Forest structure, habitat and carbon benefits from thinning floodplain forests: Managing early stand density makes a difference

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1. Introduction

Flooding is an important source of natural disturbance in floodplain forests, increasing natural thinning through mortality and maintaining a landscape mosaic of different forest types and structures (Palik et al., 1999; Kramer et al., 2008). Humans have modified many of the world’s floodplain forests through direct and indirect effects on flooding regimes and water availability (Busch and Smith, 1995). River regulation and water extraction have directly reduced flows and modified natural flooding regimes (Dynesius and Nilsson, 1994). Humans have indirectly influenced river flows by altering regional climates. In many places, this has resulted in higher temperatures, lower rainfall and more frequent severe droughts (Rood et al., 2005; Cai and Cowan, 2008). Consequently, floodplain forests fringing many large river systems around the world have experienced dramatically reduced water availability from decreased flooding. This has created conditions that are unfavourable for growth and survival of floodplain tree species (Mahoney and Rood, 1998) and has resulted in increased adult mortality and substantial changes in forest structure (Palmer et al., 2008; Cunningham et al., 2009).
The river red gum (Eucalyptus camaldulensis Dehnh.) forests of Australia’s Murray River provide habitat for a wide range of terrestrial and aquatic fauna (Emison et al., 1987; Menkhorst, 1995; Crook and Robertson, 1999; Mac Nally et al., 2001). In addition, they contribute substantial amounts of carbon to terrestrial and aquatic food webs (Baldwin, 1999). River red gum has the most extensive natural distribution of any eucalypt species, occurring in temperate to tropical and mesic to arid regions of Australia (Chippendale, 1988), so changes in forest species, occurring in temperate to tropical and mesic to arid regions of Australia (Chippendale, 1988), so changes in forest dynamics are likely to have serious regional consequences for the terrestrial carbon pool and for biodiversity conservation. These forests have been managed for timber production since the 1870s (Donovan, 1997). Therefore, it is likely that forest size-structures were considerably different prior to European settlement, with a higher abundance of large trees than occurs today (Mac Nally and Parkinson, 2005; Vesv et al., 2008). These large trees are likely to have contained more tree hollows and a wider range of hollow sizes than stands with smaller trees (Gibbons and Lindenmayer, 2002). Several studies have shown links between faunal diversity and abundance of large, hollow-bearing trees (Newton, 1994; Lada et al., 2007). Forest management needs to anticipate future requirements, such as provision of hollow-bearing trees, within individual forest stands and across the floodplain forest estate. Given that many hollow-nesting animals are highly threatened in Australian ecosystems (Bennett and Lumsden, 1994), identifying silvicultural practices that produce more large trees more quickly, are likely to benefit these species.

The productivity of river red gum and other floodplain forests around the world is highly dependent on hydrological regime, and changes to the frequency and duration of flooding have a marked effect on forest dynamics and primary production (Brinson, 1990; Robertson et al., 2001). The hydrology of the Murray River has been altered substantially by river regulation and water extraction, primarily for agriculture (Maheshwari et al., 1995; MDBC, 2005). Consequently, over the past 40–50 years, there has been a substantial reduction in the frequency (35–63%) and duration (40–84%) of flooding on these floodplains. Across south-eastern Australia, rising temperatures and pronounced rainfall deficits associated with human-induced climate change have substantially reduced inflows into the Murray River (Cai and Cowan, 2008). A recent quantitative assessment of floodplain forests of the Murray River showed that ~70% of river red gum stands were in poor or declining condition (Cunningham et al., 2009). Yet, in the absence of long-term ecological studies, our understanding of the lag effects of water extraction and a drying climate on forest structure and dynamics is limited.

Forest structure can be manipulated in two fundamental ways: (1) initial planting density, or (2) subsequent thinning (Florence, 1996). In a previous study, we showed that lower density planting produced stands with higher mortality and maximum stem diameters than higher density stands (Horner et al., 2009). Lower density stands also had reduced mortality when subjected to a steep temporal gradient of drying imposed by water extraction and a drying climate. Stand density also is manipulated routinely by thinning in many forests around the world to accelerate tree growth, minimise risk of catastrophic wildfires and restore forest-structural complexity (Tappeiner et al., 1997; Finkral and Evans, 2008; Kariuki, 2008). Thinning is relevant to management of floodplain forests because dense stands of saplings (>10 000 trees ha⁻¹) often establish after favourable flooding (Bren, 1992). For species that have rapid early growth, including the river red gum, annual (tree-level) biomass storage peaks at a relatively early age (Schöna and Coetzee, 1989). When stands are thinned before annual biomass production has peaked, there is an opportunity to accelerate growth in the retained trees, increasing crown expansion, diameter growth and the rate at which the stand collectively reaches maturity.

Understanding how thinning affects carbon storage and habitat provision in trees that live for centuries requires a long-term perspective (Reid and Ogden, 2006) which can provide important insights for developing silvicultural practices that may produce simultaneous benefits for carbon storage and biodiversity. In this study, we used a rare multi-decade, manipulative forest experiment to show how habitat quality and carbon storage of floodplain forests change in response to different thinning treatments. The aim of this study was to assess the potential for using early thinning in a floodplain forest to improve jointly carbon storage and habitat provision. To do this, we addressed the following questions: (1) How does early thinning influence long-term stand structure and habitat quality of naturally regenerating forests? (2) Does early thinning of dense, naturally regenerated river red gum stands affect the rate of carbon storage? (3) Is there an optimal thinning density that jointly enhances both habitat quality and carbon storage?

2. Methods

2.1. Study area

Barmah-Millewa Forest (35°50’S, 145°00’E), Australia’s largest extant river red gum forest (65 000 ha), is located on a lowland, depositional floodplain on the eastern reaches of the Murray River. The climate is semi-arid with predominantly winter rainfall (mean annual rainfall = 435 mm, pan evaporation = 1530 mm, 1950–2007, BoM, 2007a). High river flows enter the floodplain forest through an extensive network of distributary creeks. The Barmah-Millewa floodplain supports a diverse mosaic of vegetation communities, including forests, woodlands, grasslands and marshlands. Plant community structure is driven by gradients in geomorphology and flooding regime. River regulation, water extraction, burning, timber harvesting (historical and recent), and grazing management have substantially modified floodplain forest structure and composition (Mac Nally and Parkinson, 2005).

2.2. Experimental system

During the first half of the 20th century, widespread recruitment of dense stands of river red gum on the Barmah-Millewa floodplain prompted the (then) Victorian Forests Commission to investigate effects of thinning on timber production. In 1965, a thinning trial was established in a dense, naturally regenerated forest, then aged 26 years. The trial consisted of three replicate plots of three thinning treatments: 270, 560 and 750 trees ha⁻¹ (residual densities) as well as three replicate unthinned plots, with ~4000 trees ha⁻¹ (Table 1). Each plot was 0.08 ha. Extensive flooding in the mid-1970s caused high mortality in four plots (one plot from each treatment), and these data were removed from the analysis. Pre-thinning stem densities for all treatments were similar (Table 1). Plots were resurveyed ten times (1967, 1972, 1973, 1976, 1979, 1982, 1987, 1991, 1996 and 2007). Stem diameter at breast height over bark (dbh) of all trees was measured during each survey.

To determine the effect of thinning on habitat quality, we conducted a ground survey in 2008 to estimate the abundance of habitat (hollow-bearing) trees (Harper et al., 2004). We assessed 390 trees for presence of hollows across all treatments. Each tree was observed from four perpendicular aspects using 10 × 42 binoculars. All observations were made by the same two observers, who cross-checked all potential hollows. A hollow was defined as a cavity with a minimum estimated diameter and depth of ~5 cm. Average search time was 22.5 ± 1.7 min plot⁻¹.
In 2007, an independent tree-hollow survey was conducted to determine whether there was a relationship between river red gum tree size (dbh) and habitat quality (hollow abundance). We also wanted to assess whether this relationship was evident at the larger, forest scale. The survey was conducted in the forest adjacent the thinning trial, over an area of ~20 000 ha. In this survey, 323 trees were assessed at 13 sites, stratified across a representative range of stand types based on relative stand age and predominant crown size.

To assess the effect of thinning on standing carbon stocks and rates of carbon storage, we estimated the total amount of aboveground biomass (AGB) using an existing relationship established from trees in the Barmah-Millewa Forest (Robertson et al., 2001). A linear, allometric relationship: \( \log_{10}(AGB) = 2.3075 \log_{10}(dbh) \) (Harmon et al., 1990).

<table>
<thead>
<tr>
<th>Thinning treatment (trees ha(^{-1}))</th>
<th>Pre-thinned density 1965 (trees ha(^{-1}))</th>
<th>Post-thinned density 1965 (trees ha(^{-1}))</th>
<th>Observed median dbh (cm)</th>
<th>Estimated median dbh (cm)(^a)</th>
<th>Estimated ( \lambda ) (^a)</th>
<th>Estimated ( \alpha )</th>
<th>Estimated ( \lambda )</th>
<th>dbh(_{90})</th>
</tr>
</thead>
<tbody>
<tr>
<td>270</td>
<td>4006 (470)</td>
<td>276 (7)</td>
<td>48.4</td>
<td>48.5 (3.4)</td>
<td>6.8 (1.0)</td>
<td>51.2 (3.5)</td>
<td>62.7</td>
<td></td>
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<tr>
<td>560</td>
<td>4046 (748)</td>
<td>560 (120)</td>
<td>41.7</td>
<td>41.8 (3.9)</td>
<td>5.1 (0.7)</td>
<td>45.2 (4.1)</td>
<td>61.1</td>
<td></td>
</tr>
<tr>
<td>750</td>
<td>4005 (856)</td>
<td>754 (99)</td>
<td>36.4</td>
<td>35.6 (2.5)</td>
<td>4.7 (0.5)</td>
<td>38.5 (2.7)</td>
<td>52.5</td>
<td></td>
</tr>
<tr>
<td>4000 (no thinning)</td>
<td>4621 (732)</td>
<td>4621 (732)</td>
<td>22.0</td>
<td>22.3 (1.8)</td>
<td>2.3 (0.2)</td>
<td>26.4 (2.0)</td>
<td>49.0</td>
<td></td>
</tr>
</tbody>
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\(^a\) Posterior probabilities that median dbh values differed among thinning treatments were >0.88 in all conditional comparisons.

Table 1
Effects of thinning on observed and modeled median dbh values. Modeled median dbh values were obtained from modeled Weibull distributions. Excluding pre- and post-thinned columns, all results are from 2007. Parentheses contain standard deviations.

To quantify stand structural variation among thinning treatments, we fitted Weibull distributions to dbh data for each plot and used a hierarchical Bayesian model to determine if thinning affected stand size distributions. A Weibull distribution with shape \((\kappa)\) and scale \((\lambda)\) parameters can be used to describe a wide range of size distributions and has been used to compare species-specific size distributions in tropical and temperate forest stands (Baker et al., 2005). The Weibull distribution is unimodal for values of \(\kappa > 1\), positively skewed when \(\kappa \leq 3.6\), symmetric (approximately normal) when \(\kappa = 3.6\) and negatively skewed when \(\kappa > 3.6\). The scale parameter, \(\lambda\), is a measure of central tendency. If the dbh values of trees in a given stand follows a Weibull distribution with shape and scale parameters \(\kappa\) and \(\lambda\), the mean and median dbh for that stand are

\[
\lambda \left( 1 + \frac{1}{\kappa} \right) \quad \text{and} \quad \lambda \ln(2) \left( 1 - \frac{1}{\kappa} \right),
\]

where \(\Gamma\) is the Gamma function. For \(\kappa > 1\), \(\Gamma (1 + 1/\kappa)\) is restricted to the interval (0.88, 1) and \(\ln(2) \left( 1 - \frac{1}{\kappa} \right)\) to the interval (0.69, 1).

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

\[
dbh_{i,p} \sim \text{Weibull}(\kappa_{i,p}, \lambda_{i,p}); \quad \kappa_{i,p} = e^{\theta_{i,p}^{(1)} + \varepsilon_{i,p}^{(1)}}, \quad \lambda_{i,p} = e^{\theta_{i,p}^{(2)} + \varepsilon_{i,p}^{(2)}}.
\]

Here, \(dbh_{i,p}\) is the dbh of the \(i\)th tree in plot \(p\) with thinning treatment \(t\). The shape \((\kappa)\) and scale \((\lambda)\) parameters for each plot were modeled as log-linear functions of treatment effects \(\alpha_{t}\), and \(\delta_{t}\) and plot-level random error terms \(\varepsilon_{i,p}^{(1)}\) and \(\varepsilon_{i,p}^{(2)}\). Use of the log-link function ensured that estimated shape and scale parameters were positive. We used Bayesian estimation because it provides a consistent, flexible framework for parameter estimation and for statistical inference (Ellison, 2004; McCarthy, 2007). We used Markov chain Monte Carlo (MCMC) sampling to fit the hierarchical model (Wikle, 2003), with uninformative prior distributions for all model parameters, independent normal priors for treatment means, and exchangeable normal priors for plot-level error terms:

\[
\alpha_{nt} \sim N(0, 1000); \quad \varepsilon_{np} \sim N(0, \sigma_{n}^{2}); \quad \sigma_{n}^{2} \sim U(0, 10), \quad n = 1, 2.
\]

We tested for effects of thinning treatment on tree-size distributions by comparing the posterior distributions for expected shape and scale parameters for each treatment, \(\kappa = \exp(\alpha_{t})\) and \(\lambda = \exp(\delta_{t})\). We estimated 95% credible intervals for each parameter and the corresponding posterior mean and median dbh values for each thinning treatment. We also calculated posterior probabilities (PP) that each parameter value for a given thinning treatment exceeded the corresponding values for each higher density, e.g. \(Pr(\kappa_{70} > \kappa_{560})\).

For all Bayesian models, we ran three MCMC chains of 100 000 iterations after a 50 000 iteration burn-in. MCMC mixing and convergence were confirmed with Gelman-Rubin statistics and by inspection of chain histories and autocorrelation plots (Brooks and Gelman, 1998). Conservative posterior predictive probability checks (range: 0.2 < PPP < 0.8) confirmed that all models fitted the data adequately (Gelman et al., 1996). PPP values are equivalent to Chi-square goodness of fit tests, with ideal fit = 0.5.

To assess whether thinning influenced AGC storage rates, we used a continuous, piecewise, spline model to estimate the storage rate for all treatments (Beckage et al., 2007). The model allowed for the possibility of a change in the rate of AGC storage at some (unknown) point in time, i.e. countedenpend possible non-linear rates of storage over the 42 years. Note that while the model allowed only one (or zero) change in slope, in the Bayesian framework used, gradual changes in the rate of storage were accommodated by averaging over multiple models with slope changes at different times. We calculated posterior probabilities of non-linearity and their corresponding odds ratios (OR, Jeffreys, 1961). OR < 1 indicates no evidence of non-linearity, 1 < OR < 3 indicates some evidence, and OR > 3 indicates strong evidence.

The model was

\[
y_{yp} = \alpha_{t} + \beta_{t} y + k_{t} \delta_{t} (y - \theta_{t}) + \varepsilon_{p} + \varepsilon_{yp}.
\]

Here, \(y_{yp}\) is the estimated AGC stored in plot \(p\) at year \(y\), \(k_{t}\) is the number of changes in slope (i.e. changes in AGC storage rate) for treatment \(t\) (and is either 0 or 1), \(\beta_{t}\) is the constant (if \(k_{t} = 0\)) or initial slope of the carbon storage rate (if \(k_{t} = 1\)) for treatment \(t\), and \(\delta_{t}\) is the change in slope, if any, that occurs at year \(\theta_{t}\) for treatment \(t\). The notation \((y - \theta_{t})\) is shorthand for “if \(y < \theta_{t}\), then \(y - \theta_{t}\).” By using reversible-jump MCMC sampling (Lunn et al., 2006), we were able to treat the number \(k\) and timing \(\theta\) of slope changes for each thinning treatment as unknown parameters to be estimated as part of the model. The posterior distributions of \(k\) and
indicated the probability that there were changes in AGC storage rates (i.e. $\Pr(k = 1)$) and the likely timing of any such changes, 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 (0.5/42) to each of the 28 (1966–2007) possible models with one change in slope. The prior probability of a non-linear relationship was therefore 0.5. Specifying prior distributions of parameters, and the associated uncertainty, is a fundamental principle of Bayesian methods. As we had no existing information about the variances of the slope parameters, we used a conservative default prior that corresponds to the use of the Bayesian information criterion (George and Foster, 2000). Use of other priors [e.g. $k \sim \text{Bernoulli}(1/7)$] did not change rank order of models, indicating our prior choice seemed robust.

3. Results

3.1. Individual tree size

After 42 years, higher median and maximum dbh were associated with greater thinning intensity (Fig. 1a, Table 1). Stands thinned to lower densities produced larger trees than less intensively thinned stands. In 2007, the estimated median dbh of trees from the 270 trees ha$^{-1}$ treatment was 48.5 ± 3.4 cm (posterior median ± SD), compared to a median dbh of 22.3 ± 1.8 cm for trees from the unthinned (4000 trees ha$^{-1}$) treatment. Median dbh values for a given treatment exceeded the corresponding values for each higher density treatment in all comparisons (posterior probabilities > 0.91).

3.2. Stand size structure

In 2007, stand dbh distributions differed among all thinning treatments (Fig. 2). Unthinned stands were dominated by many slender trees, mostly in the <25 cm dbh classes, whereas thinned stands produced a higher proportion of large trees, resulting in negatively skewed distributions and higher maximum dbh (dbh$_\text{max}$) values (Table 1). The estimated $k$ parameters for the fitted Weibull distributions increased with increasing thinning intensity (Table 1). For the most severe thinning treatment, the estimated $k$ parameter was 6.8 ± 1.0 (posterior median ± SD), compared to 2.3 ± 0.2 for the unthinned treatment, indicating a shift from positive to negative skew with increasing thinning intensity. Estimated $k$ values for the thinned treatments ($k_{270}$, $k_{560}$ and $k_{750}$) exceeded the $k_{4000}$ value in all comparisons (posterior probabilities > 0.99). The estimated $\lambda$ parameters for the fitted Weibull distributions also increased with increasing thinning intensity (Table 1). The estimated $\lambda$ parameter was 51.2 ± 3.5 for the heaviest thinning treatment, compared to 26.4 ± 2.0 for the unthinned treatment. Estimated $\lambda$ values for a given treatment exceeded the corresponding values for each higher density treatment in all comparisons (posterior probabilities > 0.88). The $k$ and $\lambda$ results suggested that severe thinning (270 trees ha$^{-1}$) resulted in at least a two-fold increase in median stem diameter compared to the unthinned treatment (Table 1).

3.3. Mortality

Throughout the trial, unthinned stands experienced substantially higher mortality than thinned stands (Fig. 1b). From 1965 to 2007, the density of unthinned stands declined from 4621 ± 583 to 1518 ± 323 trees ha$^{-1}$ (69%), whereas the 270, 560 and
750 trees ha\(^{-1}\) treatments densities declined by 14%, 14% and 32%, respectively. Mortality was higher in the earlier stages of development than in the later stages (Fig. 1b).

3.4. Habitat (hollow-bearing) trees

Only 4% of trees in the thinning trial contained hollows; no hollows were observed in the unthinned stands (Fig. 3). The thinning treatments had similar numbers of hollow-bearing trees, ranging from \(19 \pm 6\) to \(21 \pm 8\) trees ha\(^{-1}\) (\(\bar{x} \pm\) SEM). Hollows typically were small (5–10 cm diameter) and appeared to have formed as a consequence of branch abscission or cracking of the bole bark.

In the independent survey conducted in 2007 over a much broader area, the overall mean number of hollows was \(2.3 \pm 0.2\) hollows tree\(^{-1}\). The presence of hollows was associated with tree size (Fig. 4). No hollows were observed in trees with dbh < 50 cm. Of trees that were > 50 cm dbh, 69% contained at least one hollow, with a mean of 4.0 \pm 0.4 hollows per tree.

3.5. Aboveground carbon (AGC) storage rates and standing carbon

The unthinned control (4000 trees ha\(^{-1}\)) had the lowest AGC storage rate at 1.6 t C year\(^{-1}\) (95% C.I. 1.3–1.9 t C year\(^{-1}\)), whereas the 560 trees ha\(^{-1}\) treatment had the highest rate of AGC storage 4.1 t C year\(^{-1}\) (95% C.I. 3.7–4.3 t C year\(^{-1}\), Table 2). AGC storage rate for the 560 trees ha\(^{-1}\) treatment exceeded the corresponding values for all other treatments (posterior probabilities > 0.99), whereas the AGC storage rate for the unthinned control was consistently lower than the corresponding values for all thinning treatments (posterior probabilities > 0.99). AGC storage for the 270 and 560 trees ha\(^{-1}\) treatments appeared to be linear (OR 0.4 and 1.4, respectively, Fig. 1c). However, fitted storage curves of the higher density treatments (750 and 4000 trees ha\(^{-1}\)) appeared to taper off after 1990 (Fig. 1c). The odds ratios for the high-density treatments were 73 and 2.7, respectively, indicating there were overwhelming evidence of a decline in AGC storage for the 750 trees ha\(^{-1}\) treatment and some evidence for the 4000 trees ha\(^{-1}\) treatment.
In 1965, the 4000 trees ha$^{-1}$ treatment had the highest standing AGC (100.4 ± 1.3 t C ha$^{-1}$; $\bar{x}$ ± SEM), whereas the AGC of the other treatments (post-thinning) were <50 t C ha$^{-1}$ (Fig. 1c). However, in 2007, the 560 trees ha$^{-1}$ treatment had the highest AGC at 200.2 ± 9.6 t C ha$^{-1}$, followed by the 750, 4000 and 270 trees ha$^{-1}$ treatments at 171.0 ± 1.4, 165.1 ± 31.1 and 157.7 ± 8.7 t C ha$^{-1}$, respectively.

4. Discussion

Thinning had a pronounced effect on stand development, tree growth, mortality, habitat quality and aboveground carbon (AGC) storage rate of these red gum stands on the eastern reaches of the Murray River floodplain (Figs. 1 and 4). Short-term studies have shown that reducing stand density by thinning reduces overall stand production while increasing the productivity of individual trees (Schönau and Coetzee, 1989; Kariuki, 2008). However, few studies have used long-term empirical data to investigate compromises between timber production, habitat quality and carbon storage. Large trees are important for the conservation of hollow-dwelling animals because they produce more hollows and a greater range of hollow sizes than do small trees (Vesk and Mac Nally, 2006). Large trees also have a higher capacity to provide food resources such as flowers, leaves, insects (Recher, 1996), foraging substrates and shelter (Mac Nally et al., 2001). Thinned stands produced more large trees more quickly (Recher, 1996), foraging substrates and shelter (Mac Nally et al., 2007). Given that fallen hollow-bearing trees and the proximity to fallen timber (Lada et al., 2007) were associated with a steep temporal decline in water availability associated with increasing water extraction and a warming regional climate (NLWRA, 2001; BoM, 2007b)—but only in stands planted at >1000 trees ha$^{-1}$—stands planted at lower densities experienced little or no mortality when water became limiting. Therefore, we suggested that thinning may ameliorate the impacts of declining water availability on developing floodplain forests. Our results support this notion by demonstrating that mortality was highest in the thinned (high-density) stands and lowest in the thinned (lower density) stands. Early thinning of dense (~4000 trees ha$^{-1}$), developing stands appeared to increase the amount of water available to the retained trees, reducing the risk of rapid mortality and substantial losses from the terrestrial carbon pool (Fig. 1b). Further long-term, stand-level studies are required to determine if this is true for a wider range of forest structures and environmental conditions.

We also hypothesised that AGC storage rates of stands thinned to different densities, on a mesic floodplain over 40 years ago, would relate to stand density. Our spline analysis supported this hypothesis by demonstrating that AGC storage rates were highest in the thinned stands and lowest in the unthinned stands (Table 2). Higher rates of carbon storage in our thinned stands, particularly in the 560 trees ha$^{-1}$ treatment, most likely were due to differences in tree growth and biomass allocation among different thinning treatments (Fig. 1a and c). At high stand density, individual tree growth is limited by crown size at the time of canopy closure. Higher tissue respiration demands relative to photosynthetic area mean less photosynthate is available for allocation to growth (Lundqvist, 1994). While this was most obvious in the reduced diameter growth of the trees (Fig. 1a), allocation to leaf production also is reduced greatly in high-density river red gum stands (Bernardo et al., 1998) reducing net primary production (Law et al., 2001).

Evidence of a decline in AGC storage rates in the higher density treatments (Fig. 1c, Table 2), were associated with a steep temporal gradient of drying resulting from regional reductions in water availability, which began in the 1990s (BoM, 2007b; Horner et al., 2009). The drying gradient is due to the combined effects of increasing water extraction, a warming regional climate, decadal ...

Table 2

<table>
<thead>
<tr>
<th>Thinning treatment (trees ha$^{-1}$)</th>
<th>Rank order</th>
<th>Overall modeled carbon storage rate (t C year$^{-1}$)</th>
<th>Probability of non-linear (carbon vs. time) relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>270</td>
<td>2</td>
<td>3.3 (3.0–3.5)</td>
<td>0.23 (0.4)</td>
</tr>
<tr>
<td>560</td>
<td>1</td>
<td>4.1 (3.7–4.3)</td>
<td>0.59 (1.4)</td>
</tr>
<tr>
<td>750</td>
<td>2</td>
<td>3.1 (2.8–3.4)</td>
<td>0.99 (73.1)</td>
</tr>
<tr>
<td>4000 (no thinning)</td>
<td>3</td>
<td>1.6 (1.3–1.9)</td>
<td>0.73 (2.7)</td>
</tr>
</tbody>
</table>

\[1 \equiv \text{Strong evidence of non-linearity, } 0.1 \equiv \text{Indicates some evidence, OR} \equiv \text{Indicates no evidence of non-linearity}\]
rainfall deficits and reduced flooding frequency. This reflects a lowering of the productivity of these forests as the primary limiting resource – water – becomes increasingly scarce (Boisvenue and Running, 2006). The decline in AGC storage rates is likely to continue given that, by 2030, climate change is predicted to further reduce river inflows by ~30% across the Murray River catchment (Cai and Cowan, 2008). If water availability continues to decline, judicious thinning of dense (~4000 trees ha⁻¹), developing stands may be the best option for conserving some remnants of floodplain forest habitat in a rapidly drying climate.

Some workers have advocated thinning to increase structural complexity of forests, mitigate the risk of carbon loss from catastrophic wildfires (e.g. Allen et al., 2002) and enhance wildlife habitat values (Thyssell and Carey, 2001). Quantifying future tree-hollow availability under alternative management regimes is important, given the predicted increases in stand-replacing disturbances caused by climate change (Millar et al., 2007). While our results suggest that thinning stands to densities of 560 trees ha⁻¹ is likely to optimise carbon storage rates and growth of hollow-bearing trees, it would be unwise to expect that one thinning regime will be appropriate for all forest types across the range of environmental conditions and uncertainties associated with future climate. It would be prudent to establish a wider range of thinning treatments monitored and evaluated as part of a landscape-scale experiment. Results could be used to predict carbon storage and habitat benefits, informing management where stand density should be higher or lower.

Given the important contribution that forests make to the global terrestrial carbon pool (Gough et al., 2008), an understanding of temporal trends of carbon storage in response to declining water availability and different forest management regimes is crucial (Balboa-Murias et al., 2006; Campbell et al., 2009). In our study, thinning of the forest produced concurrent benefits for both carbon storage and habitat provision. Moderately thinned stands had the highest carbon storage rate, standing carbon stocks and densities of hollow-bearing trees, whereas the “do-nothing” strategy produced the lowest carbon storage rate and no hollow-bearing trees. Therefore, reducing stand density by early thinning should be considered as one component of a broader approach to enhancing carbon storage capacity while maintaining or increasing habitat values of developing floodplain forests.

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