

Mortality of developing floodplain forests subjected to a drying climate and water extraction

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Abstract

River regulation and water extraction have altered the hydrology of rivers resulting in substantial changes to forest structure and the dieback of floodplain forests globally. Forest mortality, due to water extraction, is likely to be exacerbated by climate change-induced droughts. In 1965, a plantation trial was established within a natural floodplain forest to examine the effect of planting density on timber production. We used data from this trial to investigate the effect of initial stand density on the structure and dynamics of *Eucalyptus camaldulensis* (Dehnh.) forests. Highest density stands (8000 trees ha⁻¹) were dominated by many slender trees, mostly < 10 cm in diameter, whereas the lowest density stands produced size distributions with a wider range of stem diameters and higher mean and maximum stem diameter. After 1996, the study area experienced a sharp decline in water availability due to a substantial lowering of the water table, reduced flooding frequency, a pronounced rainfall deficit and increased maximum temperatures. The drought coincided with a dramatic increase in mortality in the high-density stands, yet remained little changed in low-density treatments. Our results highlight the importance of initial stand density as a key determinant of the development of forest structure. Early thinning of high-density stands is one component of a broader management approach to mitigate impacts of human-induced drought and water extraction on developing floodplain forests.

Keywords: climate change, drought, *Eucalyptus camaldulensis*, floodplain forests, mortality, river regulation, stand density, water extraction, water-table

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Introduction

Floodplain forests are both ecologically and economically important because of their high biodiversity and productivity (Tockner & Stanford, 2002). Flooding plays a vital role in determining the structure and function of floodplain forest ecosystems (Junk *et al.*, 1989). River regulation and water extraction for irrigation have changed the hydrology of rivers globally, disrupting river-floodplain connectivity, reducing flooding frequency and depleting water tables (Ward, 1998). Whenever humans have disrupted ecological processes, such as river flow, there have been 'winners' and 'losers', e.g. species declines, species invasions and subsequent shifts in forest structure (e.g. Shafroth *et al.*, 2002). These

changes have created conditions that are often unfavorable for the growth and survival of floodplain tree species (Braatne *et al.*, 2007), and have resulted in substantial changes to forest structure and the dieback of floodplain forests globally (e.g. Palmer *et al.*, 2008). Increasing global temperatures associated with climate change are likely to increase the frequency and intensity of droughts in many of the major floodplain ecosystems of the world (IPCC, 2007), which may exacerbate existing forest decline due to water extraction (Braatne *et al.*, 2008). Widespread forest mortality has the potential to cause large and possibly uncontrollable losses in plant and soil carbon pools (IPCC, 2000; Stephens, 2005).

The extensive river red gum (*Eucalyptus camaldulensis* Dehnh.) forests of Australia's Murray-Darling Basin (the fourth longest river system in the world) provide one of the world's most dramatic examples of floodplain forest dieback (Cunningham *et al.*, 2009; Palmer

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et al., 2008). River red gums dominate watercourses and their floodplains across tropical, temperate and semi-arid regions of Australia (Chippendale, 1988), providing habitat for a diverse flora and fauna (Crook & Robertson, 1999; Leslie, 2001) and contributing substantial amounts of carbon to terrestrial and aquatic food webs (Baldwin, 1999). The biomass of these forests is comparable to forests in higher rainfall areas (ca. 1200 mm, Bren 1988), suggesting that they are dependent on additional water from flooding and the water table (Akeroyd *et al.*, 1998). River regulation has substantially reduced the frequency, duration and seasonality flooding in the Murray-Darling Basin (Maheshwari *et al.*, 1995). Between 1930 and 1991, mean annual water extraction from the Murray River increased by 73%, reducing the natural mean annual flow by 50% (Thompson, 1992). In the Barmah-Millewa Forest, Australia's largest extant river red gum forest (65 000 ha), medium-sized floods have been reduced from 92 to 57 per century (MDBFC, 2005). A recent quantitative survey of river red gum forests on the Murray River floodplain indicated that 70% of river red gum stands were considered to be in poor or declining condition (Cunningham *et al.*, 2009), supporting earlier observations of substantial forest dieback in the lower reaches of the Murray River (Margules *et al.*, 1990).

There is strong evidence that rising temperatures and declining rainfall, associated with human-induced climate change, have substantially reduced inflows into the Murray-Darling Basin since the 1950s (Cai & Cowan, 2008). The predicted warmer and drier conditions in the coming decades are likely to accelerate the decline of floodplain forests already stressed by river regulation and water extraction (IPCC, 2007). In general, a reduction in water availability along an environmental gradient leads to a decrease in forest productivity and leaf area per unit area of ground (leaf area index) over that gradient (Grier & Running, 1977; Specht & Specht, 1989). Along the Murray River there is a distinct east to west gradient in floodplain forest productivity and condition that is associated with decreasing flooding frequency, due in part to water extraction. Regional reductions in water availability due to water extraction and a warming regional climate will superimpose a temporal gradient of drying – from the past to the future – over this spatial gradient of floodplain forest productivity. For long-lived organisms such as trees, temporal changes in site productivity due to decreasing water availability led to reductions in leaf area and stand density (Specht & Specht, 1989). Historical levels of leaf area will need to be reduced due to the lowered water availability. This can be achieved by leaf loss of individual trees or by reduction of stand density, or

both. This may imply that stands that have had historically low leaf areas or stem densities due to past management practices or poor recruitment may be less susceptible to dieback and decline induced by decreasing water availability. Understanding how stand density and water availability interact to influence forest dynamics requires a long-term perspective (Reid & Ogden, 2006), but may provide important insights for developing management regimes that can buffer floodplain forests from the effects of decreasing water availability.

In this study, we use a rare, multidecade forest management experiment to evaluate how the growth and mortality of river red gum stands on a productive site in the eastern reaches of the Murray River have changed in the face of an irregular, but long-term, decline in water availability. The primary goal of this project was to understand the links between floodplain forest structure and susceptibility to a changing environment. To do this we have addressed the following questions: (1) How does early stand density influence long-term patterns of tree size and stand structure? (2) Do high early stand densities predispose river red gum forests to higher mortality? and (3) Are long-term changes in stand structure and dynamics associated with particular environmental conditions?

Materials and methods

Study area

Barmah-Millewa Forest (35°50'S, 145°00'E) is located in south-eastern Australia on the eastern reaches of the Murray River. The climate is semi-arid with predominantly winter rainfall (mean annual rainfall and pan evaporation 435 and 1530 mm, respectively (1950–2007, Bureau of Meteorology, 2007). High river flows enter the floodplain forest through an extensive network of distributory creeks. The Barmah-Millewa floodplain supports a diverse mosaic of vegetation communities, including forests, woodlands, grasslands and marshlands. Plant community distribution is driven by gradients in geomorphology and flooding frequency. River regulation, water extraction, burning, timber harvesting (historical and recent) and grazing have modified plant community distribution and composition (Mac Nally & Parkinson, 2005).

Experimental system

In 1965, a river red gum plantation trial was established at Black Swamp in the south-west of Barmah-Millewa Forest. The trial consisted of three replicate plots of five density treatments (600, 1000, 2000, 4000 and

8000 trees ha⁻¹). The plots were established such that two extra rows of trees surrounded each plot to minimize edge effects; these trees were not included in the analysis. Plots were resurveyed eight times in the subsequent 42 years (1974, 1976, 1979, 1982, 1987, 1991, 1996 and 2007). Stem diameter at breast height over bark (dbh) of all trees was measured during each survey. Tree height was measured for a subset of trees across the diameter range. There was a linear relationship between tree height and the natural logarithm of dbh (Tree height = 9.3 log(dbh) - 10.1, $R^2 = 0.90$), which was subsequently used to estimate tree height.

Analysis

We fitted Weibull distributions to dbh data for each plot and used a hierarchical Bayesian model to determine if initial planting density affected stand size distributions. We used Bayesian estimation because it provides a logically consistent and flexible framework for parameter estimation and for statistical inference (Ellison, 2004; McCarthy, 2007). Bayesian estimation using Markov chain Monte Carlo (MCMC) is advantageous for fitting hierarchical models with nonnormal data, and for performing multimodel inference (Wikle, 2003).

A Weibull distribution with shape (κ) and scale (λ) parameters can be used to describe a wide range of size distributions, and has been used to compare species-based size distributions of tropical and temperate forest stands (Baker *et al.*, 2005). If the dbh of trees in a given stand follows a Weibull distribution with shape and scale parameters κ and λ , the mean and median dbh for that stand are given by

$$\lambda\Gamma(1 + 1/k) \text{ and } \lambda\ln(2)^{1/k}, \text{ respectively,}$$

where Γ is the Gamma function and median dbh = $\lambda\ln(2)^{1/k}$. Note that for $k > 1$, $\Gamma(1 + 1/k)$ is restricted to the interval (0.88, 1) and $\ln(2)^{1/k}$ to the interval (0.69, 1).

We estimated shape and scale parameters for each plot with the following hierarchical model:

$$dbh_{itp} \sim \text{Weibull}(\kappa_{tp}, \lambda_{tp}); \kappa_{tp} = e^{\alpha_{1t} + \varepsilon_{1p}}; \lambda_{tp} = e^{\alpha_{2t} + \varepsilon_{2p}}.$$

Here, dbh_{itp} was the dbh of the i th tree in plot p with planting density t . The shape (κ) and scale (λ) parameters for each plot were modeled as log-linear functions of treatment effects α_{1t} and α_{2t} and plot-level random error terms ε_{1p} and ε_{2p} . Use of the log-link function ensures that estimated shape and scale parameters are positive. We used uninformative prior distributions for all parameters, with independent normal priors for treatment means and exchangeable normal

priors for plot level error terms:

$$\alpha_{nt} \sim N(0, 1000); \varepsilon_{np} \sim N(0, \sigma_n^2); \sigma_n^2 \sim U(0, 10), n = 1, 2.$$

We tested the effects of planting density on size distributions by comparing the posterior distributions for expected shape and scale parameters for each treatment, $\kappa_t = \exp(\alpha_{1t})$ and $\lambda_t = \exp(\alpha_{2t})$. We estimated 95% credible intervals for each parameter and corresponding expected mean and median dbh values for each planting density. We also calculated posterior probabilities that each parameter value for a given planting density exceeded the corresponding values for each higher density. For example, $\Pr(\kappa_{600} > \kappa_{1000})$.

Density-dependent mortality is a useful indicator of stand carrying capacity in growth trials. Hence, we tested for discrete temporal changes in density (due to mortality) across the range of planting densities using a change-point analysis. Changes in the slopes of density vs. year regressions were identified separately for each planting treatment. We used a continuous piecewise linear spline model with up to one change-in-slope (knot):

$$y_{py} = \alpha_p + \beta_1 y + k\beta_2(y - \theta)_+ + \varepsilon_{py}.$$

Here, y_{py} is the density of plot p at year y , $k = 0$ or 1 is the number of change-points, β_1 is the constant (if $k = 0$) or initial ($k = 1$) slope (mortality rate), and β_2 is the change in slope, if any, that occurs at year θ . The notation $(y - \theta)_+$ is shorthand for 'if $(y - \theta) < 0$ then 0, otherwise $(y - \theta)$ '. By using reversible jump MCMC sampling (Lunn *et al.*, 2006), we were able to treat the number k and timing θ of any change points as unknown parameters to be estimated as part of the model. The posterior distributions of k and θ indicated the probability that there was a distinct change in mortality rate and the likely timing of that change, respectively.

We assigned a prior probability of 0.5 to the constant-slope model [i.e. $k \sim \text{Bernoulli}(0.5)$] and equal prior probabilities ($= 0.5/28$) to each of the 28 (2005–1977) possible models with one change-point. We used an approximation to the unit information prior (George & Foster, 2000) for the prior variances of the slope parameters. Use of other priors [e.g. $k \sim \text{Bernoulli}(1/7)$] did not change model ranks. Analyses performed on \log_{10} and untransformed data generated indistinguishable results, so we present results for the untransformed data.

For all Bayesian models, we ran three MCMC chains of 100 000 iterations after a 50 000 iteration burn-in period. MCMC mixing and convergence were substantiated with Ruben–Gelman statistics and by inspection of chain histories and autocorrelation plots. We verified

model-fit adequacy by calculating posterior predictive probabilities for all models (Gelman *et al.*, 1996).

The relationship between stand density and mortality was investigated by plotting the stand growth pattern on a graph of $\log_{10}(\text{biomass})$ against $\log_{10}(\text{density})$ of surviving trees. Aboveground dry mass of river red gum from Barmah-Millewa Forest (ADM; trunk and branches >1 cm diameter) was calculated using a regression model developed by Robertson *et al.* (2001): $\log_{10}\text{ADM} = 2.31 \log_{10}(\text{dbh}) - 0.78$ ($R^2 = 0.99$).

Environmental trends

Water-table data were obtained from the Victorian Department of Sustainability and Environment (DSE) for six bores within a 1.7 ± 0.3 km, radius of the study site. The bores are located in areas with comparable hydro-geomorphology to the study site, for example, all bores were located on the same undulating plain with similar flooding frequency to the study site. Soil profiles from all bores revealed consistent patterns of alternating layers of silty clay and sand at comparable depths, similar to soil samples taken from the study site. Barmah-Millewa Forest rainfall data were obtained from an interpolated climate dataset maintained by the Queensland Department of Natural Resources and Mines (Jeffrey *et al.*, 2001). Murray River daily flow data were supplied by the Murray-Darling Basin Commission from Tocumwal ($35^{\circ}48'S$, $145^{\circ}33'E$, gauging station no. 409202A).

Results

Individual tree size

Over the 42 years of the trial, mean dbh and (expected) mean tree height increased with decreasing planting density (Fig. 1, Table 1). Trees grown at lower densities grew larger and taller than trees grown at higher densities. The estimated mean dbh of trees grown at 600 trees ha^{-1} was 25.3 cm (95% CI 22.2–28.8 cm), compared with an estimated mean dbh of 9.3 cm (95% CI 7.9–10.8 cm) for trees grown at 8000 trees ha^{-1} . Posterior probabilities that mean dbhs differed were >0.95 in all cases. The mean height of trees grown at the 600 trees ha^{-1} treatment was 22.9 ± 0.3 m, whereas, the mean tree height of trees grown at the 8000 trees ha^{-1} treatment was 18.7 ± 0.3 m.

Stand size structure

Stand dbh distributions differed among planting densities (Fig. 2). The highest density treatment (8000 trees ha^{-1}) produced a positively skewed distribution (skew-

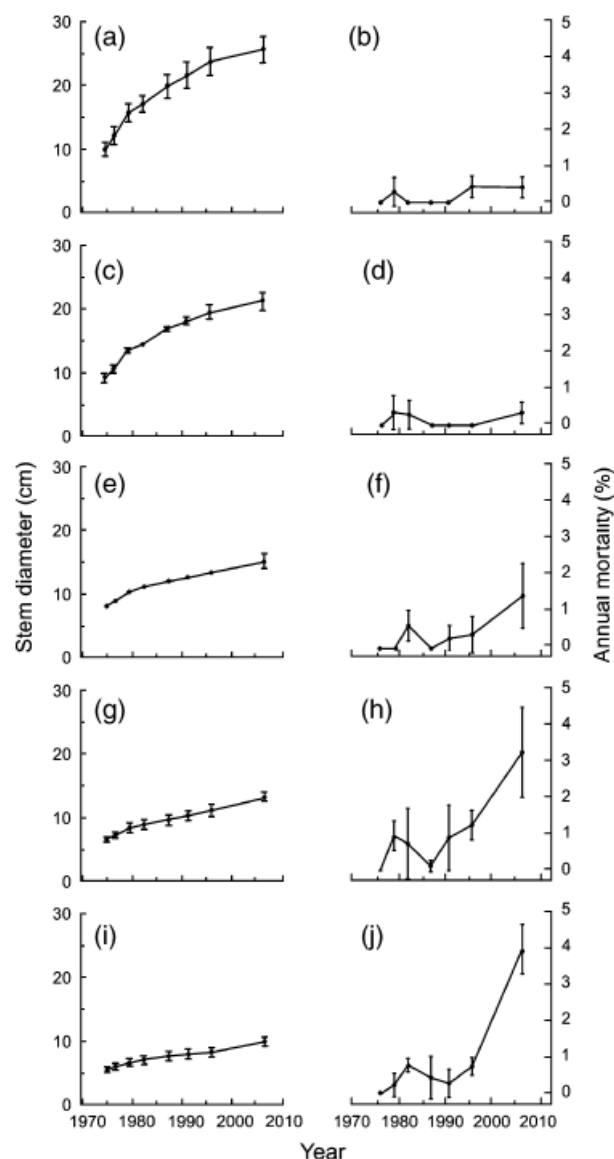


Fig. 1 Stem diameter growth (left column) and stand mortality (right column) from 1974–2007 at planting densities of 600 (a, b), 1000 (c, d), 2000 (e, f), 4000 (g, h) and 8000 trees ha^{-1} (i, j). Mean annual mortality = $1 - (N_{\text{end}}/N_{\text{start}})^{(1/\text{end-start})}$, where N_{end} is the number of trees alive at the end of the survey period and N_{start} is the number of trees alive at the start of the period. end-start = survey interval in years. Error bars represent standard errors of the mean.

ness = +1.9); whereas the size distribution of the lowest density treatment was approximately unimodal (skewness = -0.1, Fig. 2). High-density stands were dominated by many slender trees, mostly in the <10 cm dbh classes (Figs. 2 and 3). Low-density stands produced dbh distributions with a wider range of tree sizes (Fig. 2) and higher maximum dbh (dbh_{max}) values than the high-density stands (Table 1). The mean κ

Table 1 Effects of planting density on observed and modeled mean dbh values

Planting density	Observed mean dbh (cm)	Modeled mean dbh (cm)*	Modeled mean κ *	Expected mean tree height (m)	dbh_{max}
600	25.1 (1.5)	25.3 (22.2–28.8)	3.2 (2.6–3.9)	22.9 (0.3)	42.2
1000	20.7 (1.2)	20.5 (17.9–23.5)	3.4 (2.7–4.2)	22.0 (0.2)	36.0
2000	14.9 (0.9)	14.8 (2.83–16.9)	2.6 (2.1–3.2)	20.6 (0.3)	30.3
4000	12.5 (0.6)	12.6 (10.9–14.4)	2.7 (2.2–3.2)	20.0 (0.2)	27.5
8000	9.2 (0.7)	9.3 (7.9–10.8)	2.2 (1.8–2.7)	18.7 (0.3)	30.7

Modeled mean dbh values were derived from modeled Weibull distributions. Parentheses following observed and expected means are standard errors of the mean. Parentheses following modeled means contain 95% credible intervals.

*Posterior probabilities that means were different were >0.95 in all cases.

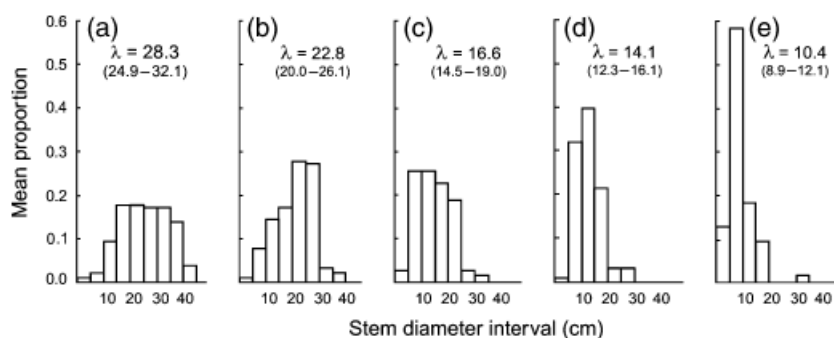


Fig. 2 Differences in stand size structure in 2007 at planting densities of (a) 600, (b) 1000, (c) 2000, (d) 4000 and (e) 8000 trees ha^{-1} . Proportions are means of three treatment plots. Estimates of mean Weibull scale (λ) are included with 95% credible intervals in parentheses.

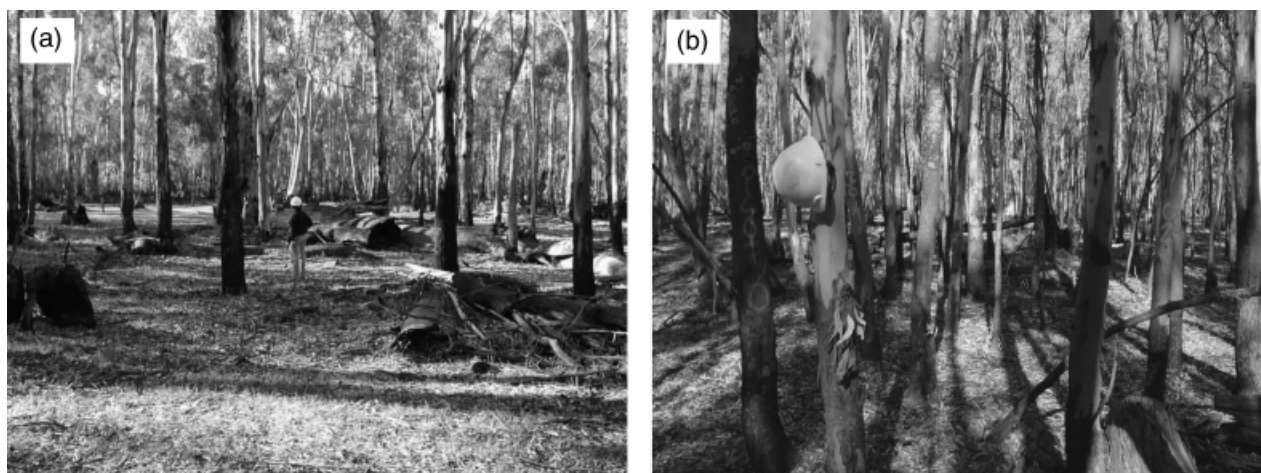


Fig. 3 Examples of (a) low- and (b) high-density treatments, planted at 600 and 8000 trees ha^{-1} respectively; photos taken in July 2007. High-density stands were dominated by many slender trees, mostly <10 cm in diameter, whereas low-density planting produced stands with a higher mean and maximum stem diameter and a wider range of stem diameters.

parameters for fitted Weibull distributions were higher for the 600 and 1000 trees ha^{-1} treatments than for the 2000 and 4000 trees ha^{-1} treatments, which in turn, were higher than the 8000 trees ha^{-1} treatment (Table 1). Posterior probabilities that mean κ s differed were

>0.88 in all cases. The mean λ parameters for the fitted Weibull distributions increased with decreasing planting density. The expected mean λ , after 42 years was 28.3 (95% CI 24.9–32.1) for the 600 trees ha^{-1} treatment but only 10.4 (95% CI 8.9–12.1) for the 8000 trees ha^{-1}

treatment (Fig. 2). Posterior probabilities that mean λ s differed were >0.95 in all cases.

Mortality

Between 1976 and 1996, mean annual mortality was $<1.2\%$ in each treatment (Fig. 1). Between 1996 and 2007, annual mortality increased substantially in the 4000 ($3.2 \pm 0.9\%$) and 8000 trees ha^{-1} ($4.0 \pm 0.5\%$) treatments (Fig. 1h and j). Over the same period, annual mortality was $0.4 \pm 0.2\%$ for the 600 and 1000 trees ha^{-1} treatments and slightly higher in the 2000 trees ha^{-1} treatment ($1.4 \pm 0.7\%$). Smaller trees (<10 cm dbh) were more prone to die than larger trees (>10 cm dbh). The two smallest size classes accounted for 93% of the observed mortality (<5 cm dbh = 51%, 5–10 cm = 42%).

The change-point model provided evidence of elevated mortality in the 4000 and 8000 trees ha^{-1} treatments (Table 2) after 1996. The model predicted a three-seven-fold increase in mortality in the 4000 and 8000 trees ha^{-1} treatments during the most recent decade, but showed no evidence of a change in mortality among the lower density stands. In contrast, the change-point model found no evidence of significant changes in mortality rates at any stand density in any of the measurement periods before 1996. Despite having higher mortality, high-density treatments had higher 'final' stand densities (consisting predominantly of slender trees) than lower planting density treatments (Fig. 5a).

Planting density affected the relationship between tree biomass, stand density and mortality (Fig. 4). Growth trajectories of the 4000 and 8000 trees ha^{-1} stands began at the lower right, approached an upper limit, and then shifted abruptly to the left (lower density, higher biomass). The apparent self-thinning threshold for these stands has a slope of ca. -1.5 , consistent with theoretical predictions and empirical observations in other plant monocultures (Yoda *et al.*, 1963; Harper, 1977). Among the 600–1000 trees ha^{-1}

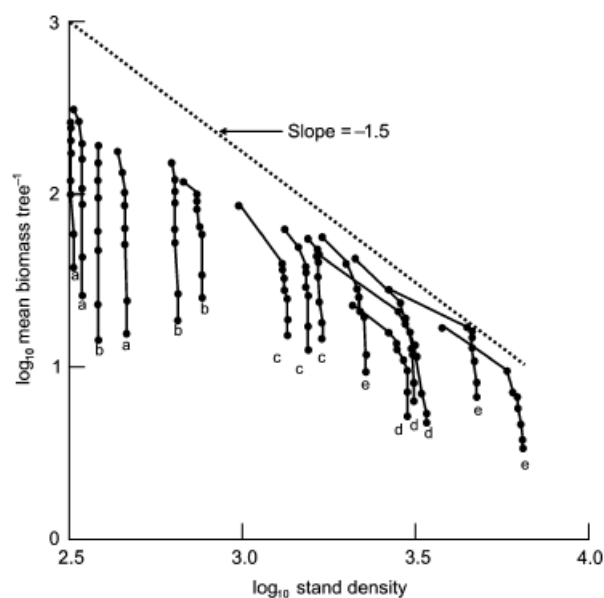


Fig. 4 Relationship between mean tree biomass and stand density from 1974 to 2007 at planting densities of (a) 600, (b) 1000, (c) 2000, (d) 4000 and (e) 8000 trees ha^{-1} . Each trace represents the response of a single stand. Filled circles represent the sequence of measurement years (1974, 1976, 1979, 1982, 1987, 1991, 1996 and 2007), starting with 1974 at the bottom and finishing with 2007 at the top. The apparent upper limit of the biomass – density relationship (..), with slope of -1.5 , is included.

treatments, growth trajectories increased in mean biomass per tree without lowering density (Fig. 4).

Environmental trends

Between 1987 and 2007, the depth to the water table dropped by 2.7 ± 0.6 m at six bores within a 1.7 ± 0.3 km, radius of the study site (Fig. 5b). The water-table began falling in the mid-1990s. No water-table data are available for the period before 1987. Two extremely dry years occurred during the study (1982 and 1994), followed by an extended drought (2001–2007, Fig. 5c). Between 1996 and 2007, mean annual rainfall at Barmah-Millewa Forest was 20% below the long-term average (1950–2007, Fig. 5c). The six year total rainfall averaged over the Murray-Darling Basin from November 2001 to October 2007 was the equal driest six year period on record (BoM, 2007). Between 2001 and 2007, average maximum daily temperatures for the Murray-Darling Basin (and Australia) were 1.3° above the long-term average (1961–1990, BoM, 2007). During the same period mean annual flow of the Murray River at Tocumwal was 46% below the long-term average (1908–2007, Fig. 5d). The 12-month flow for 2007 was the lowest on record, 84% below the long-term average.

Table 2 Discrete temporal changes in mortality across the range of planting densities 1975–2006

Planting density	Slope pre-1996	Slope post-1996
600	-0.09 (1.22)	-0.11 (1.45)
1000	-0.20 (1.25)	-0.22 (1.50)
2000	-3.78 (3.15)	-4.78 (4.39)
4000	-19.4 (4.25)	-60.8 (10.40)
8000	-19.3 (4.21)	-133.4 (9.72)

Slopes represent the number of trees died $\text{ha}^{-1} \text{yr}^{-1}$. Standard deviations are presented in parentheses.

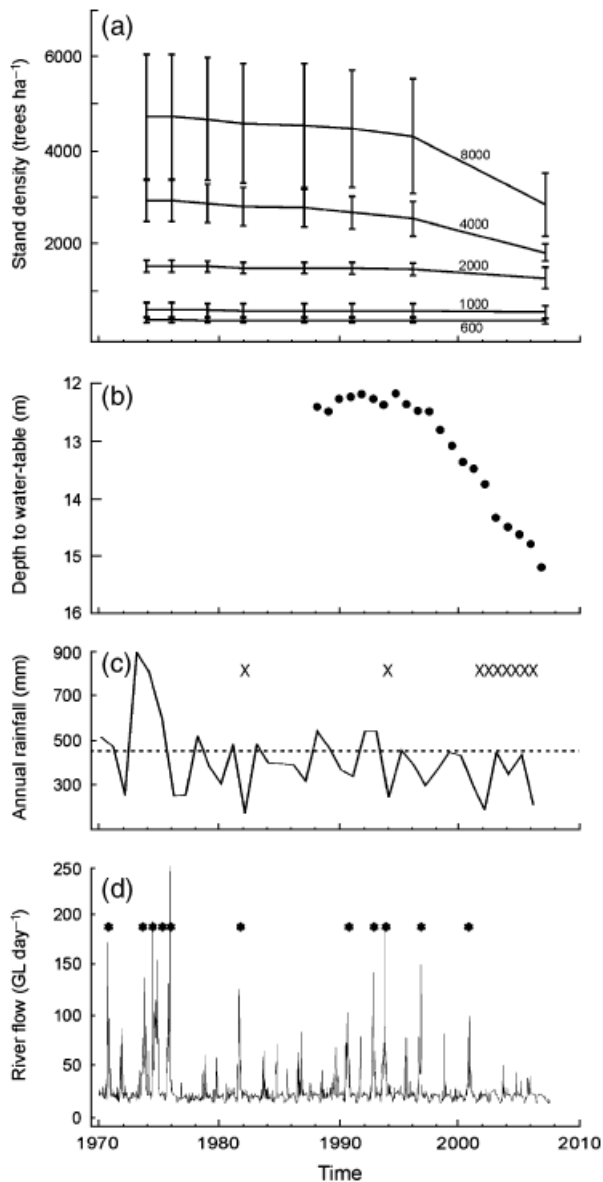


Fig. 5 Trends in stand density and water availability 1970–2007 including (a) stand density, across the range on planting densities, (b) water-table depth from a representative bore, (c) mean annual rainfall, (---) represents 1950–2007 mean annual rainfall, (X) indicates extreme droughts, (d) daily Murray River flow at Tocumwal gauging station. Flows greater than 80 000 ML day⁻¹, marked by an asterisk (*), cause extensive flooding at the study site. The study site and surrounding bores are located on an undulating, low relief, alluvial fan, suggesting that the water table decline measured at the bores is representative of the study site.

Discussion

In the past century, humans have directly modified many of the world's great river systems through damming and water extraction, primarily for irrigated agri-

culture (Busch & Smith, 1995). In recent decades, humans have also had an indirect influence on river flows through altered regional climate regimes, which have resulted in higher temperatures and dramatic rainfall deficits. As a consequence, the floodplain forests that fringe many large river systems have had dramatically reduced water availability from flooding, which is essential for germination, growth and recruitment of new trees (Stone & Bacon, 1994) and critical for avoiding physiological stress and increased risk of mortality (Lichtenthaler, 1996). In water-limited biomes of the northern hemisphere, decreasing water availability has led to both linear and exponential reductions in net primary productivity (Knapp & Smith, 2001; Loik *et al.*, 2004). For river systems, such as the Murray, that pass through semi-arid landscapes, reduced flooding frequency, lowering water tables (Busch & Smith, 1995) and drying conditions have led to widespread floodplain forest decline (Stromberg *et al.*, 2007; Palmer *et al.*, 2008). In part, this reflects a lowering of the productivity of these forests as the primary limiting resource, water, becomes increasingly scarce (Boisvenue & Running, 2006). The associated dieback and mortality at the stand level occur as the trees adjust to the change in water availability.

Given these patterns, we hypothesized that stands of trees of varying density that were planted on a mesic floodplain of the Murray River over 40 years ago would exhibit responses to a long-term decline in water availability as a function of their initial density. Our change-point analysis supported this hypothesis by demonstrating that mortality was highest in the high-density stands and lowest in the low-density stands. However, the change-point analysis showed that increases in mortality rates were limited to the densest stands and the most recent measurement interval (1996–2007). Low-density stands showed no evidence of a change in mortality levels, nor did any of the stands before 1996. Mortality due to thinning is expected as a stand grows. Previous studies (e.g. Yoda *et al.*, 1963; Weller, 1987) have suggested that tree biomass increases for a given stand density up to a limit at which point either growth of individual trees stops or mortality occurs, lowering stand density. The line defining the upper limit of these size-density relationships typically has a slope of ca. -1.5 . We found that the threshold of the size-density relationship for the high-density stands was similar to the theoretical limit (Fig. 4). However, the elevated mortality observed in the high-density stands was almost certainly triggered by the substantial decline in water availability over the past decade (Fig. 5). This suggests that the decline in water availability has shifted the self-thinning threshold down (i.e. reducing the y intercept, Fig. 4), such that stands of a given

density may now undergo compensatory mortality at lower mean tree biomass (i.e. earlier stages of stand development).

Several environmental factors, including drought, reduced flooding and lowered water tables have been implicated in the dieback of high-density river red gum stands. The combination of detailed climatic data and bore data describing water-table depth permitted us to examine these putative causes of mortality. We found that over the past 40 years, the Barmah-Millewa Forest has been subjected to several periods of reduced rainfall, decreased flooding, or both (1976–1980, 1982, 1994, 2001–2007; Fig. 5c and d). The increased mortality in the high-density stands was restricted to the most recent of those periods, suggesting that drought alone is not sufficient to induce stand-wide dieback in river red gum forests. This is not surprising given that extreme droughts (and highly variable river flows) are characteristic of the regional climate (Puckridge *et al.*, 1998). The 2001–2007 drought was exceptional because of concurrent record high temperatures (Cai & Cowan, 2008), consistent with global warming that began in the 1950s (Nicholls, 2004). The higher temperatures meant that environmental conditions (and physiological stress) were more severe during the 2001–2007 drought than the previous extremely dry years (1982 and 1994).

The bore data suggest that a reduction in water-table depth may play a fundamental role in driving the observed pattern of mortality during the recent drought. The effective root zone of river red gums at Barmah Forest extends to a depth of 9 m (Davies, 1953), suggesting that the lowering of the water table, from 12 to >15 m depth, is likely to have reduced access to water. Although the bore data do not extend as far back in time as the climatic data, they do show a decade-long period (1987–1998) of relatively constant water-table depth of ca. 12.5 m (Fig. 5b). From 1998 onwards, there was a decrease of nearly 0.25 m yr^{-1} in water-table depth, such that by 2007, the water table was >15 m deep. In the absence of longer-term records, it is not possible to determine if water-table depth dropped as dramatically during previous droughts (e.g. 1976–1980). If such a lowering of the water table had occurred during that period, the water table would have had to rise quickly after 1982 to reach the recorded 1987 depth of 12.3 m, which seems unlikely given that 1980–1987 was a period of relatively low flooding and slightly below-average rainfall (Fig. 5c and d).

In recent decades, the increasing removal of water from the Murray River for irrigated agriculture has changed the total water volume available to floodplain ecosystems (NLWRA, 2001). Between 2000 and 2002, groundwater extraction in the Murray-Darling Basin increased on average by 44% (MDBC, 2006). In the past

decade, the occurrence of a prolonged and extreme drought coincided with increasingly high groundwater extraction and a receding water table, which together should have had a significant impact on water availability above- and below-ground and led to reductions in the productivity of the floodplain ecosystem (Boisvenue & Running, 2006). In our study, this led to high levels of mortality in the densest stands. Similar patterns have been documented in mid-western North America where water table declines of $\geq 1 \text{ m}$ resulted in 88% mortality of riparian *Populus* over a 3-year period (Scott *et al.*, 1999). Elevated tree mortality in floodplain forests, as observed at Barmah-Millewa, is likely to have profound consequences for a wide range of important ecosystems services including carbon storage (Fig. 5; Boisvenue & Running, 2006), nutrient cycling between floodplains and rivers (Baldwin, 1999), maintaining water quality (Hansen *et al.*, 2007) and providing habitat for fauna (Mac Nally *et al.*, 2002).

Elevated mortality in our high-density stands, as a result of decreasing water availability, is most likely due to differences in growth rate and biomass allocation among the different density plantings. At high densities, growth of individual trees is limited by crown size at the time of crown closure. High tissue-respiration demands relative to total individual photosynthetic area mean less photosynthate is available for allocation to growth (Lundqvist, 1994). While this was most obvious aboveground in the reduced diameter growth of our trees (Fig. 1), belowground allocation to tap root growth (Bernardo *et al.*, 1998) is also greatly reduced in high-density stands of river red gum, making the trees more susceptible to drought-induced mortality.

In addition to influencing the resilience of stands to lowered water availability, initial stand density has significant impacts on stand structure and many values associated with floodplain forests. In our study, low-density stands exhibited greater variation in tree size and had more large trees than high-density stands (Fig. 2). Large trees are important for the conservation of hollow-dwelling animals because they produce more hollows and a greater range of hollow sizes than small trees (Vesk *et al.*, 2008). In high-density stands ($>1000 \text{ trees ha}^{-1}$) growth of lateral branches is inhibited, limiting branch and crown size (Vesk & Mac Nally, 2006), which are important precursors of tree hollows and fallen timber (Vesk *et al.*, 2008). Similar trends have been obtained from a range of species in many biomes (Brendenkamp, 1987; Guan *et al.*, 2008). The higher growth rate of individual trees in low-density stands also has implications for carbon sequestration in these ecosystems.

Historically, floodplain trees have regenerated in dense, localized stands of $>8000 \text{ trees ha}^{-1}$ after flood-

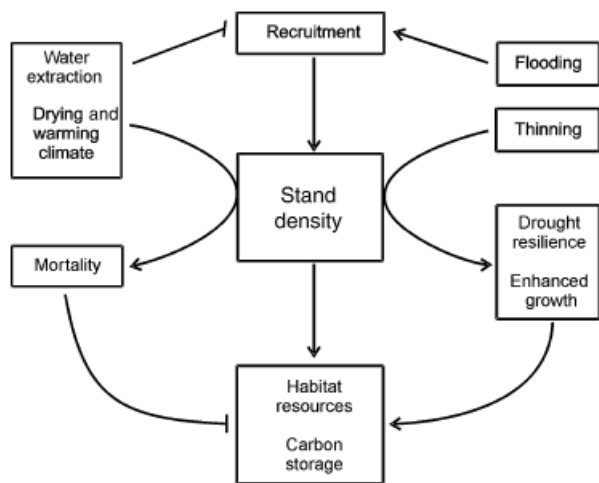


Fig. 6 Conceptual model of floodplain forest recruitment and mortality. Lines with arrows represent positive relationships, lines ending in a \perp symbol represent negative relationships.

ing (Dexter, 1978). In the face of increasing water extraction and decreasing water availability, floods are likely to occur less frequently and conditions are likely to support fewer trees. Our results suggest that careful management of stand density either at the time of stand initiation, through planting, or later in stand development, through thinning, may be important for ameliorating the impacts of declining water availability on forest dynamics (Fig. 6). Owing to the substantial uncertainties associated with future climate change and water management policies, it would be unwise to expect that one stand density will be appropriate for all species and all environments. While our results suggest that maintaining stands with densities <1000 trees ha^{-1} is likely to maximize growth and survival under declining water availability, it would be worth ensuring that a wide range of stand structures occurs across the broader landscape.

In the next 50 years, climate change and increasing human water extraction, from above and belowground, will place unprecedented pressures on rivers and their floodplain forests (IPCC, 2007; Cai & Cowan, 2008). Our study provides a valuable perspective on stand density and mortality in forests vulnerable to changes in water availability. Management of floodplain forests must be underpinned by water policies that ensure ecologically sustainable distribution of water among all floodplain users. Therefore, early management of stand density through planting, or later through thinning, is one component of a broader management approach to mitigate the impacts of a drying climate and increasing water extraction on developing floodplain forests.

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