TREE RECRUITMENT AND POPULATION DEMOGRAPHICS IN THE MURRAY– DARLING BASIN

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Cover photo: Old-growth black box (*Eucalyptus largiflorens*) tree, Katarapko Floodplain (South Australia). Copyright: Susan Gehrig.

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Executive Summary

The Murray–Darling Basin Authority (MDBA) requires improved conceptualisation of viable demographics for floodplain tree species: river red gum ((*Eucalyptus camaldulensis),* black box (*Eucalyptus largiflorens*) and coolabah (*Eucalyptus coolabah*). River red gum, black box and coolabah have expected environmental outcomes (EEOs) detailed in the Basin-wide Environmental Watering Strategy (BWS) as well as objectives in Long-Term Watering Plans (LTWPs). For example, targets to measure progress towards the overall environmental objectives for water-dependent ecosystems in Schedule 7 state:

There are improvements in the following:

- a) condition, diversity, extent and contiguousness of native water-dependent vegetation
- b) recruitment and populations of native, water-dependent species including vegetation

Maintaining the extent, improving the condition (which links to population demographics) and promoting recruitment for woody floodplain trees are often annual and multi-year environmental watering priorities. Therefore, articulating what a viable population demographic should look like, and determining what the measure of success would be, will inform more detailed quantification of BWS EEOs (e.g. SMART targets) as well as inform the approach to assess tree recruitment and population demographics as part of the Basin Plan Evaluation.

This project examined forest/woodland succession and regeneration patterns, common methods to determine population structure and growth stages for MDB floodplain eucalypts (e.g. germinant, emerging and establishing seedlings, sapling, pole, mature to old growth) and factors limiting their survivorship, to develop reference representations of viable population demographics. Reference distributions characterising the potential number of individuals per age class were developed for three species river red gum, black box and coolabah, for three vegetation structural (canopy cover) classes: closed forest, open forest, woodland. These conceptual reference distributions were deliberately simplified to provide approximate numbers of individuals, representative of each age class and species, that could fit into the twodimensional (2-D) space of one hectare (1000 m^2); relevant to the structural canopy cover class (e.g. closed forest, open forest or woodland) and/or estimates of seed availability.

At a basin-wide scale, the general pattern of an inverse J-shaped curve is expected to hold true for MDB floodplain eucalypts and vegetation structure types, with a greater frequency of small age classes (i.e. juvenile growth stages) and decreasing number of large age classes (i.e. early mature to old growth stages). However, while the number of individuals in the mature age classes is expected to be greater in closed forest vegetation types, fewer individuals in the juvenile age classes are expected because there is less remaining available space (outside of the space occupied by adult trees). Conversely, woodland vegetation types may have comparatively fewer individuals in mature ages, but potential for a greater number of juvenile age classes due to more available space. Given that some growth stages are potentially more vulnerable than other stages, a range of scenarios that may result in deviations from classical age distribution patterns (e.g. limited seedling emergence, overabundance of certain age classes and so on) were explored to determine the applicability of developing reference age distributions for evaluation and reporting purposes.

Introduction

Report aims and structure

This project seeks to further examine the conceptual understanding of the aspects that define viable populations of dominant Murray-Darling Basin (MDB) floodplain eucalypts: river red gum (*Eucalyptus camaldulensis*), black box (*Eucalyptus largiflorens*) and coolabah (*Eucalyptus coolabah*). This project briefly considered forest/woodland succession and regeneration patterns, common methods for determining population structure, and the growth stages of MDB floodplain eucalypts to develop an approach to determine what reference age distributions of population structure may approximate. The developed age class distributions were then used to explore a range of commonly encountered deviations from reference patterns.

Forest/woodland succession/regeneration

Floodplain forests and woodlands, situated between uplands and rivers, are dominated by longlived woody species that typically develop at a slow rate (decades to centuries). A forest or woodland stand comprises a collection of trees, each distinguished by its size and spatial distribution. In the MDB, eucalypt forests are broadly categorised based on tree density and canopy cover: closed forests have ≥70% canopy cover, while open forests have <70% but >30% canopy cover. Eucalypt woodlands, on the other hand, are characterised by widely spaced trees with >6, but ≤30% canopy cover (Brooks 2021).

While mortality and continuous turnover of individuals is an integral feature of forest/woodland population dynamics where populations are limited by space (Turchin 2001), if a forest/woodland stand is to remain viable, the mortality of older trees must not exceed the growth of young trees. Tree regeneration in forest and woodland ecosystems involves a series of interconnected processes. These processes include seed production, canopy storage of seed, dispersal, germination, emergence of seedlings, establishment, growth into saplings, and ultimately the recruitment of small trees that meet specific maturity criteria, such as being >2 m tall and having a diameter exceeding 10 cm (DBH >10 cm) (Kaber et al. 2021). Tree recruitment, defined as the entry of trees into a population that surpasses a designated management threshold indicating maturity, within a specified timeframe, is crucial for sustaining local tree populations. In floodplain environments like the MDB, tree species have long generation times, often surviving for centuries. Therefore, it may take some time before an existing population is substituted (Auge et al. 2023).

In floodplain forests and woodlands, vacant spaces are primarily generated by disturbances such as flooding (Smith et al. 1997). Consequently, significant recruitment events are closely tied to flood regimes because flooding provides optimal conditions for widespread seed dispersal and subsequent germination (Pettit and Froend, 2001, Pettit et al. 2001). Riparian forests, situated along permanent watercourses, often experience regular opportunities for recruitment, with inter-flood intervals spanning months to years. In contrast, ephemeral floodplain woodlands encounter highly sporadic recruitment events, with intervals spanning years to decades. Single recruitment events following floods may be highly variable and patchy in space highlighting the importance of landscape scale heterogeneity. Therefore, opportunities for continuous, yet smaller-scale recruitment events (e.g. following high rainfall) are also important (Watson et al. 1997; Weigand et al., 2004) for long-term population viability,

especially for arid zone species (Watson et al.) or species less capable of storing seeds or replenishing their reproductive potential over extended dry periods (Schweiger et al., 2020).

Population structure

The viability of forest and woodland ecosystems often correlates with the distribution of age classes within their populations (Condit et al., 1998). Structural diversity is believed to enhance habitat provision, resilience to disturbances, and resistance to drought (Pretzsch and Hilmers, 2024). Structural diversity is measured through allometric growth parameters such as tree height, diameter, canopy dimensions, basal area, and vertical canopy stratification. DeLiocourt (1898), mathematically described the expected pattern of tree diameter distribution in forests, resulting in an 'inverse J-shaped curve' when plotted as a frequency histogram (Figure 1) to understand forest population structure. This curve typically shows a steep decline in the number of trees per diameter class, as tree diameter increases, reflecting the natural aging and mortality of trees within the ecosystem. For example, Ngugi et al. (2022) investigated the demographic structure of floodplain tree species in the Murray-Darling Basin, including river red gum, black box, coolabah, and river cooba (*Acacia stenophylla*) in Queensland, Australia. They observed that these species exhibited an inverse J-shaped curve in their diameter distributions, although a marked scarcity of trees in the smaller diameter classes (<10 cm) was noted. Westphal et al. (2006) suggest some species may exhibit irregular-shaped tree diameter (age) distributions that deviate from the classic inverse J-shaped pattern. Therefore further understanding of tree diameter distributions for MDB floodplain eucalypts is needed, as conceptually explored in this report.

Figure 1: Example of the Inverse J-shape curve pattern of forest population age structure

Uncertainty aging floodplain trees

Monitoring forest/woodland population structure can provide valuable insights into the dynamics of forest regeneration, resilience to environmental stressors, and the overall ecological health of forested landscapes. Measurements of stem diameter at breast height (DBH) and tree height are widely used to estimate forest/woodland attributes, such as total basal area, tree volume, biomass, tree size distributions (Zhang et al 2023). Measuring tree diameter using diameter tape and/or callipers is relatively straightforward, although regular

measurements over large areas can be time-consuming and labour intensive. Furthermore, there have also been instances where seemingly juvenile black box trees (<2 m tall and DBH <10 cm) believed to be only a few years old, were found to be over 50 years old (George 2004), indicating that the relationship between size and age is not always straightforward for MDB floodplain eucalypts.

Dendrochronology, the study of tree rings, provides a method for aging trees (Argent 1995, George 2004, Argent et al. 2004). In regions with predictable climates, one growth ring typically forms per year, but in areas like MDB floodplains with variable flooding frequencies, growth rings may form irregularly, or multiple rings may form within a single year due to sporadic flooding events. Distinguishing growth rings can be challenging due to varying ring widths and indistinct boundaries caused by disturbances such as frost, fire, or insect infestations (Argent 1995). George (2004) conducted dendrochronological studies on river red gums and black box trees at Banrock Station, finding a correlation between DBH and age for some species but noted variability among others. In contrast, research on coolabah trees suggested that DBH alone does not reliably indicate age, as shown by radiocarbon dating predicting a specimen with a 21 cm DBH to be 300 years old (Gillen 2017).

Scaling dendrochronological studies to broader regions and species within the MDB is recommended but challenging due to logistical constraints, such as obtaining necessary permits for vegetation clearance and sampling difficulties posed by large, old trees with dense wood or internal rot (George 2004, Wood et al. 2010). Radiocarbon dating offers a more accurate alternative in some cases; for instance, it revealed that dendrochronology underestimated the lifespan of *Eucalyptus regnans* trees in Tasmania (Wood et al. 2010). However, radiocarbon dating can be costly. Emerging techniques like DNA-based aging tools show promise for requiring minimal tissue and being less invasive, though their applicability is still evolving (Ngugi et al. 2024).

MDB floodplain eucalypts growth stages

While a complete understanding of regeneration sub-processes and viability of MDB floodplain trees is disadvantaged by uncertainties regarding precise ageing, the categorisation of trees into developmental life stages (i.e. age-stages determined by size parameters such as tree diameter and height) is still regarded as a useful approach for understanding forest/woodland population structure and the subsequent ecological ramifications for stand production rates, wildlife habitat, aesthetics and carbon storage (Florence 2004). For instance, carbon storage and habitat quality are often maximised in forest/woodland areas characterised by fewer, very large trees, but a mixed mosaic of areas at the vegetation type scale that include the successive stages of seedlings and saplings progressively maturing are also required to ensure replacement of dying trees (Peeters and Butler 2014).

Figure 2 proposes the key developmental growth stages for MDB floodplain eucalypts: flowering/seed production; germination, emerging, establishing, maturing and old growth through the juvenile and adult growth phases.

Tree recruitment and population demographics in the MDB

Figure 2: Generalised growth stages of Murray–Darling Basin floodplain eucalypts. Fruit/seed crops and seed production within mature growth stages (blue) every year (or two years) is often prolific (i.e. millions of viable seeds per mature individual) although highly variable. Seeds are retained in an aerial seed crop, with some seed fall (a) via gravity/wind occurring continuously, and/or mass seed fall occurring episodically following flood recession, where seeds may be transported downstream (hydrochory). Within days, high germination rates (b) may occur, especially where seeds are deposited on exposed soils in open spaces. Significant mortality is expected in the first weeks to months of seedling emergence (c) as above and below ground biomass increases and competition for available space and resources increases. As seedlings and saplings establish (d), resilience improves, although thinning rates may still be high as size (biomass/height) increases. As trees reach maturity (e) (i.e. become reproductive adults), tree height and tree crown will continue to expand, canopy branching will become more complex and seed production will *increase, although growth rates will be slower compared to juvenile growth stages. As trees transition to the old growth phase (i.e. very large trees with spreading canopies), growth rates and seed production will diminish.*

Seed production

Flowering

The broadscale dispersal of eucalypts, such as river red gum, black box, and coolabah, hinges significantly on their seed production, which is intricately linked to flowering patterns influenced by environmental conditions. River red gums typically flower from late spring to midsummer, specifically from December to February, often following periods of flooding (Dexter 1967; Boland et al. 1981; Roberts and Marston 2011). Flowering in river red gums does not occur annually but rather prolifically every two years (Cunningham et al. 1992; Jensen et al. 2008). Similarly, black box trees flower primarily between August and January, with variability noted in South Australia where flowering may occur from May to October (Boland et al. 1980; Roberts and Marston 2000). Coolabah trees mainly flower from December to February (Blakely 1994; Brooker and Kleinig 2004), aligning their summer flowering with increased chances of widespread rainfall and flooding. However, both coolabah and black box species exhibit variability in flowering times among individuals and across different years or regions. Despite

the appearance of abundant flowering or a promising initial bud crop, only a modest proportion of these flowers or buds typically result in a good seed crop for most eucalypt species.

Seed crops

River red gums produce woody, hemispherical to ovoid fruits that contain yellow-brown, nondormant seeds, typically around only a few millimetres in size. Black box, on the other hand, bear cup-shaped to barrel-shaped fruits that encase brown ovoid seeds measuring approximately 4 mm long and 3 mm wide. Unlike some other eucalypt species, floodplain eucalypts generally do not maintain a significant soil seed bank (Greet 2016, Greet et al. 2012b), instead they retain their seeds as an aerial seed crop in their canopies for extended periods, sometimes two years or more, awaiting suitable conditions for dispersal (Dexter 1967). According to Gunn (2001), river red gums yield an average of about 6000 viable seeds per 10 grams, while black box produces approximately 5000 viable seeds per 10 grams. Coolabah generally produces around 4000 seeds per 10 grams on average, with considerable variation depending on region (Boland et al., 1980). In optimal seeding years, a large mature river red gum tree can yield between 5 to 10 kilograms of seed (Harwood, 1990), hence one mature river red gum may produce a crop of up to 6 million viable seeds suggesting considerable fecundity.

Seed fall/dispersal

Eucalypt seeds are small and can be dispersed by gravity and wind (Turnbull and Doran 1987, Roberts and Marston 2011). River red gums typically begin shedding some seeds nine months after flowering, whereas black box and coolabah trees shed their seeds within a few months after flowering. However, hydrochory, or water dispersal, is a critical dispersal mechanism for floodplain eucalypts. Mass seed fall often occurs during flood recession periods, when seeds are transported downstream and deposited in favourable germination sites (Mahoney and Rood 1998, Greet 2016, Greet et al. 2012b). Seeds of river red gum, black box, and coolabah can float for up to 10 days (Casanova 2015), facilitating their distribution along floodplains. As a result, emerging seeds are commonly found in organic litter at the maximum reach of floodwaters (Roberts and Marston 2011).

Germination

The germinant stage marks the initial growth phase of a seed when it begins to sprout and develop roots, typically occurring within days to a few weeks. Eucalypt seeds, including those of river red gum, coolabah, and black box, are generally non-dormant and exhibit high germination rates under favourable conditions. Laboratory trials have shown that river red gum seeds achieve 100% germination on 1% w/v agar under alternating dark and light conditions at 20°C (source: [https://spapps.environment.sa.gov.au\)](https://spapps.environment.sa.gov.au/). Similarly, coolabah seeds demonstrate over 95% germination within one week (Gillen 2017). While specific data on black box seed germination in laboratory conditions is not available, these seeds also germinate readily (George 2004). Therefore, even if field germination rates following flooding are lower compared to ideal laboratory conditions, the high fecundity of floodplain eucalypts, with the sheer volume of seeds produced, suggests that hundreds of thousands to millions of seeds have the potential to germinate per hectare if space is available and conditions are suitable. For instance, greater germination rates are likely to occur on exposed soils, following flood recession in open spaces, devoid of vegetation (Greet et al. 2022).

Emerging

The S1 seedling stage refers to newly emerging eucalypt seedlings (i.e. in the first weeks to months) which are <30 cm high, and not yet mature. Abundant emerging seedlings are more often observed in open spaces/gaps (i.e. not under tree canopies) (Ngugi et al. 2024). After germination, emerging seedlings will have greatly accelerated growth rates compared to mature and old growth stages. In the first growth season, S1 seedlings prioritise root development to access groundwater and/or for anchorage. Significant thinning is expected as above and below ground biomass increases and competition for available space and resources increases (Canham and Murphy 2017, Florence 2004). For example, while hundreds of thousands to millions of seeds may initially germinate per hectare, there is only physically enough space for tens of thousands of S1 seedlings with canopy dimensions of ~30 cm diameter to occupy one hectare (assuming full spatial coverage). Despite flooding providing optimum opportunities for widespread recruitment, mortality rates for S1 seedlings remain high in the early weeks and months (see below), posing a significant bottleneck and limitation in tree population dynamics (Jones et al. 1994, Canham and Murphy 2016).

Establishing

S2 seedling and sapling

The S2 seedling stage refers to establishing seedlings (possibly months to years old) which are >30 cm high but < 2 m high, and not yet mature (i.e. DBH <10 cm). The sapling stage refers to a juvenile tree which is >2 m high and not yet mature (DBH <10 cm). Typically, sapling crowns are developing, but have not reached full expansion and maturity, where lower branches are retained compared to the pole stage. Establishing seedlings and saplings continue to grow rapidly compared to mature growth stages. Although plants continue to compete for space and resources (Canham and Murphy 2017) survivorship of establishing S2 seedlings and saplings generally improves (compared to the S1 seedling emergence phase) as plants reach a critical size and develop greater resilience to drought and/or re-flooding, higher temperatures, browsing pressure and so on (Peeters and Butler 2014). Thinning rates vary widely between species (Florence 2004) but observations of hundreds to thousands of S2 seedlings and saplings per hectare are likely (Ngugi et al. 2024).

Maturing

Pole

The pole stage refers to a young, mature tree (>2 m high and >10 cm DBH), where the trees are reproductive (i.e. flowering and fruiting) but the crown/canopy has not reach full expansion and maturity, although lower branches begin to shed (compared to sapling stage). Tree trunks are often single-stemmed and very straight. If during the sapling stage sufficient self-thinning (natural thinning) does not occur (e.g. vigorous growth in high quality sites) then areas of forest or woodland may become stagnant and locked into the 'pole' stage (Florence 2004). This results in stands dominated by high densities of slender trees with poor spreading canopies and reduced seed production (Figure 2) versus stands with a few large trees, interspersed with a mosaic of mixed-aged trees of varying sizes (MacNally et al. 2011).

Early mature to mature

The early mature stage refers to reproductive trees with DBH ≥10 cm that have transitioned from the pole stage, where canopies have reached early maturity and expansion (i.e. ~10 m diameter for river red gum and black box, ~8 m diameter for coolabah). As individuals mature, river red

gums may be up to 30 to 40 m tall, with canopies expanding to 20+ m diameter. In contrast, late mature black box and coolabah individuals may be up to 20 m tall, with canopy dimensions up to 15+ m diameter [\(https://plantnet.rbgsyd.nsw.gov.au/\)](https://plantnet.rbgsyd.nsw.gov.au/). Mature individuals that can attain maximum canopy expansion are more likely to develop tree hollows (OEH 2018).

In the maturing stages, growth rates are inherently more constant compared to the accelerated growth rates in juvenile stages and decelerated growth rates of old growth stages, although growth rates will vary between species and different environments (Ngugi et al. 2015). Individual trees may start to differentiate in growth habit, based on variable access to resources (e.g. water, nutrients, light and space) leading to greater forest/woodland structural heterogeneity). Stand population structure at regional to local scales, may include several overlapping diameter classes (Kadavul and Parthasarathy 2001) or there may be distinct cohorts (i.e. similar sized age classes) (Smith et al. 1997).

Old growth

The old growth stage generally refers to very large old trees that may be decades to centuries old. Strict definitions of old growth trees are often challenging because the use of allometric growth parameters like trunk diameter, height and longevity is species specific. However, old growth trees tend to exhibit other key features such as buttressing, wide-spread canopy architecture and/or extreme height, hollow cavities and extensive bark micro-environments (Lindenmayer and Laurance 2016). Large old trees strongly influence the spatial and temporal abundance of individuals of the same species, and populations of other species, fulfilling important ecological roles not filled, or only partially filled, by the other growth stages. Trees in the old growth stage are vulnerable to drought, pest/pathogen attacks, land management (e.g. logging), landscape fragmentation and climate change. For the purposes of this report, old growth river red gums are individuals with DBH >120 cm, while for black box and coolabah, old growth trees are individuals with DBH >100 cm.

Factors limiting growth and survivorship

Seed production

Numerous factors may limit regeneration, growth and survivorship. For instance, insect and pathogen attacks, as well as moisture stress, can significantly impact the final yield of viable seeds (Cremer 1971; Loneragan 1979; Cremer et al. 1978; Boland and Martensz 1981). In general, trees in better condition generally produce more seeds (Jensen et al., 2008; Moore et al., 2016; Moxham et al., 2018), but trees in poorer condition may retain seeds for longer periods (George, 2004). Trees that dominate their environment tend to produce heavier seed crops compared to sub-dominant or suppressed trees (Jacobs, 1955). Hence seed release may range widely from approximately 1 to 2.3 million seeds per hectare (Loneragan, 1979) up to 49 million seeds per hectare (Burrows and Burrows, 1992). Regular flooding plays a crucial role in maintaining tree condition and reproductive output and flooding provides the conditions for synchronised seed fall and opportunities for widespread germination. However, if hydrological conditions such as flow frequency, timing, and duration do not meet the needs of floodplain forests and woodlands, opportunities for larger-scale, episodic seed dispersal may be severely restricted.

Germination

Germination rates may vary due to factors such as water availability, space, light, temperature fluctuations, seed predation, and pathogen risks, as well as the density of the overstorey and

conditions of the seedbed (Stoneman 1994). However, for floodplain eucalypts, flooding plays a crucial role by creating favourable conditions for germination. Flood events not only expose bare soil surfaces but also provide high soil moisture levels, which are conducive to seed germination (Dexter 1967, Dexter 1978, George 2004). In floodplain environments, eucalypt seeds tend to germinate more readily and have higher survival rates following disturbances like flooding. This is because flooding likely removes competition from understorey plants, improves seed-to-soil contact, and reduces the abundance of seed predators such as ants (Forestry Tasmania, 2010).

Emerging

Emerging seedlings are vulnerable to frost and desiccation (Roberts and Marston 2011, Frei et al. 2018). Sediment structure and poor groundwater quality, such as high salinity may limit root development (Gillen 2017, MacNally et al. 2011). Floodplain eucalypt seedlings are particularly vulnerable to saline conditions in their first growing season, although tolerance increases with age and is species specific (i.e. coolabah and black box are more tolerant than river red gums). S1 seedlings are also susceptible to being submerged if re-flooded in the first growing season, although tolerance will similarly increase with age and is species dependent (i.e. river red gums are more tolerant than black box and coolabah) (Dexter 1978, Gehrig 2010). S1 seedlings are also vulnerable to erosion and/or deposition because of fluvial processes (Stavi et al. 2015). Allelopathic effects from leaf litter or specific soil conditions can inhibit the emergence and growth of S1 seedlings, particularly where drainage is poor or soils are shallow and clay-rich (del Moral and Muller 1970). The presence of competing vegetation at the time of emergence can increase mortality rates (Ladd and Facelli 2007, Frei et al. 2018), although some vegetation may provide partial shelter, moderating climatic conditions and aiding establishment (Jones et al. 1994). S1 seedling survival is influenced by factors such as water availability, temperature, seedbed conditions, overstorey density, litter accumulation, soil properties, microclimate, seed predation (e.g., by ants), and soil pathogens (Jones et al. 1994). Herbivores also pose a significant threat to emerging eucalypt seedlings, as browsing damage can severely limit their transition to the next growth stage (S2 seedling). Some browsers selectively feed on certain species, making them more vulnerable, particularly smaller seedlings (Ladd and Facelli 2007, Moxham and Kenny 2024). High rates of natural thinning are expected as tree size increases, canopies expand, and competition for space increases (Canham and Murphy 2017).

Establishing

Establishing seedlings are likely to be more tolerant of re-flooding and submergence (compared to S1 seedlings) due to increasing size (e.g. height, stem diameter, above and below-ground biomass). However, if water availability is limited during the first few years, growth rates may slow, increasing vulnerability to inter- and intra-specific competition and/or browsing pressure. Recovery of establishing S2 seedlings from browsing is dependent on local site conditions (Kupferschmid et al. 2019) and ability to outgrow the reach of primary browsers (Ngugi et al. 2021).

Maturing

Reproductive output in early maturing trees is typically expected to be less compared to later mature trees, as crowns expand. Mature trees continue to be vulnerable to climate (Canham and Murphy 2016, 2017) and water bioavailability (Wallace et al. 2020). If resources become insufficient to meet the needs of all individuals, mortality and/or thinning may increase beyond expected natural causes (i.e. baseline mortality), where only the individuals with superior access to resources will ultimately survive (Marks and Canham 2015). Stand structure may

include several over-lapping age classes (Kadavul and Parthasarathy 2001) or there may be evidence of distinct age cohorts (i.e. similar-sized age classes) (Smith et al. 1997). Ideally a mosaic of forest succession (early maturing through to late maturing) stages are found across landscape and regional scales to ensure biological legacies are retained, because the ecological attributes of an early maturing stage will be profoundly influenced by the biological legacy carried over from the pre-disturbance stand. For example, the presence of dead trees, shrubs and other plants, living animals, seeds, spores, fungi, egg and soil communities that remain after flooding, will shape recovery patterns (Franklin et al. 2000; Lindenmayer et al. 2019).

Overall MDB eucalypts are highly fecund, and seed production is expected to be extremely high. However, the emerging and establishing growth stages are highly vulnerable and susceptible to considerable loss (i.e. thousands to tens of thousands of individuals per hectare) but rates of loss are expected to decrease (i.e. survivorship increase) as trees mature and then increase again slightly during the old growth stage as trees start to deteriorate (Figure 3).

Figure 3: predicted loss of individuals for key growth stages of MDB floodplain eucalypts from natural causes

Historical legacies

Prior to the implementation of the Basin Plan, MacNally et al. (2011) highlighted multiple stressors affecting the condition and viability of floodplain forests and woodlands across the MDB. These included a significant increase in the average inter-flood period, doubling in some areas like Barmah-Millewa and the Gunbower-Koondrook-Perricoota Forests, where historic 5 year intervals had increased to 11 years due to regulation, with projections of further increases under climate change scenarios beyond 2030. Additionally, declining groundwater levels in floodplain regions contributed to rising salinity levels in the lower Murray River. Historically, the MDB has lost a substantial number of trees, due to land use practices, although floodplain

forests were relatively spared severe clearance due to centuries of active management for timber extraction. Introduced stressors such as browsing by domestic livestock (e.g., sheep, cattle) and invasive species (e.g., rabbits, goats) have been detrimental to woody seedlings and saplings over centuries. In some areas browsing pressure from native animals like kangaroos may have also increased, due to overabundant populations and/or their confinement to diminishing remnants of native vegetation (MacNally et al., 2011). These stressors collectively pose challenges that may limit the success of various life stages of dominant floodplain tree species over the past few centuries.

Age class distributions

Approach

Reference distributions characterising the potential number of individuals per age class based on available seed/space, were developed for three species: river red gum, black box and coolabah, for three vegetation structural (canopy cover) classes: closed forest, open forest, woodland, across multiple age stages (see Figure 2). The conceptual reference distributions were deliberately simplified using the approach that there are only so many individuals, representative of each age class and species, that could fit into the two-dimensional (2-D) space of one hectare (1000 m²); relevant to the structural canopy cover class (e.g. closed forest, open forest or woodland).

For each species, a growth stage was assigned to a representative stem diameter (cm) class range along with an expected canopy diameter (m) range indicative of that stem diameter class (Appendix 1 to 3). Although the precise age of trees may vary considerably between the three species, black box and coolabah trees are assumed to be more similar in their growth patterns compared to river red gum. Black box and coolabah are typically smaller and are expected to have a reduced range of stem diameter age classes, with the old growth stage assumed to be when tree diameters exceed 100 cm DBH. On the other hand, river red gums are assumed to have a greater stem diameter age class range, with old growth stage assumed to be when tree diameters exceed 120 cm DBH.

The canopy diameter estimates (per stem diameter class) were then used to calculate the projected canopy area (m²) of an individual tree; assuming a circular shaped canopy (i.e. A= πr^2 , where A = area, r = radius). For the mature growth stages, the projected canopy areas were then used to calculate the maximum number of river red gum, black box or coolabah individuals that could fit within the specified vegetation structural canopy cover class (assuming there is no vertical stratification (i.e. single layered), individuals are the same size and representative of the same stem/age classand species assemblages were mono-specific (i.e. no co-dominance). For example, the maximum number of entire circles that represent mature river red gum individuals that fit into one hectare (100 x 100 m) of closed forest with >70% canopy cover (Figure 4; Appendix 1 to 3) versus the number of individuals (per stem class) that fit within a hectare of open forest with canopy cover >30 but <70%) along with the number of individuals (per stem class) that fit into a hectare of woodland with canopy cover (>6% but <30%). (Figure 4; Appendix 1 to 3). To determine the number of juvenile individuals that may be present per hectare, it was assumed that juvenile age stages would only fit into the remaining open space (i.e. the canopygaps - outside of the space occupied by mature trees) for each vegetation structural (cover) scenario. For example, the closed forest scenario, the number of juvenile river red gum

individuals (per stem diameter class) that would fit into the remaining space (<30%) was calculated (Figure 4; Appendix 1 to 3). The analysis assumes opportunities for germination and growth occur through the different age classes. The calculated number of individuals, per hectare for each stem diameter class, were then plotted to provide reference age class distributions for river red gum, black box and coolabah for the following vegetation structural (cover) classes:

- o closed forest (>70% cover)
- o open forest (30-50% cover) and (50-70% cover)
- o woodland (<30% cover)

Figure 4: Schematic illustrating how many mature individual trees of same age class ((blue circles) may fit into one hectare if the vegetation structural type was: >70% canopy cover (closed forest), 50-70% and 30-50% canopy cover (open forest) or <30% canopy cover (woodland). The number of juvenile age classes per hectare, for each vegetation structural type, were calculated as the number that fit within the remaining available space (yellow brown).

Reference distributions

Figures 5 to 7 highlights that the shape of the tree diameter distributions should approximate an inverse J-shaped curve pattern, exhibiting much greater numbers of small juvenile growth stages (S1 seedling, S2 seedling) and a steadily decreasing number of establishing (sapling) to maturing growth stages (pole to old growth). Note a logarithmic scale (y-axis) was used for ease of comparison.

Predictably there are greater numbers of sapling and mature age-classes (i.e. >5 cm DBH) in the river red gum closed forest (>70% canopy cover) scenario compared to the open forest (50-70% cover, followed by open forest (30-50% cover) and woodland (<30% cover) scenarios. But the more space that is expected to be occupied by established trees in the closed forest scenario, means there is less space for germinating and emerging phases (germinant, S1 seedling and S2 seedling) compared to open forest and woodland scenarios that have less canopy cover (e.g. hundreds S2 seedlings/hectare in closed forest compared to thousands S2 seedlings per hectare in the latter scenarios) (Figure 5).

Similarly, the shape of the age distributions for black box and coolabah diameter distributions approximates an inverse J-shaped curve pattern for all vegetation structural (cover) classes, with a greater number of juvenile growth stages compared to the adult, larger growth stages with the reverse true for the germinant, S1 and S2 seedling stages (Figure 5 and Figure 6). However, since coolabah and black box trees are not expected to be as large (and expansive) as river red gums, greater densities of mature (stem diameter classes >20 cm DBH) black box and coolabah trees per hectare are expected.

*Figure 5: Expected diameter distribution (cm) for river red gum (*Eucalyptus camaldulensis*) vegetation types: closed forest (>70% canopy cover); open forest (50-70% and 30-50% canopy cover) and woodland (<30% canopy cover) as per Brooks 2021 vegetation structure classifications; Appendix 1 to 3.*

*Figure 6: Expected diameter distribution for black box (*Eucalyptus largiflorens*)) vegetation types: vegetation types: closed forest (>70% canopy cover); open forest (50-70& and 30-50% canopy cover) and woodland (<30% canopy cover) as per Brooks 2021 vegetation structure classifications; Appendix 1 to 3.*

It is acknowledged that there are several assumptions underpinning this approach, which may under- or over-estimate the number of individuals representative of each stem class per hectare. For instance, the method assumes a circular canopy-shape, but in the field, floodplain eucalypt canopies are rarely perfectly circular. Likewise, in the field, tree canopies may overlap. Furthermore, the canopy area measurements used to represent each growth stage/stem class, were assumed, and may not be wholly representative of canopy development for each growth stage. Also, while many MDB floodplain forests and woodlands stands are often mono-specific (in terms of the overstorey), this approach did not allow for mixed woodland types, nor the presence of other under- and mid-storey species that may occupy (and compete for) the space that is largely presumed to be available for the juvenile growth stages (i.e. open gaps). The approach also assumes that there are no missed opportunities for seed dispersal/germination and that the volume of seed available at any one time, will likely provide enough seed to fully cover any available space. This approach also assumes that all the remaining space (that may not be occupied by establishing to mature stages) is available for germination, which is not possible. Especially as this approach does not account for dead trees or the presence of fallen timber, which are also valuable characteristics of forest/woodland structural complexity and habitat quality. Not to mention the numerous aforementioned factors that may limit the growth and survivorship of each growth stage (see above).

However, this approach does highlight that the magnitude of the x and y axis scales are expected to differ between species and structural canopy classes and hence the patterns of the age class distribution are expected to differ across different vegetation types (Lorimer and

Halpin 2014). Differences in reference age class distributions may also be expected if the sampling approach was stratified and delineated for other attributes such as hydrological regime, climate, and so on. Therefore, the approach seeks to highlight the value of providing a benchmark age-class distribution that may then be used as a reference to evaluate what population structures should look like and how the population structure across different MDB forests/woodland types compares.

From an ecological perspective, the classic inverse J-shaped curve in tree diameter distributions is predicated on the assumption of equal mortality rates across diameter classes (DeLiocourt 1989, Leak 1996). However, mortality rates may follow patterns characterised by more pronounced, higher mortality rates among younger (smaller) and much older (larger) trees compared to mid-sized trees (Goff and West 1975, Westphal et al. 2006; Figure 7), which as proposed earlier, is likely the expected mortality pattern for MDB floodplain eucalypts (Figure 3).

Thus, growth stage dependent mortality patterns mean some species may exhibit irregularshaped age distributions. For example, Lorimer (1980) observed irregular age distributions in mixed-species virgin beech forests of North America, with peaks in certain age classes indicating periods of favourable recruitment and growth, offset by losses in other age classes due to disturbances. Similarly, Korpel (1995) documented a bimodal curve shape in virgin beech forests in Slovakia. In northern hardwood stands in New Hampshire, USA, Gove et al. (2008) found either an inverse J-shaped curve or a rotated sigmoid distribution. Long-term studies of unmanaged sugar maple hardwoods in Michigan also revealed rotated sigmoid patterns (Lorimer and Frelich 1984). This pattern is characterized by a plateau in mid-diameter classes, suggesting very low mortality rates compared to other age classes (see Figure 5). Hytteborn et al. (1987) proposed that browsing by moose in montane virgin forests of northern Sweden resulted in static survivorship curves, preventing certain tree species from developing into a tree layer. Thus, while it is generally accepted that diameter distributions of old growth forests will typically show a descending curve, the specific shape of this curve and the factors influencing deviations from the classical inverse J-shape require further investigation (Westphal et al. 2006).

Furthermore, pronounced deviations from the expected patterns are also likely to be explained by a range of factors influencing the mortality and survival of growth stages. Conceptual

frameworks concerning floodplain forests and woodlands emphasise the critical link between inundation patterns and plant survival, but often neglect the significance of other influential factors shaping emergence dynamics (de Jager et al. 2019). These factors include competition, climate conditions, browsing pressure, pests, pathogens, salinity levels, and various anthropogenic stressors (MacNally et al., 2011). Understanding how flooding impacts plant survival and regeneration at local scales is essential for deciphering its broader implications on successional processes across landscape scales (de Jager et al., 2019).

Deviation from reference age class distributions

For MDB floodplain eucalypts it is likely that certain grow stages will be disproportionately impacted, therefore a range of common scenarios were developed (Table 1) to explore the influence that these scenarios may have on the classic inverse J-shaped curve pattern. The scenarios were compared to the expected reference age distribution for a river red gum open forest type with 50-70% canopy cover (Figures 8 to 13).

Table 1: Proposed scenarios and possible causes influencing regeneration sub-processes

When compared to the reference age distribution pattern, the detection of no germinant or S1 seedlings growth stages (Scenario 1, Figure 8) is clear, as are similar observations of very few germinant and S1 seedling growth stages relative to the reference age distribution (Scenario 2, Figure 9). While scenario 1 may suggest that no opportunities for seed fall/dispersal, such as flooding, are occurring, scenario 2 may suggest either i) limited opportunities for seed fall are occurring, ii) opportunities for seed fall are occurring, but seed production is limited (e.g. poor parent tree condition, poor pollination), iii) germination is limited (e.g. limited space, unfavourable site conditions, moisture stress, seed predation) and/or iv) S1 seedling emergence is limited due to factors such as browsing stress, competition and so on. However, there would be too many uncertainties because seed fall may be spatially scattered, clumped or in bands (VTAG 2019). In addition, germinant and S1 seedling stages may only be present for days to weeks, and therefore they could be easily missed, or under reported, in a monitoring network where plots are randomly positioned. Thus, the inclusion of the germinant and S1 seedlings growth stages in the reference age distribution curves may be less suited to Basin-wide, large scale and long-term population structure monitoring (i.e. monitoring program) and better suited

to more frequent, targeted event-based (before/after), site- specific sampling approaches at regional/local scales (i.e. research program). Seedlings in the S2 seedling growth stage may take several years to establish (depending on the species), and therefore the S2 seedling category is likely the best representation of an early age class for longer term monitoring programs.

At a basin-wide scale, repeated, poor observations of S2 seedling individuals relative to the reference age distribution (Scenario 3, Figure 10) may suggest seedling recruitment is i) highly episodic or ii) limited by a range of confounding system-wide stressors such as browsing pressure, moisture stress, soil/groundwater salinisation, competition and so on.

Repeated observations of greater than expected numbers of individuals within certain cohorts (relative to the reference age distributions) may suggest periods of favourable recruitment and growth. However, repeated observations of an overabundance of sapling, pole and early mature stages (Scenario 4, Figure 11) may warrant further investigation as there is risk that floodplain eucalypt population structures are skewed towards even-aged stands of straight 'poles', which may diminish structural complexity (Mac Nally et al. 2011).

Observations of irregular age distribution patterns, with missing or diminished mature growth age classes relative to the reference age distributions (Scenario 5, Figure 12) may highlight episodic recruitment strategies, or legacies of past catastrophic disturbances.

A contracted range of age classes compared to the expected range of age classes in the reference distributions, may suggest that population structure is skewed towards small to midsized age classes and a lack of larger, old growth stands/trees, possibly because of historical legacies or more recent mortality (Scenario 6, Figure 13).

Figure 9: Reference age class distribution for river red gum open forest vegetation type (50-70% cover) compared to Scenario 1: no seed dispersal

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Figure 10: Reference age class distribution for river red gum open forest vegetation type (50-70% cover) compared to Scenario 2: low germination and seedling emergence

Figure 11: Reference age class distribution for river red gum open forest vegetation type (50-70% cover) compared to Scenario 3: low seedling establishment

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Figure 12: Reference age class distribution for river red gum open forest vegetation type (50-70% cover) compared to Scenario 4: overabundance of certain cohorts

Figure 13: Reference age class distribution for river red gum open forest vegetation type (50-70% cover) compared to Scenario 5: missing cohorts

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Figure 14: Reference age class distribution for river red gum open forest vegetation type (50-70% cover) compared to Scenario 5: contracted range of age classes

Next steps

Further discussions and investigations regarding the applicability of developing reference age distributions are recommended as it is acknowledged that the reference age distributions developed here may not be suitable for some, if not all, species and vegetation types (VTAG 2021, Westphal et al. 2006).

Classification of vegetation types differs amongst jurisdictions, but the revised Australian National Aquatic Ecosystem (ANAE) classification for the MDB (Brooks 2021) provides a higher classification level and consistency that could be applied at the basin scale. Therefore, it is recommended that the Basin-wide monitoring program consider a consistent approach to vegetation classification/stratification (as illustrated here) to minimise the variability in tree diameter distributions observed. Stratification may be based on:

- species (e.g. including river cooba, *Acacia stenophylla*)
- other vegetation types (e.g. swamps)
- environmental gradients (flooding, climate, salinity)

An agreed strategy to representative stratification will influence the determination of the minimum number of plots to survey (i.e. power analysis), because sampling too few plots may over- or under-represent certain age classes (Westphal et al. 2006). The scenario-based analysis presented herein, highlights that the minimum and maximum time between surveys also needs to be considered, depending on the overarching objective. For instance, germination and seedling emergence growth stages (S1 seedlings) may be highly ephemeral because they

either die or progress to the next stage within months, therefore monitoring these growth stages at longer time scales (i.e. years) may be unsuitable and better suited to adaptive targeted (short term (weeks to months), site-based) research projects (e.g. after flooding and/or environmental watering events). Additionally, experimental trials may need to be established to investigate the influence of non-hydrologic factors on recruitment success, such as browsing pressure.

VTAG (2019) developed a standardised approach to monitoring populations demographics, which has been successfully adopted; however, further discussions regarding the best approach for the analysis and reporting are also encouraged to improve consistency. For instance, whether tree stem diameter distributions are reported using: absolute numbers, numbers per hectare and/or proportions? Whether stem diameters are rounded-up then grouped into diameter classes? Whether age distributions are presented as histogram approximations or a smoothing of the distribution? (Garcia 1991).

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Appendices

*Appendix 1: Predicted growth stages for river red gums (*Eucalyptus camaldulensis) *and representative stem diameter class (cm); estimated canopy diameter (m) and projected canopy areas (m2) used to calculate the number of mature individuals/Ha (pole to old growth stages) occupying the canopy extent within a closed forest (>70%); open forest (50-70% and 30*50%) and woodland (<30%) vegetation types; and the number of juvenile individuals/ha (germinant to sapling) outside of the canopy extent within a closed forest (i.e. <30%); open forest (30-50% and 50- 70%) and woodland (>70%). .*

seed crop estimates are based on minimum to maximum number of mature trees per hectare x 5 kg seed per tree x 600,000 viable river red gum seeds per kilogram

**estimated number of germinants must be less than maximum number of potential viable seeds per hectare ^age estimates are variable and uncertain. In suitable conditions, river red gum seedlings may reach maturity quite rapidly (within a few years)

**canopy/crown diameter range for all growth stages are approximate and assume canopy shape is circular.

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Appendix 2:

*Predicted growth stages for black box (*Eucalyptus largiflorens) *and representative stem diameter class (cm); estimated canopy diameter (m) and projected canopy areas (m2) used to calculate the number of mature individuals/Ha (pole to old growth stages) occupying the canopy extent within a closed forest (>70%); open forest (50- 70% and 30*50%) and woodland (<30%) vegetation types; and the number of juvenile individuals/ha (germinant to sapling) outside of the canopy extent within a closed forest (i.e. <30%); open forest (30-50% and 50-70%) and woodland (>70%). .*

seed crop estimates are based on minimum to maximum number of mature trees per hectare x 3.75 kg seed per tree x 500,000 viable black box seeds per kilogram

**estimated number of germinants must be less than maximum number of potential viable seeds per hectare ^age estimates are variable and uncertain. In suitable conditions, river red gum seedlings may reach maturity quite rapidly (within a few years)

**canopy/crown diameter range for all growth stages are approximate and assume canopy shape is circular.

Tree recruitment and population demographics in the MDB

*Appendix 3: Predicted growth stages for coolabah (*Eucalyptus coolabah) *and representative stem diameter class (cm); estimated canopy diameter (m) and projected canopy areas (m2) used to calculate the number of mature individuals/Ha (pole to old growth stages) occupying the canopy extent within a closed forest (>70%); open forest (50- 70% and 30*50%) and woodland (<30%) vegetation types; and the number of juvenile individuals/ha (germinant to sapling) outside of the canopy extent within a closed forest (i.e. <30%); open forest (30-50% and 50-70%) and woodland (>70%). .*

seed crop estimates are based on minimum and maximum number of mature trees per hectare x 3 kg seed per tree x 400,000 viable black box seeds per kilogram

**estimated number of germinants may be less if seed production is less

^age estimates are variable and uncertain. In suitable conditions, river red gum seedlings may reach maturity quite rapidly (within a few years)

**canopy/crown diameter range for all growth stages are approximate and assume canopy shape is circular.