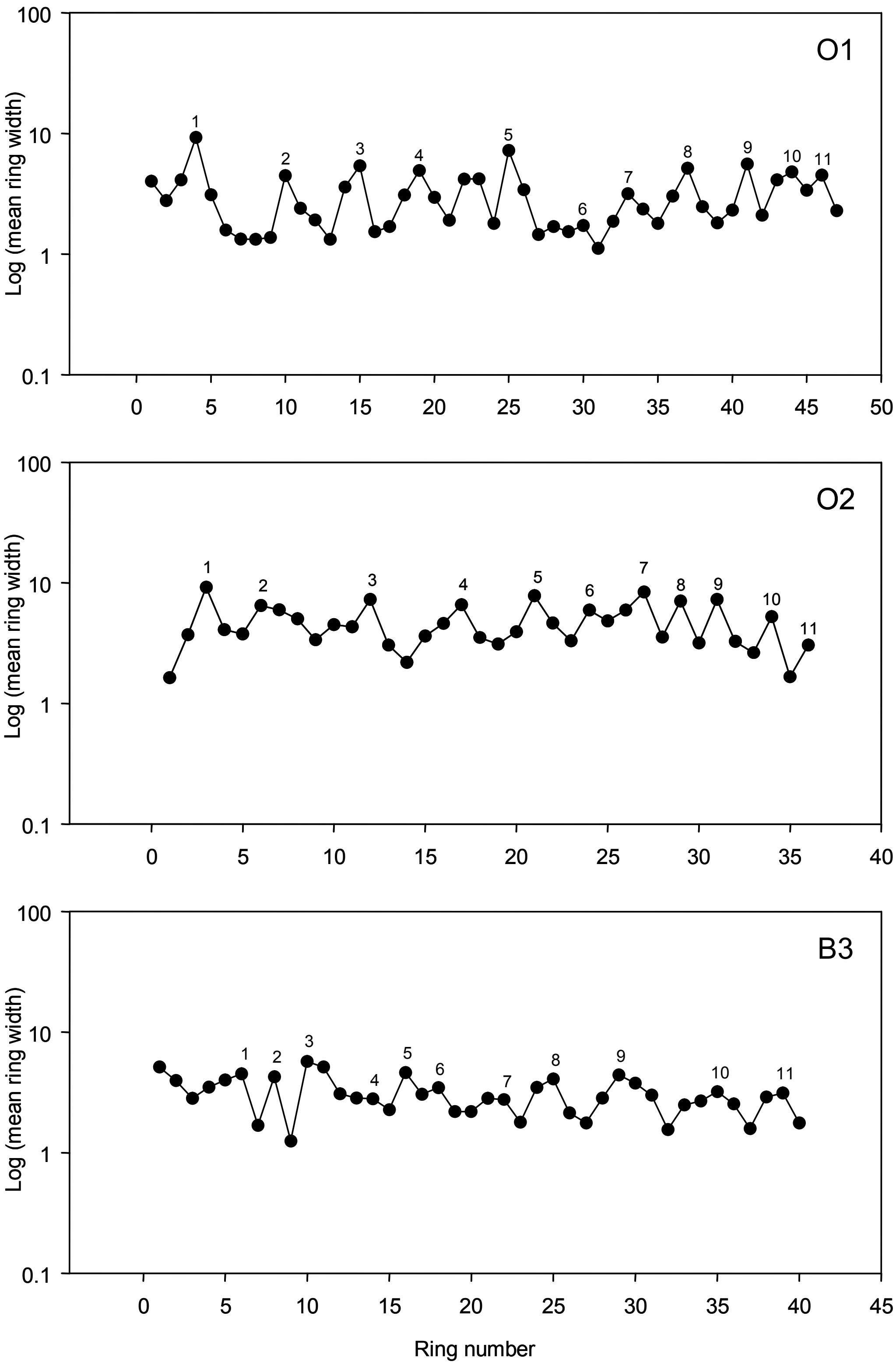


Figure 6-5 Composite ring width sequences for 1956 germinated red gums. The initial ring is next to the pith with the most recent rings towards the right of the diagram. Note that the abscissa differs relative to the total ring count of each tree. Applying differing abscissa scales allowed the *patterns* of growth to be more easily visualized.

Black box trees of the same cohort illustrated nine matching peaks (Figure 6-6). The rings in the middle of the sequences were not as easily distinguished as in red gum. Tree G2 had a more variable ring width pattern than G1. Two peaks in G2 were not directly matched with any peak from G1. The rings between peaks 3 and 4 were the most difficult with no visible association between the two trees in this area of the sequence. The magnitude of the widths varied in the same way as in the red gums resulting in a similar pattern but differing in total width.

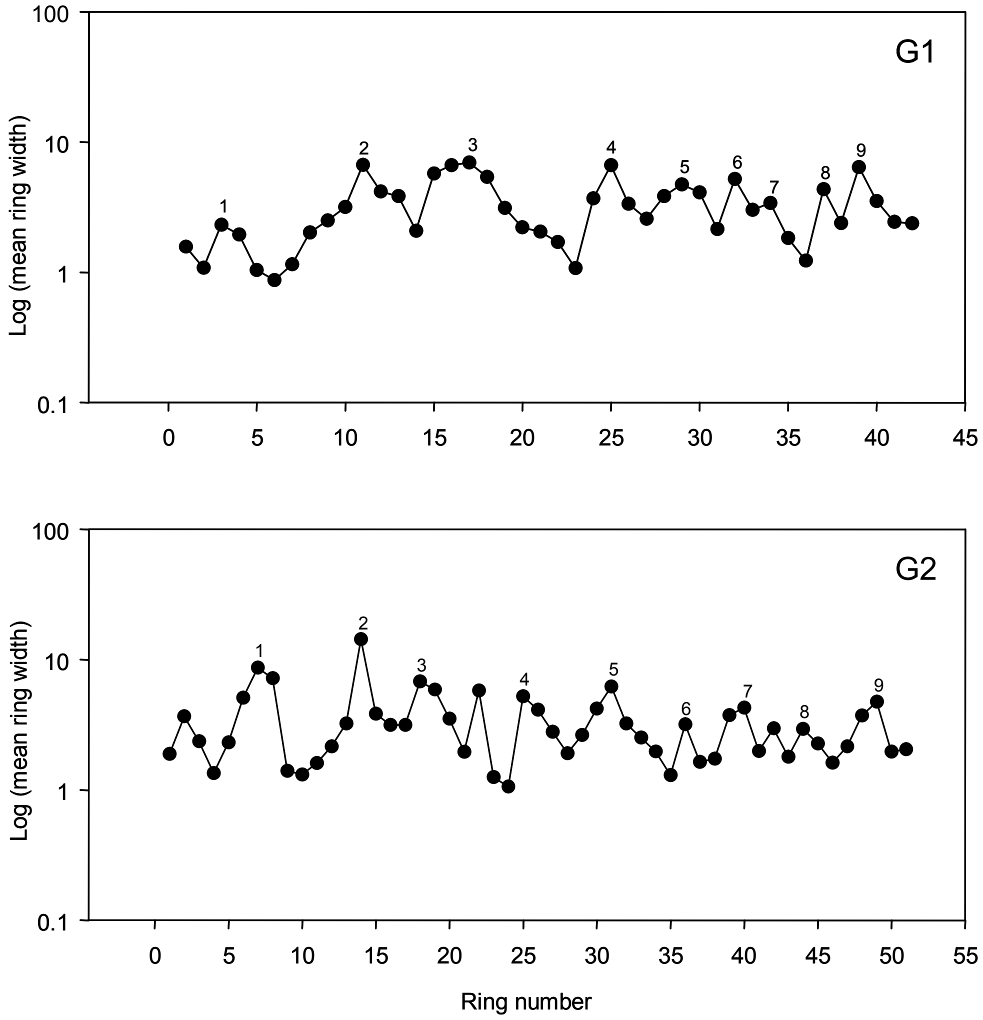


Figure 6-6 Black box composite ring sequences. The sequence begins with the first ring after the pith. Note that the abscissa differs between the trees and is associated with the total ring count. Different scales allowed easier comparisons between tree growth patterns.

A high degree of ring matching was found between red gum and black box of the same cohort, especially during the final third of the sequences. For example, peak 3 in G1 could be matched with peak 4 of O1, and peak 5 in G2 matched with peak 8 in B3. Conclusive matches occurred in nearly half of the sequences between trees G2 and O2. From peak 4 in both trees the patterns of widths change at nearly equal rates. However, overall the black box trees had fewer wide rings and less distinct growth areas.

Composite ring sequence patterns for the 1978 cohort of red gums are presented in Figure 6-7. Ring matches between these trees was comparatively equal to matches found in the 1956 cohort, but fewer matches given the younger age of the trees. Seven matches were recognizable throughout the sequences with the same middle sequence ambiguities as in the 1956 cohort. Also, as in the 1956 trees, early ring patterns were unclear and matching was unsuccessful. However, an equal number of rings were represented before the first obvious match at the sixth ring. No trees of the older cohort showed an equal number of rings before the first match. The greatest variation occurred between peaks 4 and 5 resulting in one peak unmatched in tree B1. This peak was excluded from matching since there was a high degree of association between the sequence patterns following match 5.

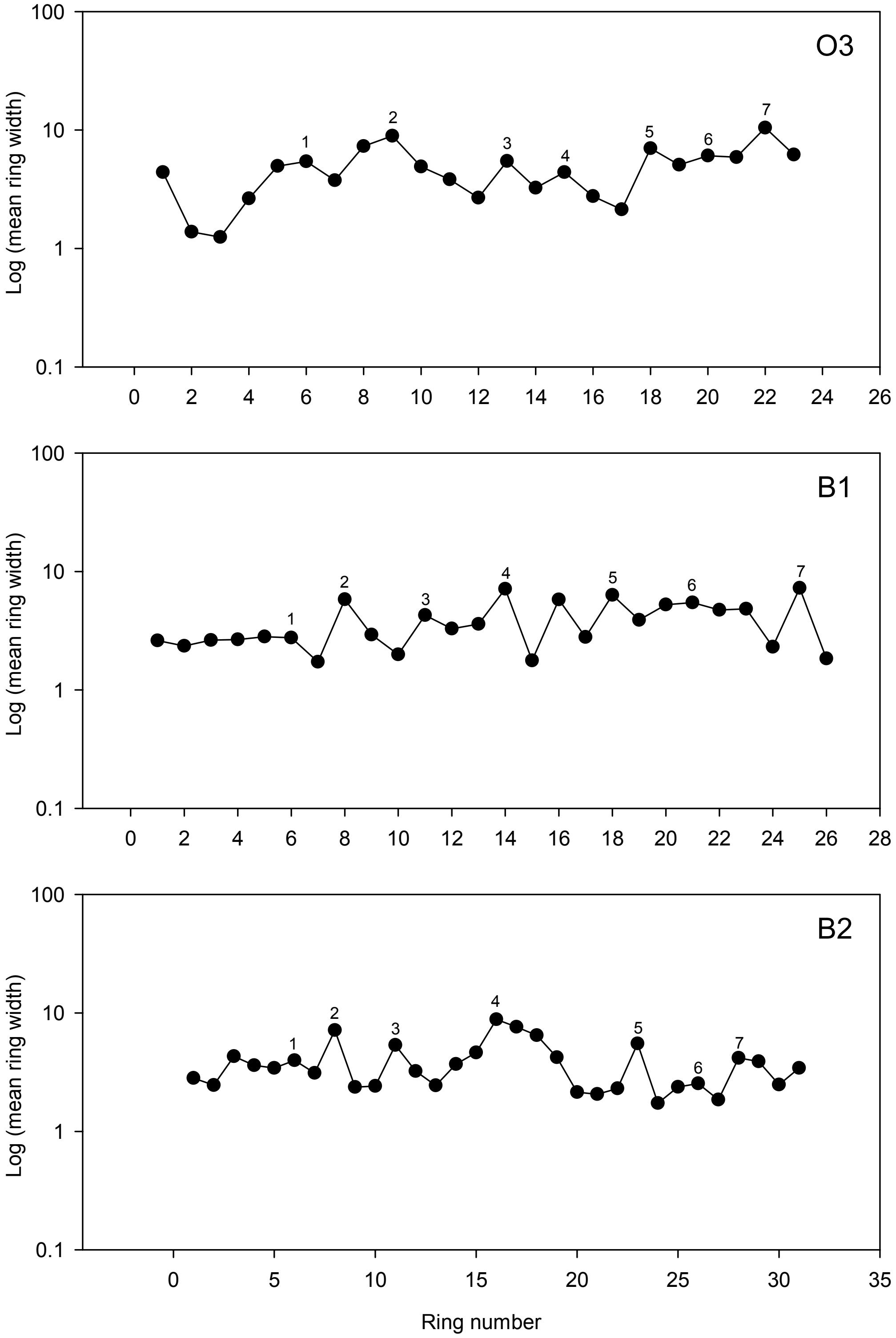


Figure 6-7 Composite ring width sequence of 1978 red gums. The pith of the tree is represented by the first ring with recent rings towards the right of the diagram. Sapwood is not included in the diagram. Again, the abscissa varies for each diagram and reflects the total ring count for each tree.

6.3.4 Hydrological requirements

6.3.4.1 Statistical evaluation

Composite ring width sequences were used to assess correlations between growth rings and river flow and rainfall values during time periods corresponding to the relative age of the tree. Ring sequences were assumed to be annual, as results from Section 6.3.2 indicated no significant deviation from expected ring counts. Naturally, mean annual flows and peak annual flows (Spearman's $r_s = 0.940$, n = 48, $p = 0.000$) as well as total annual rainfall and mean annual rainfall ($r_s = 0.860$, n = 49, $p = 0.000$) were strongly correlated. Total annual rainfall at Swan Reach was also correlated with both mean annual flows ($r_s = 0.407$, n = 48, $p = 0.004$) and peak annual flows ($r_s = 0.379$, n = 48, $p = 0.008$). Figure 6-8 illustrates the temporal association between hydrologic variables. Mean annual rainfall was not included in Figure 6-8 since it did not correlate with either flow value.

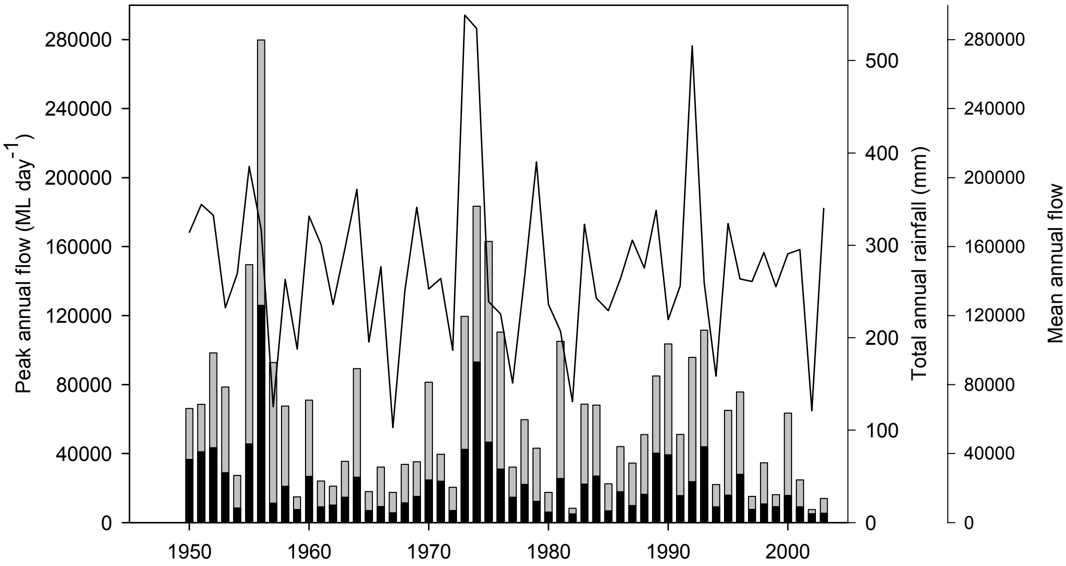


Figure 6-8 Rainfall and river flow distribution between 1950 and 2004. (Peak annual flow: light bars; mean annual flow: dark bars; Total annual rainfall: solid line). Mean annual flow and peak annual flow are represented with the same units (ML day^{-1}).

Statistically significant correlations between ring widths and available water were limited to two of the eight trees. Growth rings in tree O1 were correlated with mean annual flows ($r_s = 0.355$, $n = 46$, $p = 0.015$) and peak annual flows ($r_s = 0.328$, $n = 46$, $p = 0.026$) while tree B1 was correlated with mean annual rainfall ($r_s = 0.478$, $n = 26$, $p = 0.013$) and total annual rainfall ($r_s = 0.432$, $n = 26$, $p = 0.027$). Correlation coefficients and associated p-values are in Appendix 9. Both the 1956 and 1978 cohorts are represented by the correlations. Younger trees show a correlation with rainfall while older trees are correlated with flows. Lagged correlations were not apparent between growth rings and water availability.

6.3.4.2 Graphical evaluation

Graphical assessment of ring widths and hydrological variables suggests association and trends not quantified by the statistical tests. Again, mean annual rainfall was not included because it did not correlate with flow variables. Mean annual flow was also excluded because peak flows showed a stronger correlation with total annual rainfall than mean values.

From Figure 6-9, the 1956 red gum growth response was greatest when flows were between 40,000 and 80,000 ML day^{-1} and total rainfall was about 300 mm. A positive growth response also resulted from higher rainfalls (>300 mm) combined with lower peak flows (30,000 ML day^{-1}). Each of the red gums showed greatly reduced ring widths during excessively wet years. An example being 1973 – 1975, where flows exceeded 80,000 ML day^{-1} and total rainfall was greater than 300 mm. Within the 1956 red gums tree O2 appeared to have the most consistent and continuous ring width response to water availability. O1 showed the most variable response, which directly reflected the correlation with flows (Section 6.3.4.1).

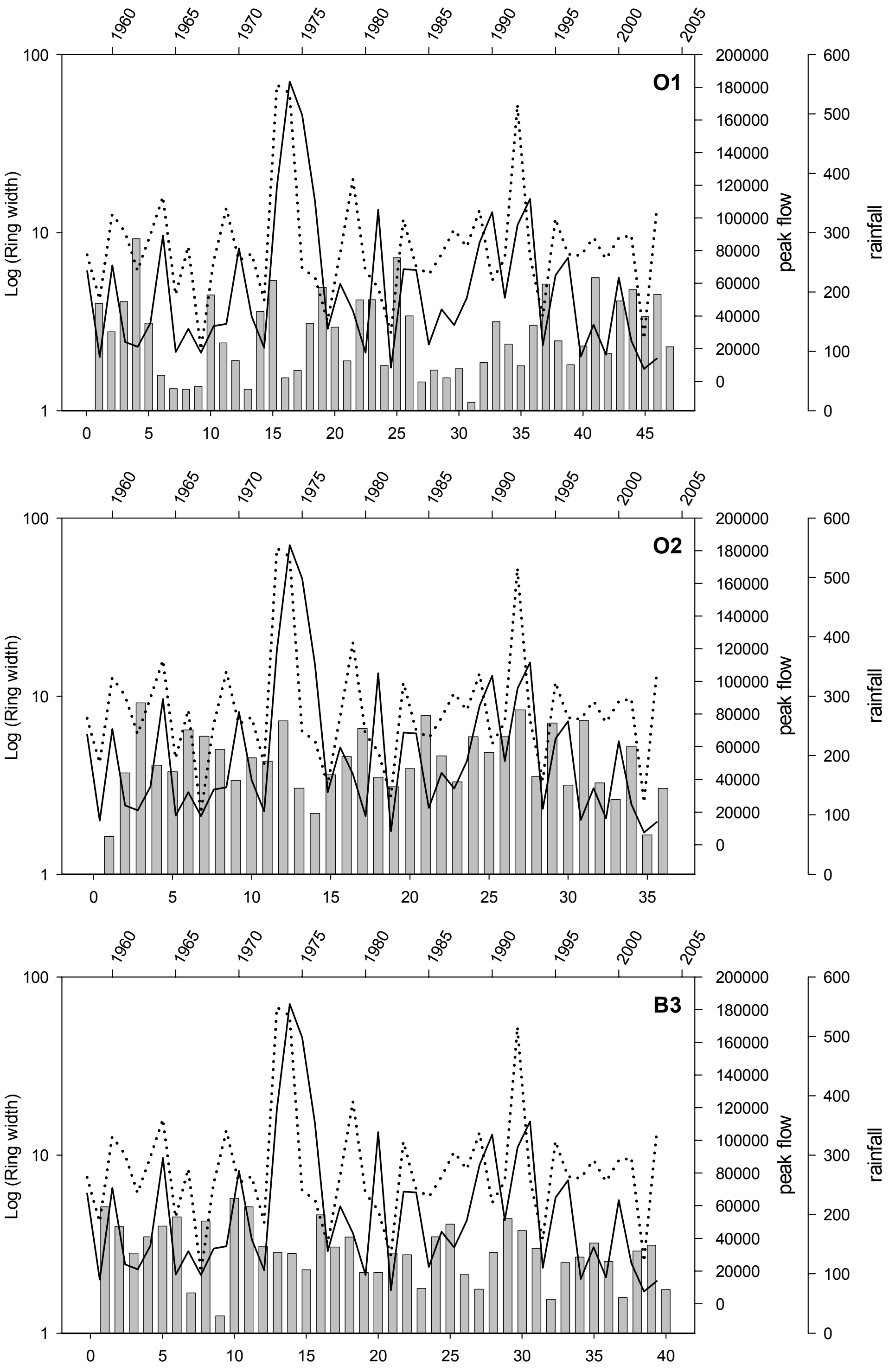
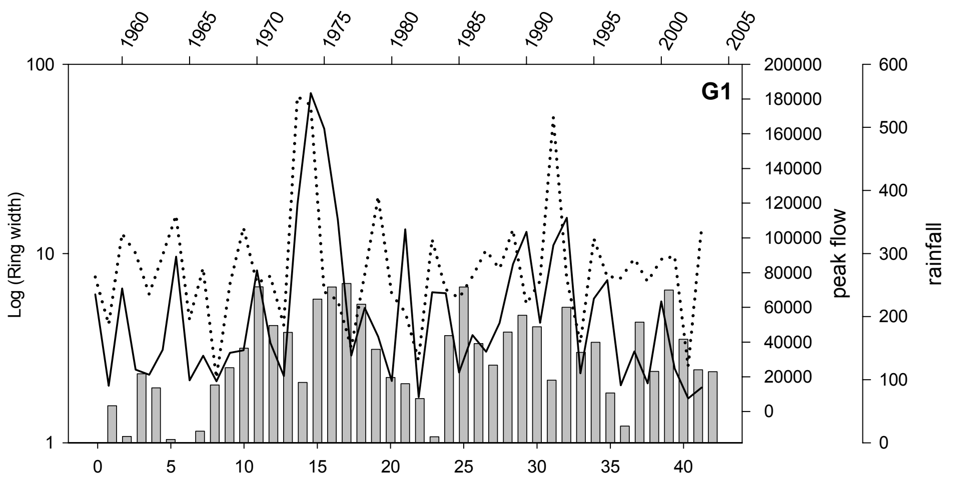


Figure 6-9 Ring pattern and associated rainfall and river flows in red gums germinated in 1956. (Bars = growth rings; dotted line = rainfall; solid line = river flow). The units for rainfall are millimeters and peak flow is ML day^{-1}.

Black box growth responses varied slightly from similar aged red gum, as shown in Figure 6-10. Favourable growth is associated with flows between 60,000 and 80,000 ML day^{-1}, rather than 40,000 ML day^{-1} for red gums, thus also responding to lower rainfall magnitudes. Growth was more responsive during high flows and rainfall in 1973 – 1975 than red gum, but growth was still reduced compared to surrounding years. Black box widths during this time were 5 – 6 mm while red gum widths for the same time period were only 2 – 3 mm. Also, black boxes have longer response duration to favourable flows and rainfall. Figure 6-10 shows that black box can respond for approximately 2 years following high levels of available water. However, red gum response occurs within the same year of high water availability, but does not generally last longer than the single year.

Ring width variation throughout the lifespan of the trees differed between the two species despite exposure to the same patterns of rainfall and flows. Red gum width variation did not fluctuate between years as dramatically as for black box, especially within the early rings. Positive ring width response to favourable water conditions was only slightly different between species. Positive responses generally resulted in widths of 3, 4 or 5 mm in black box and 4, 5 or 6 mm for red gums. Red gums O1 and B3 were exceptions to this generalisation. Tree B3 had a distinct lack of similarly wide rings compared to the other trees and O1 had simply a larger range of ring widths as well as a greater number of rings overall.



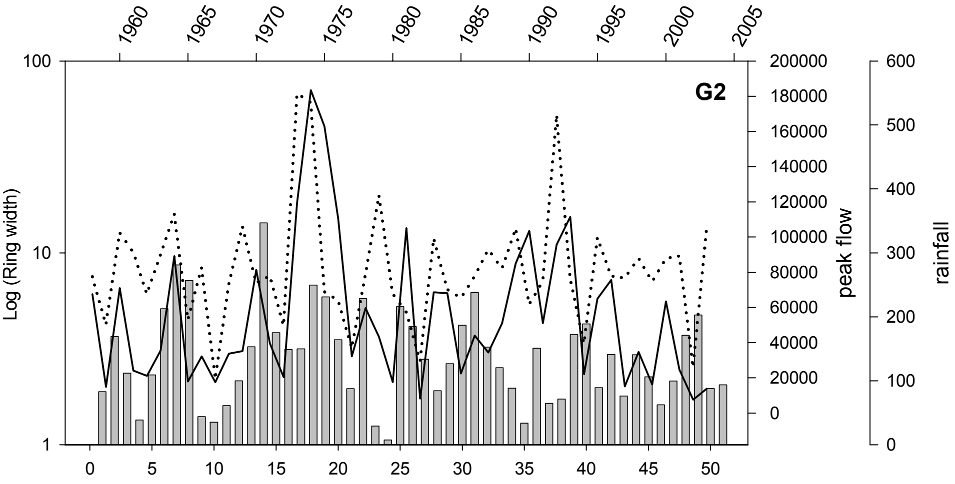


Figure 6-10 River flow and rainfall trends relative to ring numbers in black box germinated in 1956. (Bars = growth rings; dotted line = rainfall; solid line = river flow). Rainfall is shown in mm while peak flows are in ML day^{-1}.

The ring width/hydrology association for the 1978 red gum trees is shown in Figure 6-11. Individual growth responses varied most within this group of trees. None of the three trees had responses as closely associated with flow as the 1956 trees. O3 was the most similar to 1956 red gums generally responding to magnitudes between 40 and 60,000 ML day^{-1}. Like black box, O3 had a more active response to flows greater than 80,000 ML day^{-1} during 1990, but during high flows in 1993 growth was suppressed as in 1956 red gums. This tree showed a more distinct association with rainfall either responding during the same year as high rainfall or with a lag of approximately one year. Tree B1, which was correlated with rainfall, showed a related response. Ring width changes occurred during the same year as high rainfall such as 1993 or lagged behind rainfall by one year as in 1987 and 1997. The most ambiguous results were seen in tree B2. Ring widths for this tree were generally less than for the other two trees and the patterns were not primarily associated with rainfall or flows. Rather, the growth pattern switched between the two water sources. The widest rings appeared to be from high flows during 1993. Growth in the other trees during this period appeared to be suppressed by too much water, as indicated by the presence of narrow rings in the comparative growth zone. Conversely, when rainfall and flow levels were moderate, generally associated with positive growth response, growth in B2 was reduced (e.g. 1984, 2000).

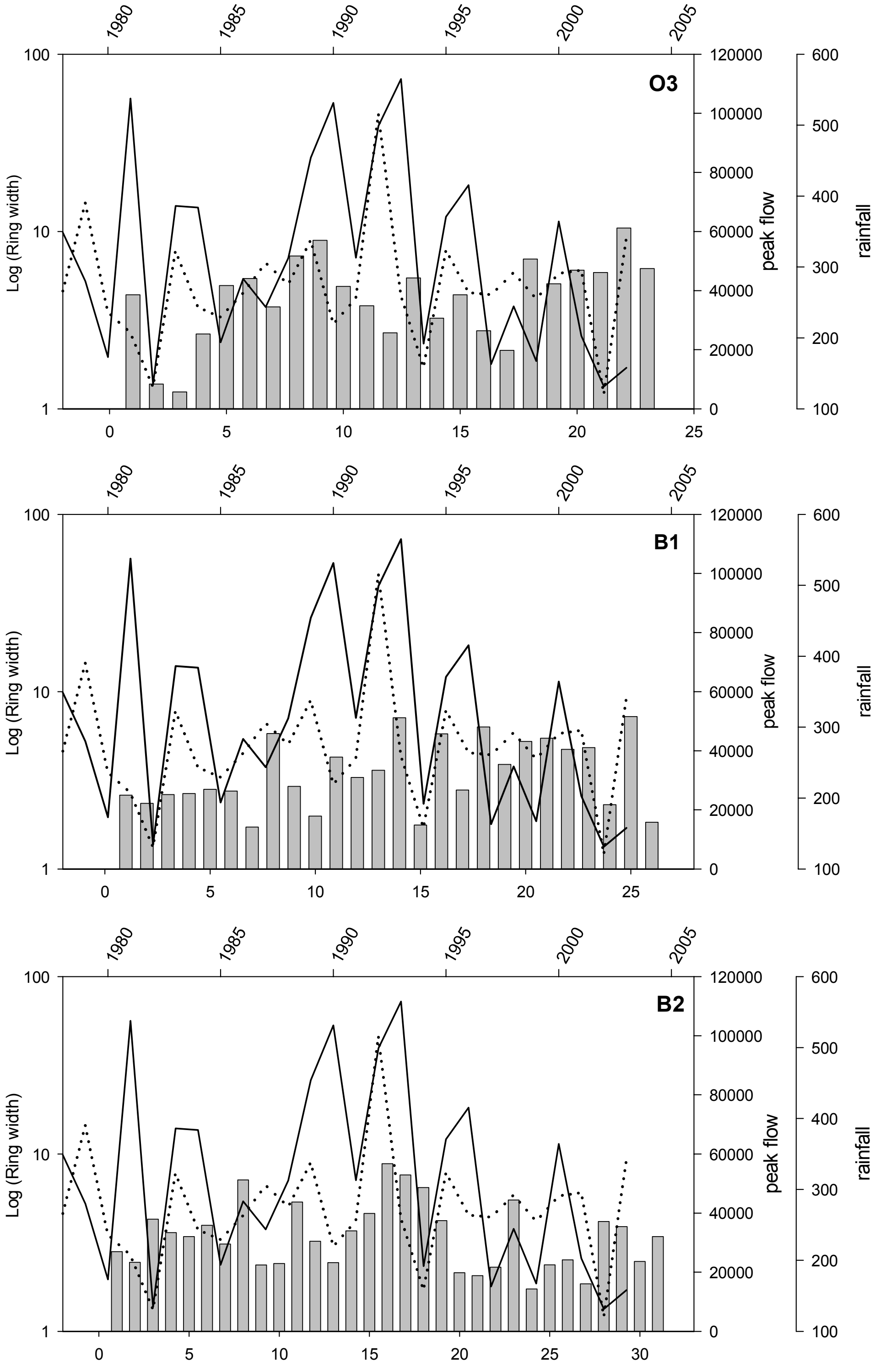


Figure 6-11 Trend for rainfall and river flow relative to red gums germinated following high flows in 1978. (Bars = growth rings; dotted line = rainfall; solid line = river flow). Rainfall is shown in mm while peak flows are in ML day^{-1}.

6.4 Discussion

6.4.1 *Age and diameter*

As illustrated in Chapter 3, the association between DBH and age can be tenuous. Even though the number of samples is small, results showed a clear distinction between the 1978 and 1956 cohorts, validating the use of DBH as a surrogate for age. If no difference had been found between the cohorts, DBH could not represent age since these trees had been verified to have germinated at different times. The DBH values obtained during this study suggest that within this region, red gums with DBH values greater than 35 cm can be classified as approximately 50 years old or greater and trees with diameters between 28 and 35 cm are approximately 25 years of age. Since this suggests a growth increment of 1 cm each year, it implies that trees taller than breast height with diameters of 10 cm are approximately 5-10 years old. These values are in accordance with the growth measurements of *E. camaldulensis* in the Mount Gambier region of South Australia (Cotterill *et al.*, 1985). Black box DBH at this site is more variable than red gums with one value similar to the 1956 red gums and the other reflecting the size of the 1978 trees. While this does suggest a very different growth pattern, it does not account for the second bole of the tree which, if included, could have provided DBH values similar only to the 1956 red gums.

6.4.2 *Age and ring number*

Growth ring enumeration was successfully correlated with tree age, as no difference was found between actual and expected ring counts. The similar number of rings exhibited within cohorts also supports the correlation between ages and rings. The strongest correlation was found in the 1978 trees since ring counts in the younger trees had the least variation between radii counts. This verified the preferential collection of younger, smaller trees with more distinct rings as proposed by Fritts (1976).

The lack of divergence between expected and actual counts suggests that ring deposition is annual despite the semi-arid climate of the region. This, naturally, does not account for any combination of missing or multiple rings that may have occurred. It does, however, imply that average growth may occur in a cyclic manner even if the cycle is not related to seasonal climatic changes.

Student's *t*-tests failed to account for the single 1956 red gum (O2) that had ring counts more closely related to the 1978 trees. While some level of intraspecific enumeration variability is expected, the statistical tests did not reflect the difference of nearly 40% between mean ring counts and actual counts in tree O2. Argent (1995) found similar discrepancies in his work with *E. camaldulensis*, determining that an 80- 90% difference in counts could exist within individual samples. However, Argent (1995) collected 76 trees while this study only included 8. Therefore, the failure to identify variation at 40% could result from the small number of samples. Fritts (1976 pg 256) points out that a minimum of 10 different trees is required for trees to be included in the International Tree-Ring Data Bank because of the large error in small samples. This suggests that by increasing the number of trees variation between rings counts could be better represented. This study was designed to be exploratory, so the limited number of samples was inherent by both the difficulties in locating suitable known-aged trees and the limitations placed on the number of trees that could be collected.

6.4.3 Cohort growth responses

The consolidated ring sequences clearly indicate that trees within this region show similar growth responses. Variation between individual trees is expected since physiological responses are unique, but the general patterns within the sequences indicated consistent changes between wide and narrow rings. The differences seen between red gum and black box reflect the differences in not only growth environment but also in physiological tolerance and response mechanisms. Because of the reduced dependency of black box on continuously available water, the number of matching rings should be less than red gums. The tolerance of dry conditions characteristic of this species should be reflected in the growth response as missing or absent rings. The close association between available water and red gum may be reflected as narrow rather than absent rings.

Early ring sequences were the most problematic for matching in all trees. It is generally accepted that early rings are wider and have more consistent growth than later rings (Fritts, 1976). The uniformity and width of initial rings could have been impacted by the presence of multiple piths in a number of the sample trees. Multiple piths may reflect the establishment of lateral branches during early growth stages. None of the trees harvested had dominant lateral branching at breast height, but given the grazing history of the site, each tree could have had any number of later branches in early growth stages because there was no direct competition from surrounding trees to prevent horizontal canopy expansion. Lateral branches would impinge and alter the shape and arrangement of rings. A number of trees also exhibited ring abnormalities common with the presence of tension and compression wood resulting from lean or tilt of the main trunk. Such forms will often set the pith off-centre, making rings compressed and indistinguishable on one side of the tree.

Ring matching in the middle of sequences was also complicated for black box and the 1978 red gum cohort. The middle of these sequences was associated with ‘double’ flows where two large flow events occurred within a short time period. The flows during the early 1970’s are an example of this. The unclear ring patterns during these times imply climatic aberrations that caused sporadic growth. These could have resulted in misidentification of boundaries thus disrupting pattern evaluation.

Fewer ring matches were found in the 1978 cohort, which is not surprising given that the 1956 trees are nearly twice as old as the younger cohort. It is expected that ring matches are directly proportional to the relative age of the tree. Rings in the younger cohort were also much more easily matched between trees. Younger trees simply could have a more rapid and obvious response to climatic conditions since translocation is not prohibited by tree size as much as in older, larger trees. The location of trees on the floodplain and within the stand could have also contributed to the more obvious matches in younger trees. Each of the younger cohort trees were located on the outer edges of the stand near flood runners and low-lying areas where standing water could easily pool during rainfall events and higher flows. The 1956 trees were in closer proximity to the river but on slightly higher elevations.

6.4.4 Hydrological links

Associations between hydrological variables and the matched growth responses were not strongly supported by statistical correlations. With only two of the eight trees showing any correlation with rainfall or flow variables, it could be concluded that measurable growth does not result from water availability. However, the statistical tests were limited by the small sample size, and probably by errors in ring identification and width measurements. Further, statistical correlations only allow for single year associations with single rings, and do not account for missing rings during drought years or multiple rings that may result during favourable water conditions. Lagged correlations suggested that the correlations could be improved, particularly if rings were more precisely assigned to specific water years or the appropriate lag between available water and active growth could be identified. Such information would provide guidelines for precise response for any given hydrological value. But, as Rayner (1992) suggests, when study objectives relate to climatic rather than physiological growth factors, generalizations may be all that are required. At the Swan Reach site only generalizations may be possible, given that regional rather than site specific hydrological data are available. Strict statistical applications may not be the most comprehensive means of determining general trends between growth and hydrology.

The two correlations resulting from the statistical analysis suggest that older trees rely on flows while younger are more dependent on rainfall. Whilst it is well established that trees are able to switch between water sources (*i.e.* Mensforth *et al.*, 1994; Thorburn and Walker, 1994) such studies make no provision for water sources relative to age. These studies used fully mature trees but as Zahner (1968) discusses it can not be assumed that the mechanisms of response will remain constant during development from seedling to sapling, pole or mature tree. Akeroyd (2002) attempted to chronicle water sources by isolating stable isotopes from individual rings, and had the work been conclusive the results could have offered support to the issue of age related water dependency. Younger trees sourcing rainfall preferentially to flow is not completely unfounded. Resource allocation between 25 and 46 year old trees should vary since they are dependent on size. An increase in size is accompanied by increased complexity in physiology, and competition for water among plant tissues is a major factor in tree form (Fritts, 1976).

The graphical representations of hydrological factors and growth sequences proved to be more persuasive than the statistical analysis. Again, the statistical analysis relies on directly correlating individual rings with individual water years, but the graphical representations do not have this limitation. They allow trends to be evaluated that are not apparent by statistical test results. Both cohorts responded favourably to moderate sized flows when coupled with average or above average total rainfall. Interestingly, these are the same flows that are most impacted by regulation and also contribute to successful regeneration and establishment as discussed in Chapter 4. The graphs further suggest that a relative threshold of 80,000 ML day^{-1} coupled with rainfall in excess of 350 mm depressed growth in all trees. The effect of the thresholds was reduced in black box but only in the magnitude of the growth response, further illustrating that tolerance varies between the species. The idea of thresholds was also shown by the work conducted by Heinrich (1990) using seedlings. The importance of this point lies in the fact that different growth stages exhibited similar responses to excessive amounts of water, so there is little benefit from flows that inundate any growth stage with exceedingly high flows or rainfall.

This does not imply there is no benefit in considering different growth stages when prescribing hydrological inputs. The graphs suggest similar results to the statistical tests regarding age dependant hydrology, implying that younger trees are more reliant and responsive to rainfall rather than river flow regardless of the magnitude. This suggests that younger trees are a better measure of water availability necessary for initiating germination, establishment, and early growth, but that older trees are necessary for defining the transitional water requirements. The necessary hydrology for maintaining viability and population expansion can be derived from older trees.

A limitation of this dendroecological assessment is the failure to directly link years with specific rings. Few trees showed extremely narrow rings indicative of dry years even though such years were visible in the hydrograph, as in 1983 or 2003. This implies that a least a few years of missing rings should be expected as well as multiple rings during high water years.

6.4.5 Confounding factors

One limitation of this study is the assumption that ring width variation resulted primarily from water availability. Severe defoliation resulting from prolonged drought, disease, or insect attack will influence ring width and number (Rayner, 1992), and such factors were not included. Further work should consider growth response from these alternative factors as well as from the effects of phenological processes on radial growth. Fritts (1976) emphasizes that buds, flowers, fruits and leaves are often associated with specific stages in cambial activity, and therefore can result in structural ring variation.

In this study, the use of vessel characteristics was relatively unsuccessful, but according to Yanosky (1983) vessel arrangements could offer a way to assign years with rings. Yanosky (1983) found ring anomalies such as earlywood vessels within latewood and 'jumbled' earlywood vessels characteristic of flooding related growth responses. This type of anomalous vessel characterization could be attempted with red gum and black box. The trees used in this study exhibited rings with distinctly different vessel arrangements that could equally represent flood years. A narrow ring with densely packed vessels may represent growth in such situations. Vessel characterization would also need to include other climatic factors such as temperature. Thomas *et al.* (2004) determined that temperatures during active growth affected water viscosity, which in turn changed the size and frequency of vessels.

Rates of cambial expansion have not be quantified for this region, but the association with hydrology apparent from this study as well as previous chapters suggests that such growth verification is pertinent for describing water requirements. Also the rate of growth in response to available water should be considered. This type of work could be easily conducted using increment bands during wet and dry years and would assess if the growth rate of 1 cm y^{-1} is feasible for Lower Murray eucalypts.

Ferguson (1970) suggests that in dendrochronological studies trees for sampling should not be too close to other trees because competition may disrupt climatic response nor should they have subsurface supplies of water. Trees chosen for this study were located in a region with confined floodplain where subsurface water would be readily available. Readily available subsurface water may induce more complacent growth in floodplain trees. While the results do not suggest complacent growth, the point should be considered by examining comparable trees from drier floodplain areas where groundwater is less accessible.

Finally, it should be noted that this study only attempted to identify hydrological associations under regulated conditions. Thus, this work should not be extrapolated to compare water requirements prior to regulation without quantifying growth responses. Older trees (100+ years old) could be used to identify patterns of growth decline relative to intense river regulation since they should show rings characterizing growth under both natural and regulated river conditions.

6.5 Conclusions

This study was developed to apply dendroecological techniques to examine the relationship between tree age and growth rings and to determine if growth reflects water availability. The findings show that DBH can be used as a relative measure of age without requiring *exact* age/DBH correlations. DBH values alone provide limited information about ages, but once quantified for a particular region, can be used for age structuring. Quantification involves relating a given age with a range of diameters. Despite the limitations of small sample sizes and variability, ring enumeration also represents relative age. Near Swan Reach it is strongly suggested that radial expansion in both red gum and black box occurs annually or at the very least in a cyclic manner.

Positive growth appears to rely on moderate river flows (40,000 – 80,000 ML day^{-1}) coupled with average rainfall (250 – 300 mm $year^{-1}$). However, active growth is interrupted by saturated conditions occurring when flows exceed 80,000 ML day^{-1} and rainfall is well above average. Tree ring widths record the opportunistic water use over time and show that growth can be maintained when flows are reduced but rainfall is high or conversely, low rainfall and moderate flows.

The two different aged cohorts provide varying information. Younger trees may be used to describe necessary water requirements for initiating and establishing early regeneration stages, while older trees provide hydrological associations for maintaining mature tree viability and contribution to eucalypt population expansion.

Chapter 7 Conclusions

The research presented in this thesis examined regeneration of river red gum (*Eucalyptus camaldulensis* Dehnh.) and black box (*Eucalyptus largiflorens* F. Muell.), the two dominant species of trees on the floodplain of the Lower River Murray, South Australia. The study aimed to identify the impacts of reduced flooding on the regeneration process, and to investigate how these impacts affect growth, establishment and survival of the trees.

A conceptual model was developed outlining the stages of the regeneration process and suggesting limitations to each stage. The thesis chapters explored these limitations and included comparisons between *E. largiflorens* and *E. camaldulensis* to elucidate variations between species and attempt to define their associations with floodplain processes. Because discussions were included with each component of the study, this chapter serves simply to recapitulate the findings of each of the preceding chapters.

7.1 Demography

While the demographic structure of populations does not directly limit regeneration, it indicates long-term population sustainability. Demography is a balance between mortality and regeneration. Thus, knowledge of regeneration and demography highlight the effects of reduced flooding for tree populations. The study incorporated regeneration stages VIII-X of the sapling, pole and mature growth stages. The density of each species was lower than expected with gaps occurring in size classes of both species. A size structure with gaps suggests episodic recruitment such that intermediate size classes may be absent when recruitment opportunities are limited. The viability of black box at this site suggests that the population is in decline, based on the current demographic structure. Regardless of the manipulation of proposed longevity values this species will require greater than 100% survival to maintain the population at its current level. Red gum populations are at lower risk at any longevity assuming no substantial population loss in dense copses where recruitment has been prolific. A key point resulting from this study was the identification of the role of sapling release in population maintenance at this site. Sapling release times had a larger impact on viability calculation than altering longevity. This highlights the need for further studies to identify no only the physiological triggers for sapling release, but also the ecological conditions initiating sapling release in a given stand. Where sapling release may be a competition factor in temperate stands possibly stands in semi-arid regions release may be driven by edaphic factors.

7.2 Hydrological analysis

The association between flooding and tree growth stages was developed in Chapter 4. Trees depend on available moisture to induce germination and recruitment. The current distribution of floodplain trees identified species-dependent flow responses. No surprisingly, black box require moderate to large flows and red gum require small to moderate flow magnitudes. The distribution of growth stages did not support the evident spatial differentiation between the species, as proposed in the literature. Black box were not wholly restricted to the outer edges of the floodplain and high elevations. Red gum conformed to the expected spatial pattern, located in lower depressions and along inflows where water is readily available. Information derived from flow hydrographs illustrated severe alteration of tree-dependant moderate flows between natural and regulated conditions. These findings supported the need for moderate flow re-instatement to benefit floodplain trees. However, specific ecologically significant hydrological parameters for growth stages were relatively inconclusive, permitting only generalizations. Seasonal timing was more relevant for younger growth stages, while advanced growth stages were impacted by the duration and quantity of flows. The study also found no clear patterns in hydrologic parameters to illustrate variable regeneration, concluding that the fluctuation between wet and dry conditions probably contributes more to regeneration than individual patterns. However, hydrological parameters warrant further study since the absence of associations between growth stage periods reflect the application of a regional hydrological scale or the multiple decades of hydrological inputs. Possibly a smaller time frame could elucidate stronger associations.

7.3 Reproductive potential

Regeneration cannot occur if seeds are unavailable, and seed availability begins with the parent trees. Chapter 5 addressed this issue by monitoring phenological processes in ‘healthy’ and ‘unhealthy’ trees. Visual assessments of parent tree vigour proved useful in identifying stress impacts on reproductive potential. Early stages of the regeneration cycle including seed production, budding, flowering, and fruit formation are all substantially altered by reduced parent tree health. The amounts regenerative investments are more impacted than the timing. The rates of bud development, flowering, and seed production were all lower in unhealthy trees. A key finding in this chapter was the absence of multiple capsule crops in healthy red gum. Instead of being associated with increased health, multiple crops appear to be a consequence of reduced health. No significant differences were found in the reproductive processes of the co-occurring tree species. Therefore, regardless of individual or species specific responses, reproductive processes are similar within similar areas.

7.4 Dendroecological evaluation

Chapter 6 applied dendroecological techniques to floodplain trees. Ambiguities resulting from the demography study required a closer examination of the age/size relationship for floodplain trees, and a quantitative measure of water requirements for active tree growth was needed. This chapter concluded that tree diameter could be used as a relative assessment of age and ring enumeration implied annual growth. Growth did not necessarily imply a seasonal correlation but illustrated cyclic growth responses. Growth responses of relative cohorts were similar and easily matched between individuals. This work verified the preferable selection of younger trees for dendroecological studies. Younger tree growth was correlated with rainfall while older tree growth correlated with river flows. A general range of moisture conditions was determined from the graphical evaluation of hydrology and ring widths. *E. camaldulensis* apparently showed the greatest response to annual flows between 40,000 and 80,000 ML day^{-1} combined with average total annual rainfall (300 mm). Growth response in *E. largiflorens* occurs from higher flows (60,000 to 80,000 ML day^{-1}) with similar rainfall links as *E. camaldulensis*. Extremely high flows or rainfall depresses growth responses in both species and cohorts.

7.5 Summary

This thesis has examined various stages of the regeneration cycle. Each chapter supported, in some manner, that the populations of red gum and black box along the Lower Murray are in dire condition. Unhealthy trees will not provide sufficient seed supplies to offset population losses throughout the Basin. As the remaining populations become more fragmented, the likelihood of expansive floodplain tree distribution decreases. Applications of environmental flows or environmental watering may assist in prolonging the distribution of populations, but the allocations should aim to provide water which will provide more than simply survival of floodplain trees. The work presented here offers further support to the need for ecologically significant environmental flow allocations to prevent further tree losses and promote naturally sustainable populations. Since individual hydrological parameters could not be related to specific growth stages, variability of flows would meet the needs of each growth stage as required. Fundamentally, a return of moderate sized flows, in particular, at about half of the frequency of natural conditions could begin to allay further declines. Based on these findings, it could possibly not only initiate but also maintain further regeneration along the floodplain. Increased flooding could increase parent tree health providing for increased reproductive capacity, promote establishment and allow for population expansion by maintaining age/size related diversity.

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Appendix 1

Density and dominance calculated values from tree survey data collected at Banrock Station.

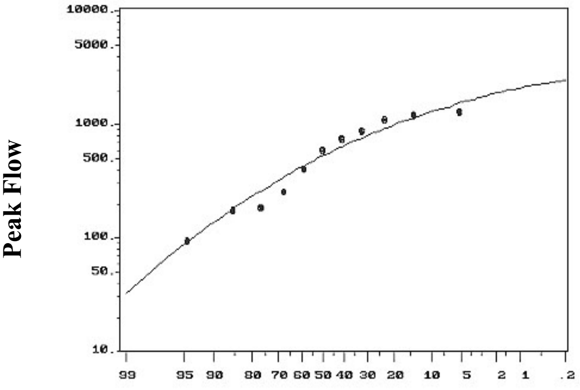
Density Measures	**Values**
Total Number of Red Gum measured	1108.00
Total Number of Black Box measured	290.00
Total Number of RG and BB measured	1398.00
Absolute Density of Trees (plot^{-1})	11.00
Absolute Density of RG (plot^{-1})	8.70
Absolute Density of BB (plot^{-1})	2.30
Absolute Density of Trees (ha^{-1})	87.60
Absolute Density of RG (ha^{-1})	69.40
Absolute Density of BB (ha^{-1})	18.20
Area of Sample Plot (m^2)	1256.60
Number of Sample Plots (ha^{-1})	8.00
Relative Density of RG	79.30
Relative Density of BB	20.70
Density of RG greater than 10 cm DBH (stems ha^{-1})	25.10
Density of BB greater than 10 cm DBH (stems ha^{-1})	14.00
Density of RG less than 10 cm DBH (stems ha^{-1})	44.40
Density of BB less than 10 cm DBH (stems ha^{-1})	4.20

Dominance Measures	**Values**
Total Absolute Dominance (m^2 plot^{-1})	1.70
Total Basal Area (cm^2)	2183976.70
Total Basal Area (m^2)	218.40
Basal Area of BB (cm^2)	878861.40
Basal Area of RG (cm^2)	1305115.30
Basal Area of BB (m^2)	87.90
Basal Area of RG (m^2)	130.50
Absolute dominance of RG (m^2)	1.00
Absolute dominance of BB (m^2)	0.70
Absolute Dominance per ha (m^2)	13.70
Absolute Dominance of RG (m^2 basal area ha^{-1})	8.20
Absolute Dominance of BB (m^2 basal area ha^{-1})	5.50
Total Percent of Ground Surface Covered	0.10
Percent of Ground Cover (RG)	0.10
Percent of Ground Cover (BB)	0.10
Relative Dominance of RG	59.80
Relative Dominance of BB	40.20
Frequency of RG	40.90
Frequency of BB	40.20
Relative Frequency of RG	50.50
Relative Frequency of BB	49.50

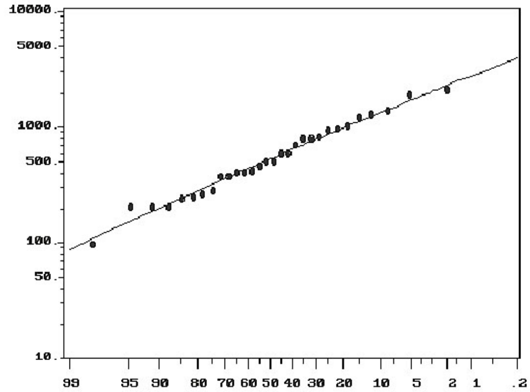
Appendix 2

Flow frequency curves for growth stage time periods under regulated conditions. Frequency curves are Log Pearson Type III distribution curves derived using AQUAPAK software. Growth stages represent the flows for both red gum and black box during each time period.

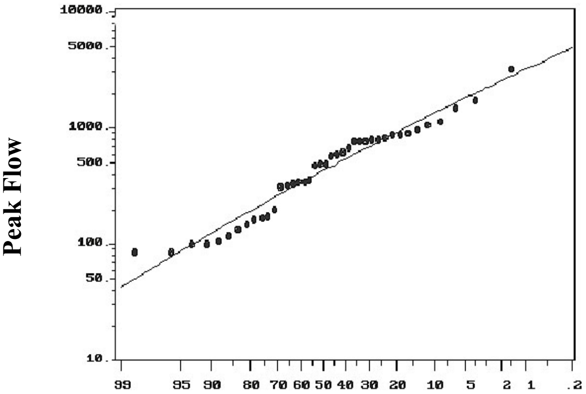
Seedling



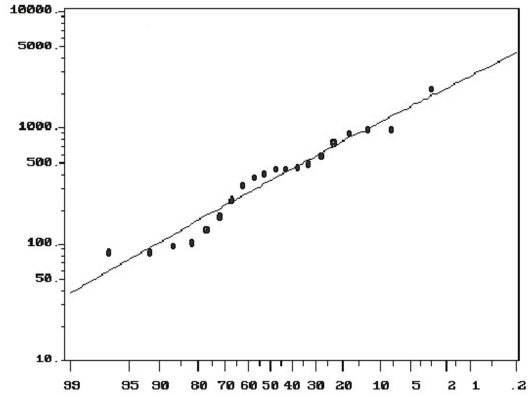
Sapling



Pole

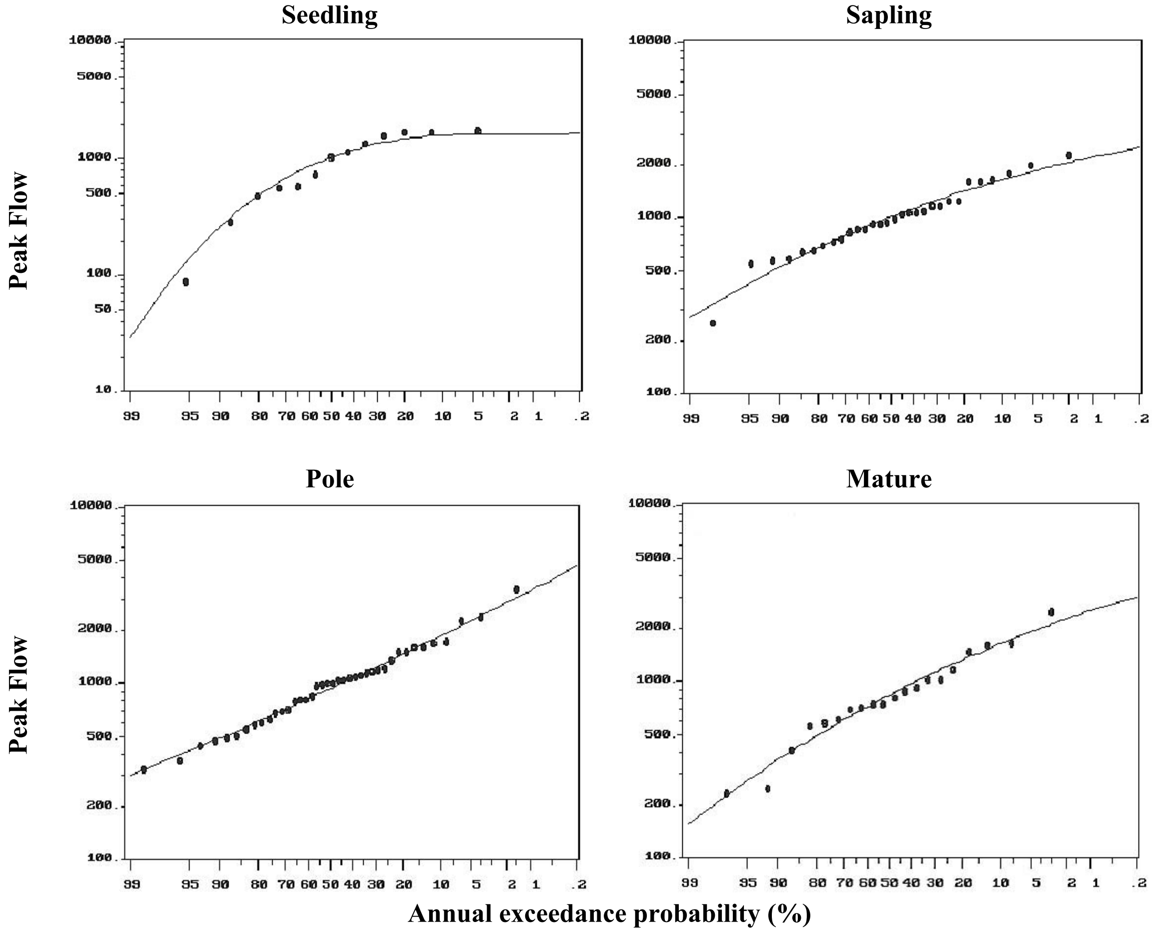


Mature



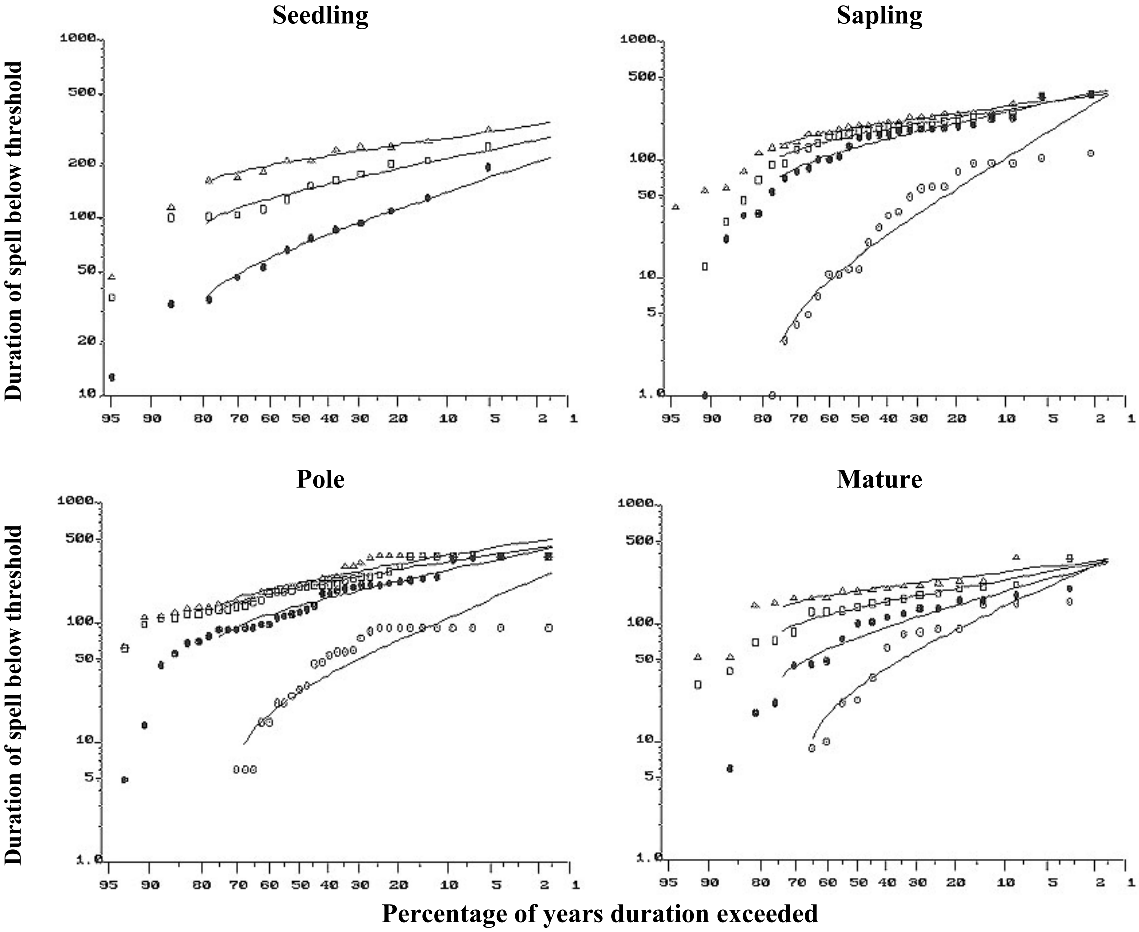
Annual exceedance probability (%)

Flow frequency curves for growth stage time periods under natural conditions. Frequency curves are Log Pearson Type III distribution curves derived using AQUAPAK software.

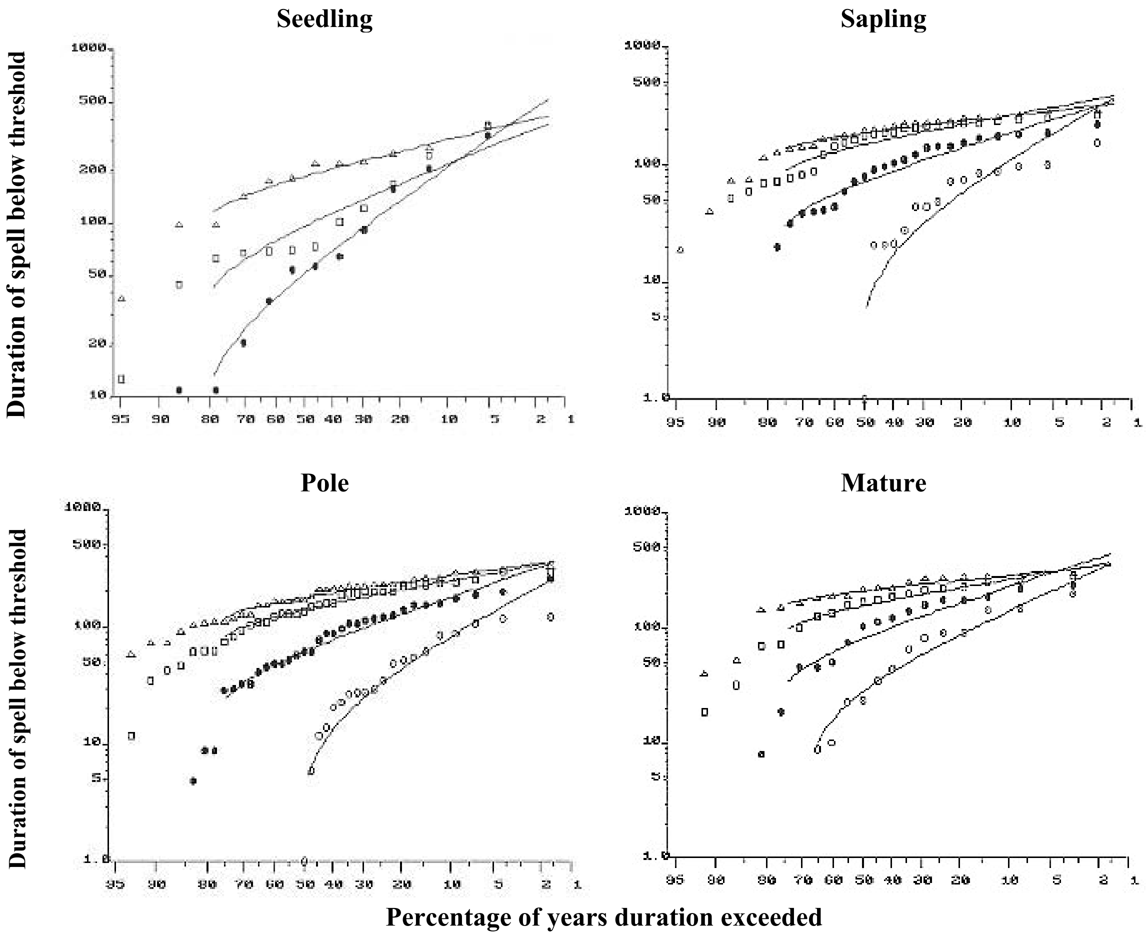


Appendix 3

Spell duration curves for growth stage time periods under regulated conditions. The software program applies threshold values at 20 (○), 40 (●), 60 (□), and 80 (Δ) percent of the mean daily flow. Duration represented as the number or days.

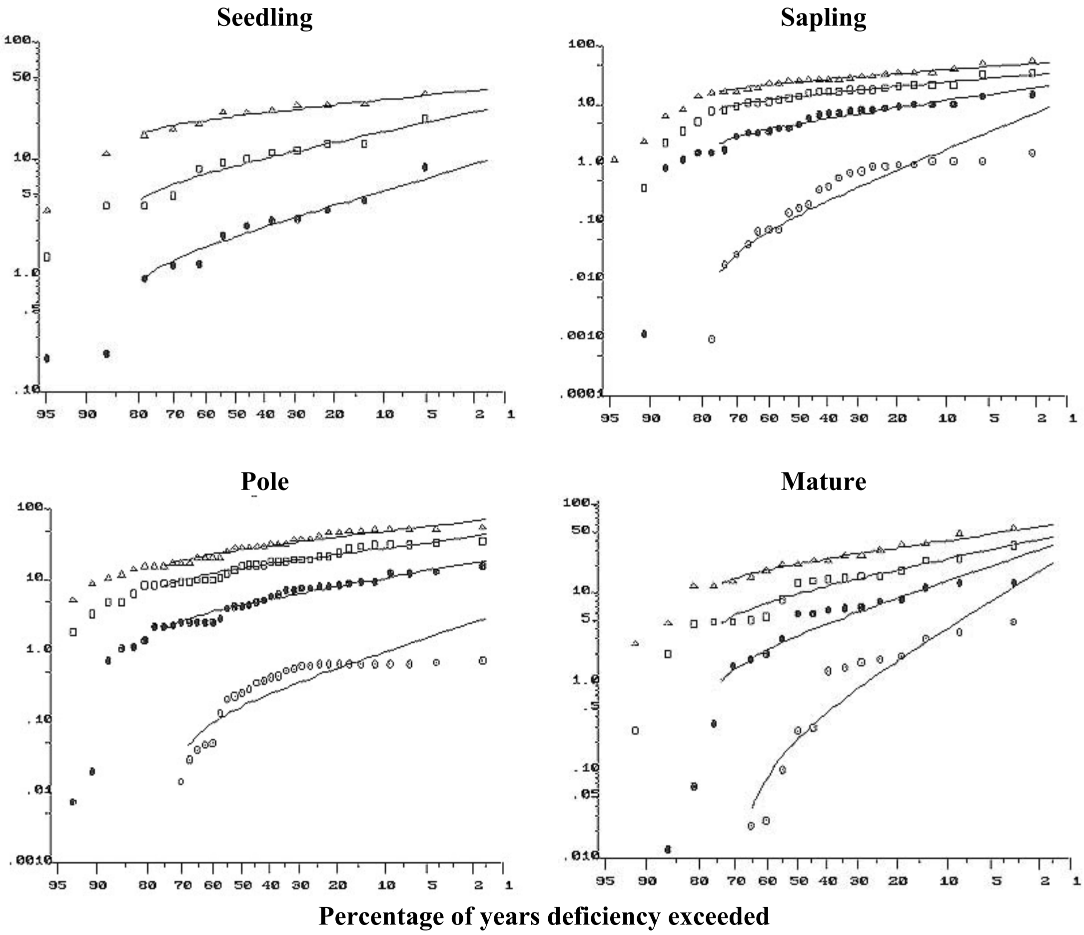


Spell duration curves for growth stages under natural flow conditions. Threshold values represented include 20 (○), 40 (●), 60 (□), and 80 (Δ) percent of the mean daily flow.

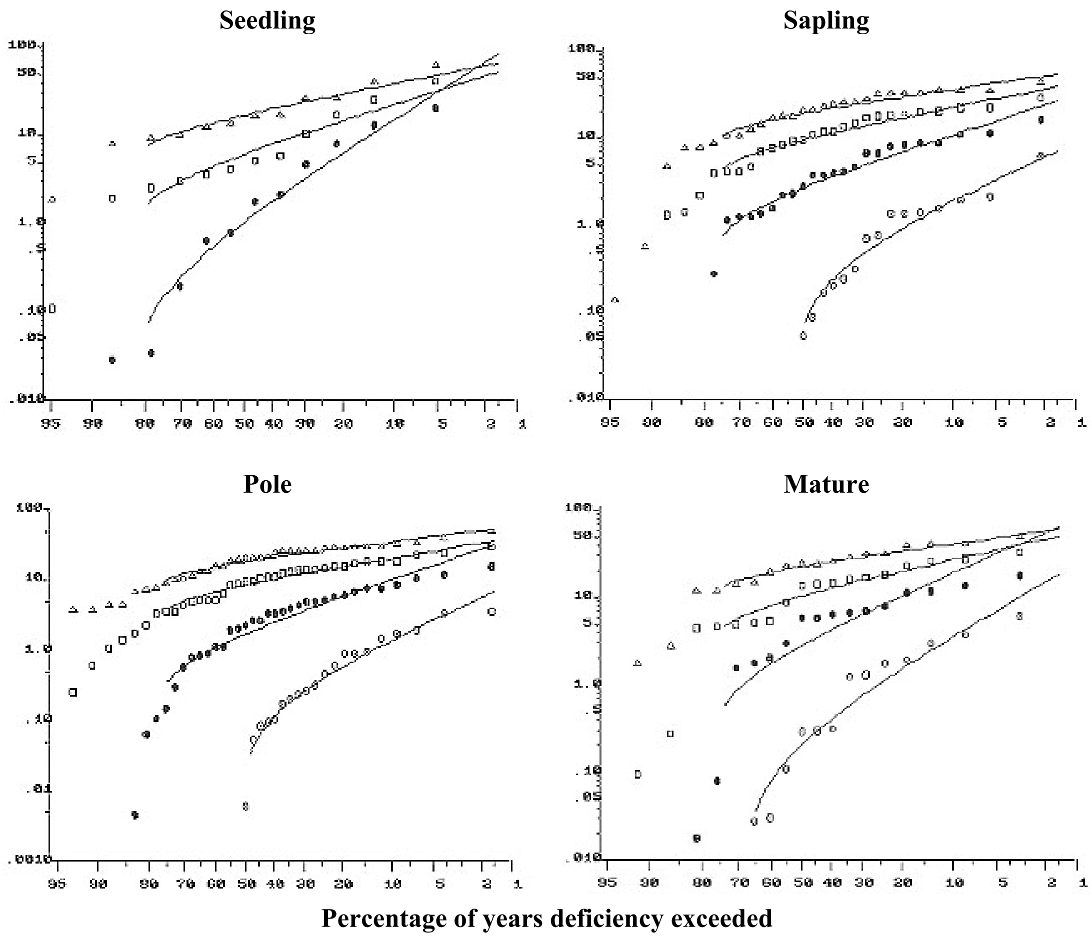


Appendix 4

Spell deficiency volume for growth stage time periods under regulated conditions. Threshold values represented include 20 (○), 40 (●), 60 (□), and 80 (Δ) percent of the mean daily flow. Ordinate axis is the deficiency volume expressed as the percent of the mean annual flow.



Spell deficiency volumes for growth stages under natural flow conditions. Threshold values represented include 20 (○), 40 (●), 60 (□), and 80 (Δ) percent of the mean daily flow. Ordinate axis is the deficiency volume expressed as the percent of the mean annual flow.



Appendix 5

Crown condition data collected for sample trees at Banrock Station. Scores and ratings were calculated using the methods outlined by Grimes (1987).

Tree	**Crown position**	**Crown size**	**Crown density**	**Dead Branches**	**Crown epicomic growth**	**Total crown score**	**Rating**	**dmai***
BBG3	4	4	5	3	2.0	18.0	average	0.298
BBG4	3	5	9	4	2.5	23.5	good	0.749
BBG6	4	4	9	3	2.5	22.5	good	0.648
BBG8	5	5	9	4	2.5	25.5	excellent	0.975
BBG9	5	4	9	4	2.5	24.5	excellent	0.858
BBG10	5	5	9	4	2.5	25.5	excellent	0.975
BBP1	4	3	3	3	2.5	15.5	poor	0.176
BBP2	3	3	5	2	1.5	14.5	poor	0.142
BBP7	3	2	1	1	1.0	8.0	very poor	0.124
BBP8	3	2	1	1	1.5	8.5	very poor	0.113
BBP9	3	2	1	1	1.5	8.5	very poor	0.113
BBP10	2	1	1	1	1.5	6.5	very poor	0.170
RGG1	5	4	7	4	2.5	22.5	good	0.648
RGG2	5	5	7	4	2.5	23.5	good	0.749
RGG4	3	3	7	4	2.5	19.5	average	0.396
RGG8	4	4	9	4	2.0	23.0	good	0.697
RGG9	5	5	9	4	3.0	26.0	excellent	1.037
RGG10	4	3	5	2	1.5	15.5	poor	0.176
RGP1	5	3	5	3	1.5	17.5	average	0.269
RGP2	3	4	5	3	1.5	16.5	average	0.218
RGP3	5	4	3	2	1.5	15.5	poor	0.176
RGP4	4	3	3	3	1.5	14.5	poor	0.142
RGP5	5	2	5	1	1.0	14.0	poor	0.128
RGP9	4	4	3	2	1.5	14.5	poor	0.142

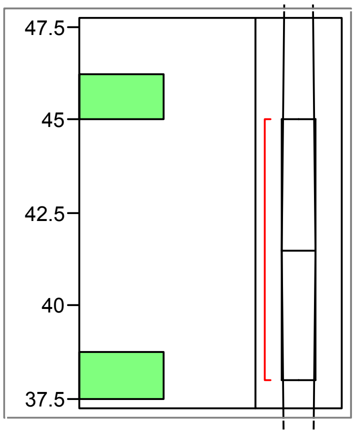
Total Crown Assessment	less than 12	Very Poor
	12 – 15.9	Poor
	16 – 19.9	Average
	20 – 23.9	Good
	24 - 27	Excellent

*dmai: mean annual diameter breast height increment, representing the expected amount of incremental diameter growth reflected in crown condition factors.

Appendix 6

Comparison of mean ring counts with expected mean ring counts. Testing was conducted using JMPIN Version 4.0.3, SAS Institute Inc. The graphs show the distribution of radii values measured for each tree.

O1

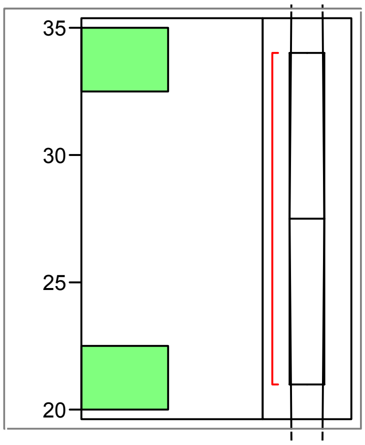


Test Mean=value

Hypothesized Value	46
Actual Estimate	41.5
df	1
Std Dev	4.94975

	t Test
Test Statistic	-1.2857
Prob > |t|	0.4208
Prob > t	0.7896
Prob < t	0.2104

O2

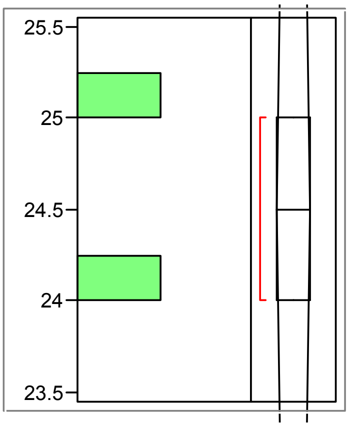


Test Mean=value

Hypothesized Value	46
Actual Estimate	27.5
df	1
Std Dev	9.19239

	t Test
Test Statistic	-2.8462
Prob > |t|	0.2151
Prob > t	0.8925
Prob < t	0.1075

O3

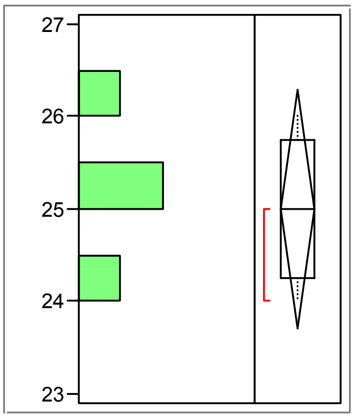


Test Mean=value

Hypothesized Value	24
Actual Estimate	24.5
df	1
Std Dev	0.70711

	t Test
Test Statistic	1.0000
Prob > |t|	0.5000
Prob > t	0.2500
Prob < t	0.7500

B1

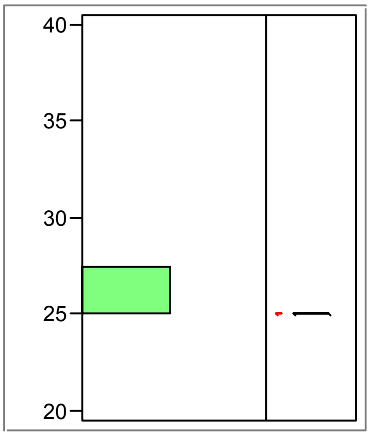


Test Mean=value

Hypothesized Value	24
Actual Estimate	25
df	3
Std Dev	0.8165

	t Test
Test Statistic	2.4495
Prob > |t|	0.0917
Prob > t	0.0459
Prob < t	0.9541

B2

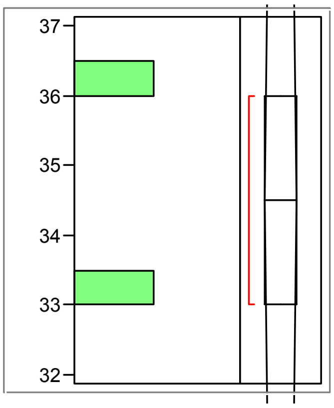


Test Mean=value

Hypothesized Value	24
Actual Estimate	25
df	1
Std Dev	0

	t Test
Test Statistic	.
Prob > |t|	.
Prob > t	.
Prob < t	.

B3

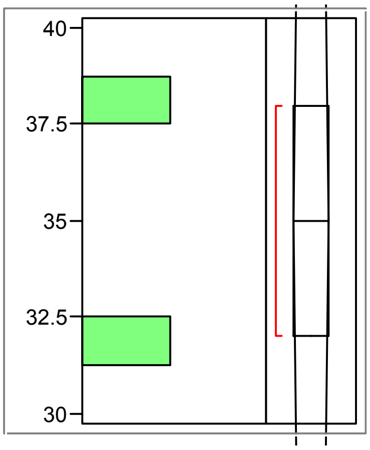


Test Mean=value

Hypothesized Value	46
Actual Estimate	34.5
df	1
Std Dev	2.12132

	t Test
Test Statistic	-7.6667
Prob > |t|	0.0826
Prob > t	0.9587
Prob < t	0.0413

G1

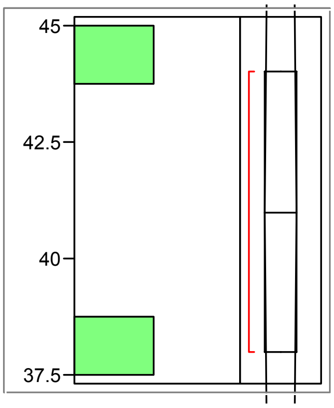


Test Mean=value

Hypothesized Value	46
Actual Estimate	35
df	1
Std Dev	4.24264

	t Test
Test Statistic	-3.6667
Prob > |t|	0.1695
Prob > t	0.9152
Prob < t	0.0848

G2



Test Mean=value

Hypothesized Value	46
Actual Estimate	41
df	1
Std Dev	4.24264

	t Test
Test Statistic	-1.6667
Prob > |t|	0.3440
Prob > t	0.8280
Prob < t	0.1720

Appendix 7

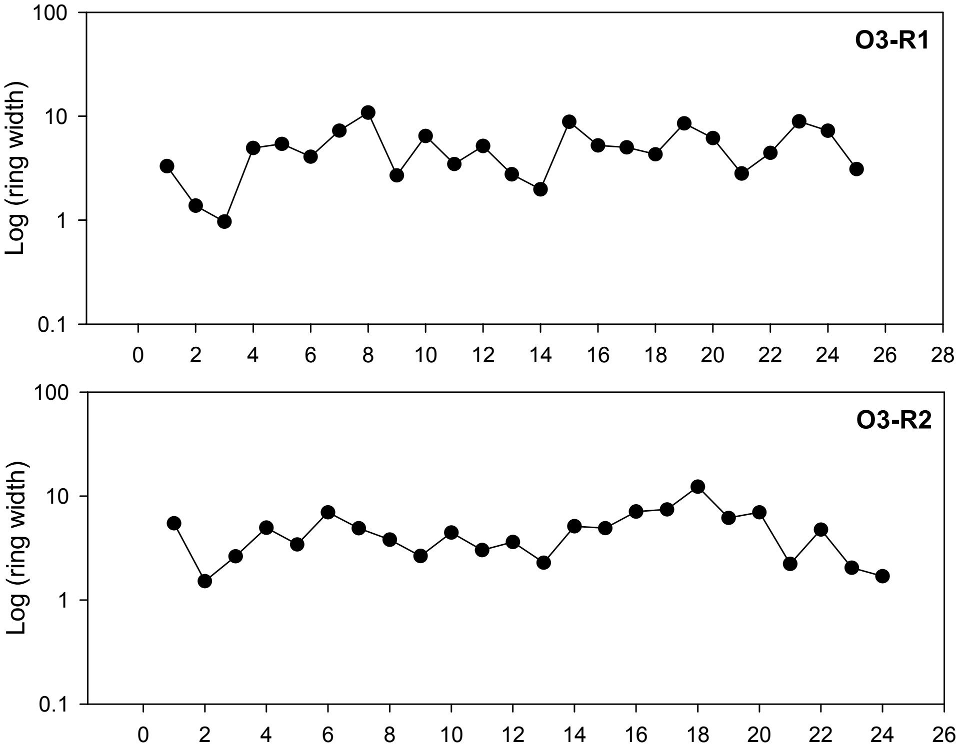
Individual tree ring width values in mm.

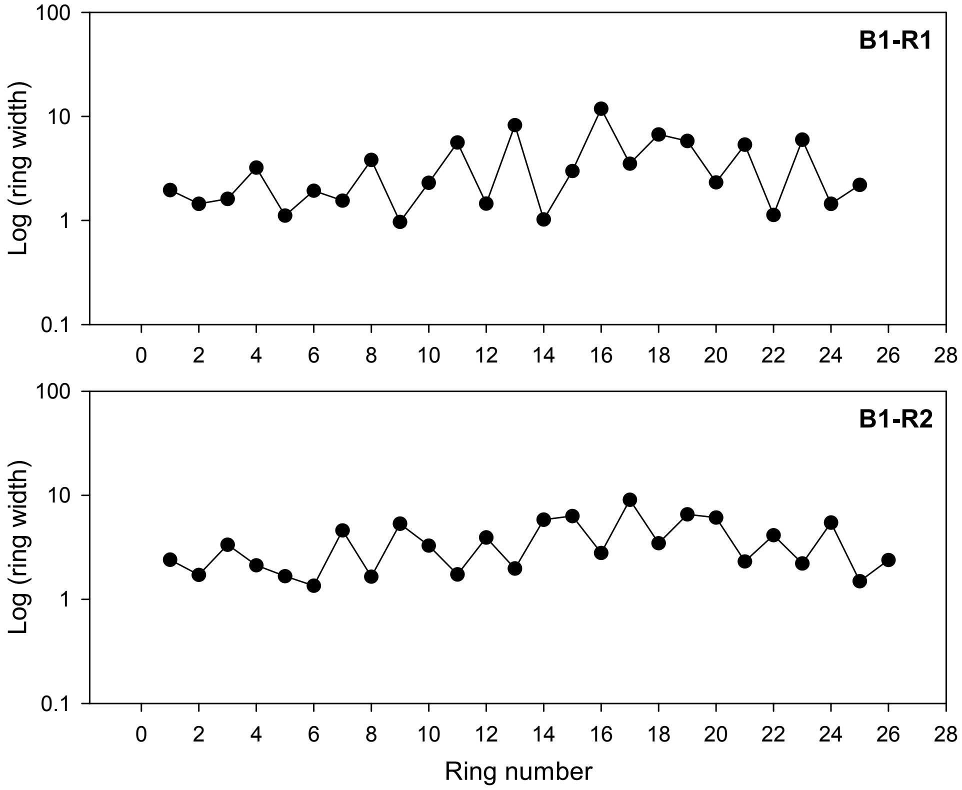
E. camaldulensis 1956						*E. camaldulensis* 1978						*E. largiflorens* 1956			
O1		**O2**		**B3**		**O3**		**B1**		**B2**		**G1**		**G2**	
R1	*R2*	*R1*	*R2*	*R1*	*R2*	*R1*	*R2*	*R1*	*R2*	*R1*	*R2*	*R1*	*R2*	*R1*	*R2*
3.36	4.65	1.63	5.55	4.65	5.60	3.31	5.48	2.82	2.40	2.80	2.83	2.32	1.57	4.95	1.89
2.48	3.07	3.70	5.19	3.59	4.33	1.38	1.52	2.97	1.72	2.06	2.84	2.07	1.08	2.36	2.37
4.11	10.01	9.17	4.19	2.44	3.20	0.97	2.64	2.63	3.35	4.00	4.58	0.96	2.31	1.24	1.45
8.50	3.11	4.09	2.57	3.48	3.09	4.95	4.97	1.98	2.12	3.41	3.80	1.15	1.83	2.31	1.57
3.09	1.58	3.76	3.99	3.99	1.32	5.43	3.43	3.51	1.67	3.10	3.74	1.69	1.04	5.11	1.05
1.87	1.33	7.36	2.62	5.91	2.67	4.09	7.00	3.84	1.35	4.00	3.93	2.29	0.78	8.66	1.31
6.34	0.77	6.71	5.65	2.05	0.97	7.28	4.90	2.10	4.60	3.60	2.61	3.16	2.35	12.79	1.60
2.57	1.37	5.84	3.04	5.85	4.63	10.84	3.82	6.99	1.65	5.78	8.51	6.28	2.69	1.75	2.06
5.96	2.59	4.16	2.05	1.53	3.73	2.70	2.66	4.20	5.32	2.15	2.58	5.24	7.06	2.25	3.24
1.90	2.40	5.02	3.53	6.79	3.02	6.47	4.46	1.99	3.28	2.41	3.40	3.70	2.86	13.50	15.17
3.09	2.00	5.99	6.02	6.51	3.17	3.47	3.02	3.22	1.73	7.31	2.99	1.92	3.08	4.11	3.56
6.57	1.26	8.87	3.51	3.12	3.09	5.18	3.62	5.47	3.93	3.22	3.69	5.48	3.96	3.48	3.14
2.94	1.32	2.33	2.68	2.51	3.99	2.76	2.29	10.32	1.97	1.89	4.62	6.49	2.25	6.20	2.83
2.52	3.60	3.71	6.42	2.51	2.37	1.98	5.13	1.57	5.82	8.39	9.24	6.01	5.99	4.55	7.39
3.32	4.83	4.59	6.42	2.27	2.72	8.84	4.92	5.50	6.32	7.62	6.46	1.32	6.80	1.84	7.24
2.72	2.79	7.15	5.20	5.24	2.19	5.23	7.09	3.63	2.79	3.00	5.42	3.68	7.87	6.26	3.52
5.72	2.00	3.52	8.65	3.72	1.33	5.02	7.45	4.31	9.01	1.98	2.30	6.15	5.39	1.25	2.08
1.92	1.53	3.92	8.76	4.21	1.72	4.31	12.36	3.92	3.46	2.06	7.83	2.56	3.12	0.51	5.31
2.28	1.47	7.79	2.70	3.05	1.60	8.53	6.18	4.79	6.56	2.30	1.73	2.15	2.21	7.11	1.61
1.35	3.29	4.62	2.48	3.91	3.91	6.17	6.98	7.15	6.12	3.19	2.37	3.77	2.05	4.90	3.36
2.42	1.29	3.30	2.56	2.76	4.47	2.81	2.23	5.53	2.31	3.42	1.64	4.76	1.71	1.50	3.35
2.31	4.19	5.43		1.97	2.13	4.45	4.76	2.40	4.13	4.11	1.85	4.10	0.83	4.20	2.79
2.15	5.07	4.83		3.04	1.64	8.91	2.05	9.02	2.21	3.66	4.22	2.87	7.14	4.81	2.32
1.46	0.87	5.42		3.71	3.03	7.24	1.70	2.18	5.46	3.08	4.13	5.82	4.12	2.52	2.64
3.55	7.22	8.38		1.89	3.89	3.10		4.45	1.49	3.42	1.87	3.83	2.99	1.97	7.64
1.58	1.10	1.87		2.64	3.77				2.39			3.41	3.91	1.55	3.23
7.34	0.98	5.47		4.92	2.43							1.83	4.68	2.17	1.04
2.54	1.10	3.17		3.56	1.71							1.50	1.41	1.83	4.19
1.81	1.53	5.79		1.39	2.49							5.25	4.58	3.37	1.45
2.04	1.72	3.81		1.81	3.54							7.55	2.18	1.71	1.73
5.59	0.88	2.78		1.24	3.21							3.58	3.39	3.46	3.75
2.85	1.58	5.23		3.20	2.53							3.22	0.95	1.69	5.16
2.12	3.16	1.66		1.73	1.93								3.43	3.18	2.25
2.54	1.18	3.51			2.89								2.38	2.26	2.45
1.96	2.00				3.04								5.27	1.45	2.31
2.06	3.02				1.79								3.47	2.60	1.95
2.49	2.93												1.64	3.82	1.90
2.12	2.40												2.37	1.57	2.70
	2.58														1.78
	1.34														2.15
	6.14														4.84
	7.03														5.66
	4.79														2.36
	6.51														2.05
	2.45														

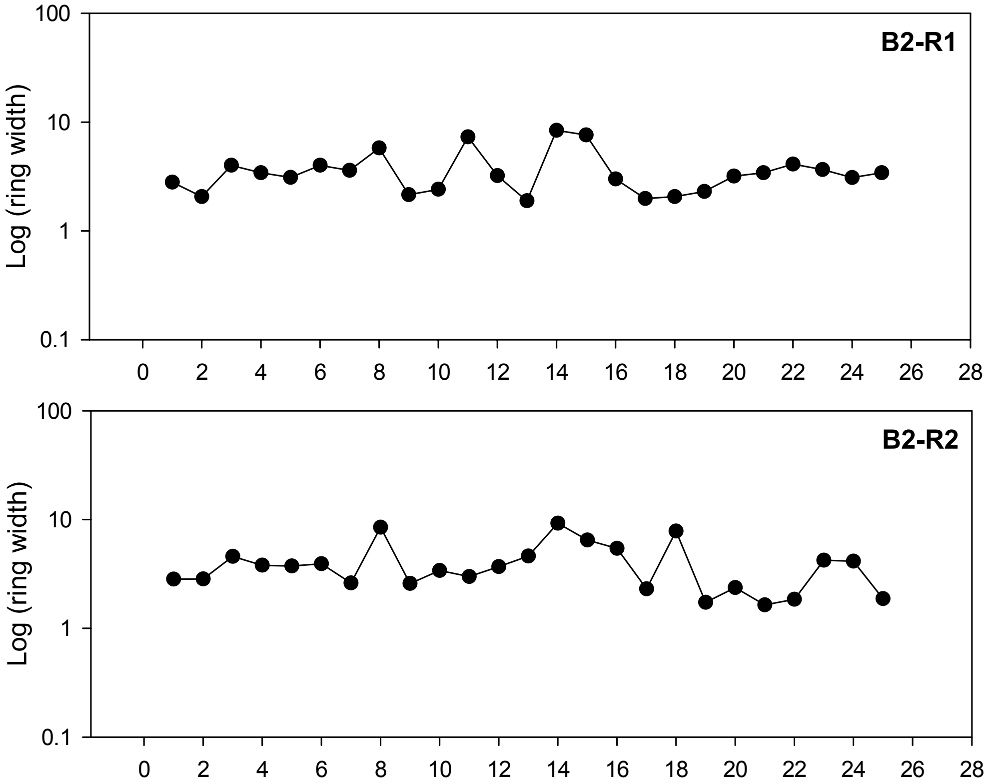
R: radius

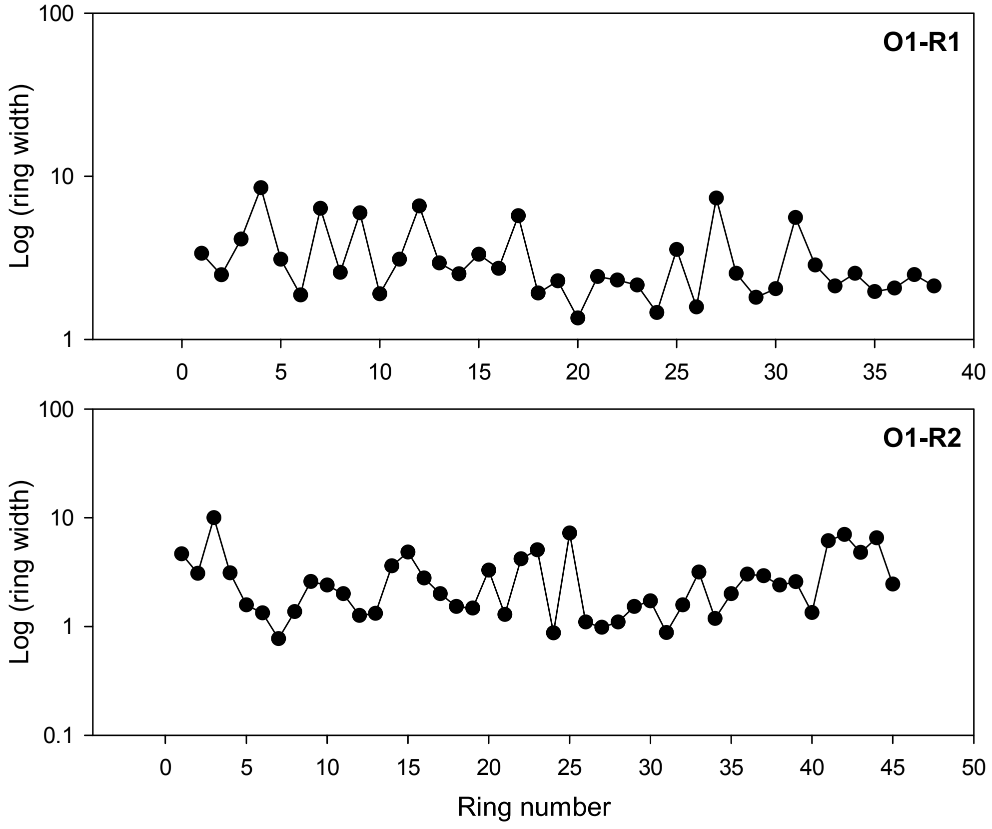
Appendix 8

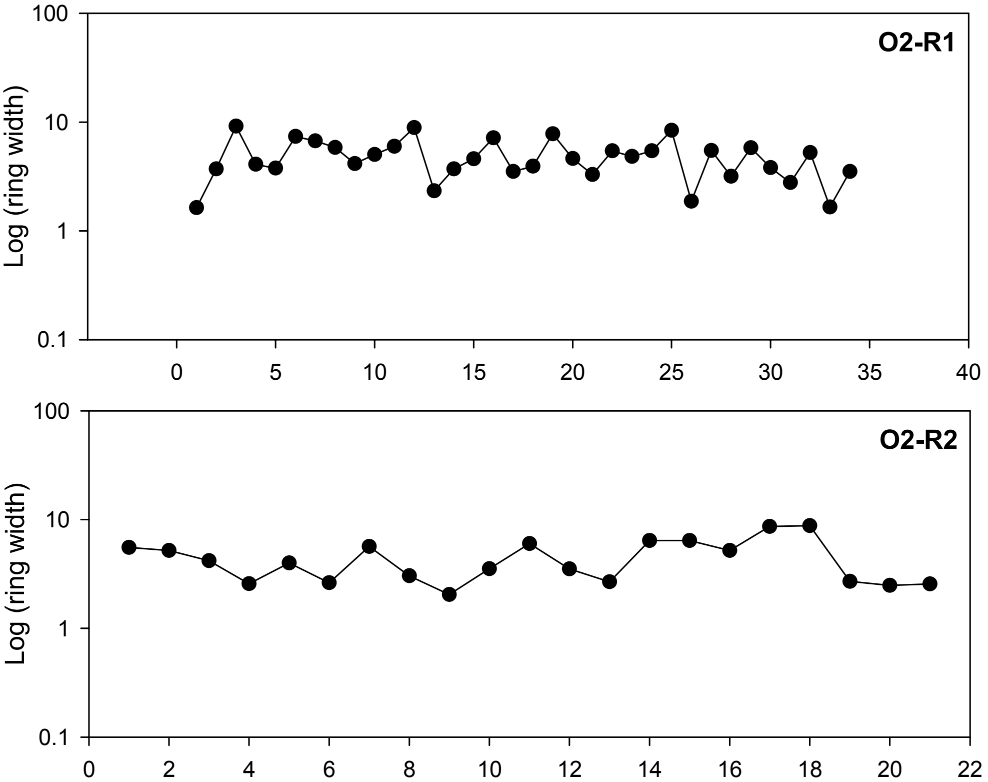
Figures illustrating individual radii for each tree.

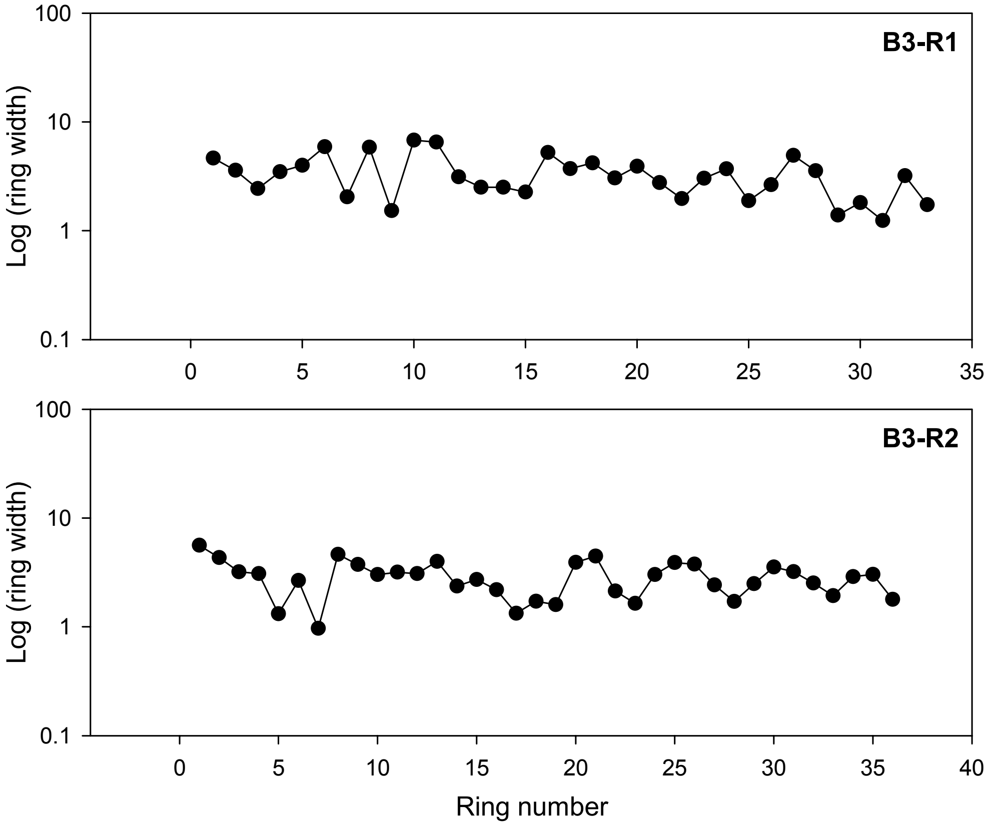


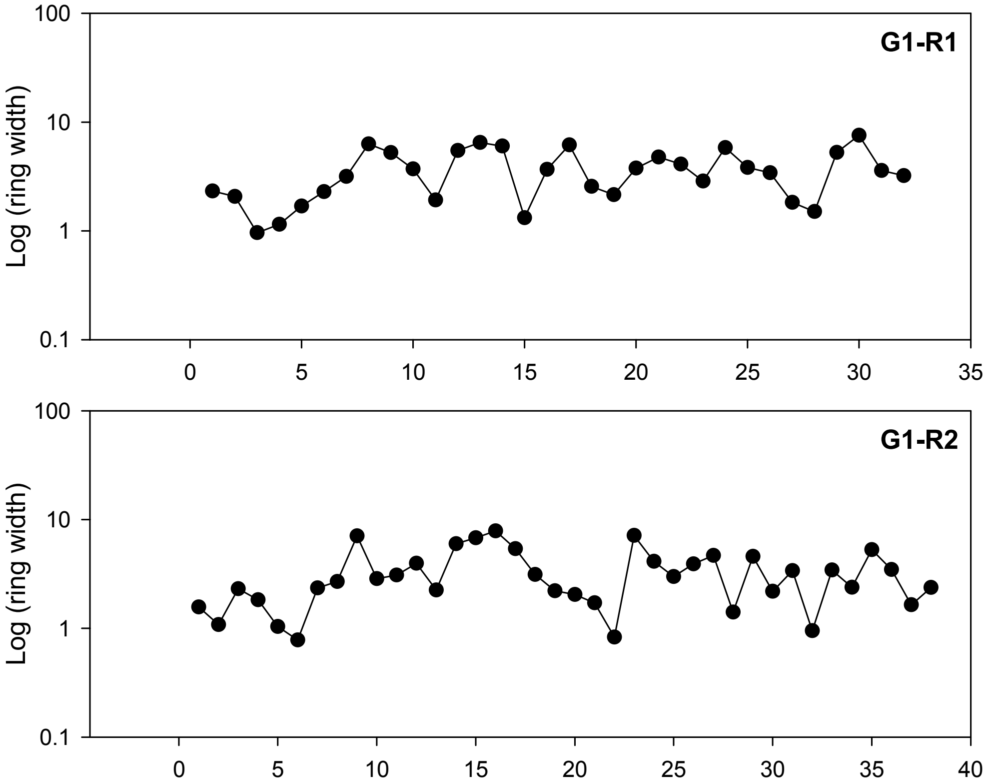


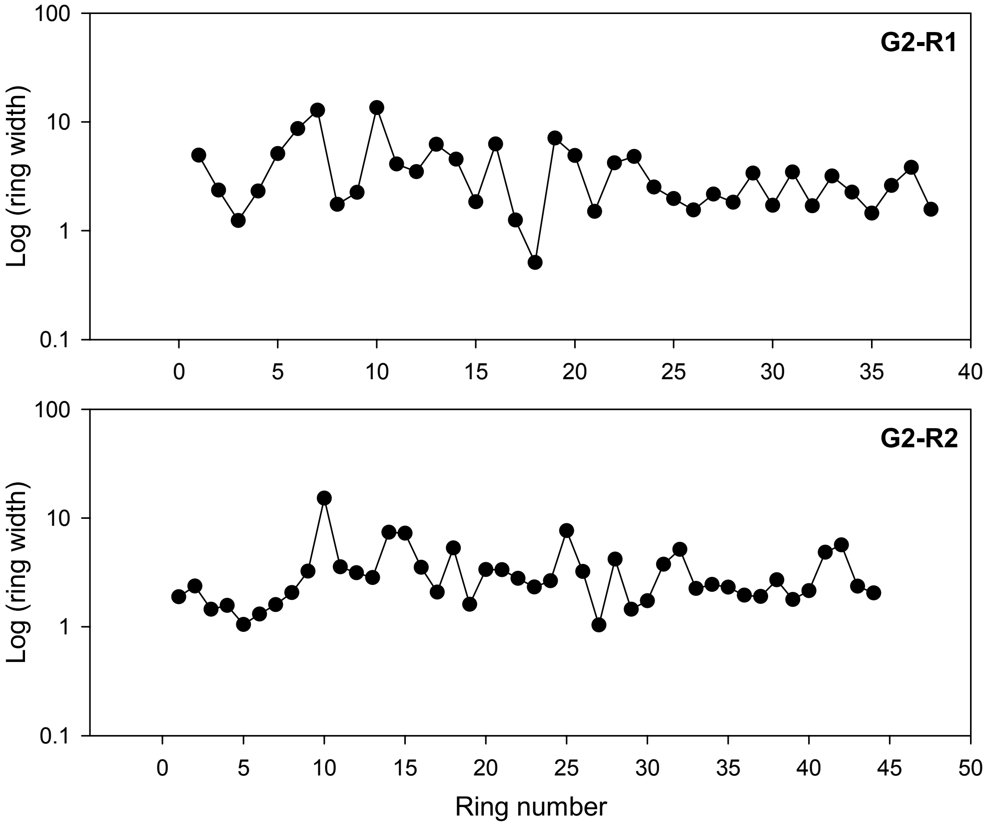

B2-R1
B2-R2
Log (ring width)
100
10
1
0.1
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28


O1-R1
O1-R2
Log (ring width)
100
10
1
0.1
0
5
10
15
20
25
30
35
40
45
50
Ring number


O2-R1
Log (ring width)
100
10
1
0.1
0
5
10
15
20
25
30
35
40
O2-R2
Log (ring width)
100
10
1
0.1
0
2
4
6
8
10
12
14
16
18
20
22


B3-R1
Log (ring width)
100
10
1
0.1
0
5
10
15
20
25
30
35
B3-R2
Log (ring width)
100
10
1
0.1
0
5
10
15
20
25
30
35
40
Ring number


G1-R1
Log (ring width)
100
10
1
0.1
0
5
10
15
20
25
30
35
G1-R2
Log (ring width)
100
10
1
0.1
0
5
10
15
20
25
30
35
40


G2-R1
Log (ring width)
100
10
1
0.1
0
5
10
15
20
25
30
35
40
G2-R2
Log (ring width)
100
10
1
0.1
0
5
10
15
20
25
30
35
40
45
50
Ring number

Appendix 9

Nonparametric Correlations

Spearman's rho		**MAF**	**PAF**	**TAR**	**MAR**	**O1**	**O2**	**B3**	**O3**	**B1**	**B2**	**G1**	**G2**
MAF	Correlation Coef.	1.000	.940(**)	.407(**)	.186	-.355(*)	-.003	-.151	-.333	.054	.249	.148	.229
	Sig. (2-tailed)	.	.000	.004	.205	.015	.987	.353	.121	.798	.221	.349	.125
	N	48	48	48	48	46	36	40	23	25	26	42	46
PAF	Correlation Coef.		1.000	.379(**)	.164	-.328(*)	-.026	-.106	-.403	-.023	.373	.156	.136
	Sig. (2-tailed)		.	.008	.264	.026	.880	.514	.056	.913	.061	.323	.367
	N		48	48	48	46	36	40	23	25	26	42	46
TAR	Correlation Coef.			1.000	.860(**)	-.212	.189	-.047	.222	.432(*)	.032	-.058	.040
	Sig. (2-tailed)			.	.000	.154	.269	.772	.308	.027	.875	.715	.792
	N			49	49	47	36	40	23	26	27	42	47
MAR	Correlation Coef.				1.000	-.150	.122	-.026	.367	.478(*)	-.021	-.084	.042
	Sig. (2-tailed)				.	.316	.477	.873	.085	.013	.916	.599	.779
	N				49	47	36	40	23	26	27	42	47
O1	Correlation Coef.					1.000	-.279	-.061	-.170	.132	-.090	-.072	-.185
	Sig. (2-tailed)					.	.100	.709	.438	.522	.654	.652	.214
	N					47	36	40	23	26	27	42	47
O2	Correlation Coef.						1.000	.085	-.152	-.154	-.165	.114	.042
	Sig. (2-tailed)						.	.622	.605	.585	.542	.510	.809
	N						36	36	14	15	16	36	36
B3	Correlation Coef.							1.000	-.245	-.009	-.078	.061	-.104
	Sig. (2-tailed)							.	.328	.972	.743	.707	.525
	N							40	18	19	20	40	40
O3	Correlation Coef.								1.000	.068	-.325	-.319	.163
	Sig. (2-tailed)								.	.757	.130	.171	.457
	N								23	23	23	20	23
B1	Correlation Coef.									1.000	-.198	.349	-.169
	Sig. (2-tailed)									.	.332	.121	.410
	N									26	26	21	26
B2	Correlation Coef.										1.000	-.128	-.221
	Sig. (2-tailed)										.	.570	.233
	N										31	22	31
G1	Correlation Coef.											1.000	.009
	Sig. (2-tailed)											.	.956
	N											42	42
G2	Correlation Coef.												1.000
	Sig. (2-tailed)												.
	N												51

** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

MAF: Mean annual flow
PAF: Peak annual flow
TAR: Total annual rainfall
MAR: Mean annual rainfall