



# *A model analysis of climate and CO<sub>2</sub> controls on tree growth and carbon allocation in a semi-arid woodland*

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1 A model analysis of climate and CO<sub>2</sub> controls on tree growth  
2 and carbon allocation in a semi-arid woodland  
3

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13

14 **Abstract**

15 Many studies have failed to show an increase in the radial growth of trees in response to  
16 increasing atmospheric CO<sub>2</sub> concentration [CO<sub>2</sub>] despite the expected enhancement of  
17 photosynthetic rates and water-use efficiency at high [CO<sub>2</sub>]. A global light use efficiency  
18 model of photosynthesis, coupled with a generic carbon allocation and tree-growth model  
19 based on mass balance and tree geometry principals, was used to simulate annual ring-  
20 width variations for the gymnosperm *Callitris columellaris* in the semi-arid Great Western  
21 Woodlands, Western Australia, over the past 100 years. Parameter values for the tree-  
22 growth model were derived from independent observations except for sapwood specific

23 respiration rate, fine-root turnover time, fine-root specific respiration rate and the ratio of  
24 fine-root mass to foliage area ( $\zeta$ ), which were calibrated to the ring-width measurements by  
25 approximate Bayesian calibration. This procedure imposed a strong constraint on  $\zeta$ .  
26 Modelled and observed ring-widths showed quantitatively similar, positive responses to  
27 total annual photosynthetically active radiation and soil moisture, and similar negative  
28 responses to vapour pressure deficit. The model also produced enhanced radial growth in  
29 response to increasing  $[\text{CO}_2]$  during recent decades, but the data do not show this.  
30 Recalibration in moving 30-year time windows produced temporal shifts in the estimated  
31 values of  $\zeta$ , including an increase by *ca* 12% since the 1960s, and eliminated the  $[\text{CO}_2]$ -  
32 induced increase in radial growth. The potential effect of  $\text{CO}_2$  on ring-width was thus shown  
33 to be small compared to effects of climate variability even in this semi-arid climate. It could  
34 be counteracted in the model by a modest allocation shift, as has been observed in field  
35 experiments with raised  $[\text{CO}_2]$ .

36

## 37 **Keywords**

38 Tree growth modelling, Tree rings,  $\text{CO}_2$  fertilisation, Carbon allocation, Response to climate  
39 change, Water-use efficiency.

40

## 41 **Introduction**

42 Atmospheric  $\text{CO}_2$  concentration  $[\text{CO}_2]$  has direct impacts on the photosynthesis and water-  
43 use efficiency of  $\text{C}_3$  plants (Drake et al., 1997; Ainsworth and Long, 2005; Norby and Zak,  
44 2011; De Kauwe et al., 2013). However, several studies of tree radial growth in well-  
45 watered temperate and tropical regions have failed to show increases that might be  
46 attributed to increasing  $[\text{CO}_2]$  (Kienast and Luxmoore, 1988; Gedalof and Berg, 2010;

47 Girardin et al., 2011; Peñuelas et al., 2011; van der Sleen et al., 2015). Moreover, tree-  
48 growth modelling (Boucher et al., 2014; Li et al., 2014) has suggested that the expected  
49 radial growth enhancement due to the recent [CO<sub>2</sub>] increase is quite small, compared to the  
50 effects of climate variability. A stronger response to enhanced [CO<sub>2</sub>] might be expected a  
51 *priori* in water-limited regions (Field et al., 1983; Hyvönen et al., 2007), because stomatal  
52 conductance is reduced when [CO<sub>2</sub>] is higher. This is a common empirical observation,  
53 consistent with the least-cost hypothesis (Wright et al., 2003; Prentice et al., 2014), which  
54 predicts a near-constant ratio of leaf-internal to ambient [CO<sub>2</sub>] as [CO<sub>2</sub>] increases – while  
55 the rate of increase of photosynthesis with [CO<sub>2</sub>] declines. Failure to sample water-limited  
56 environments might thus conceivably explain the apparent lack of increased stem growth in  
57 response to increasing [CO<sub>2</sub>].

58

59 An alternative explanation could be that increased primary production due to increased  
60 [CO<sub>2</sub>] has not led to increased stem growth due to a shift in carbon allocation away from  
61 stems. There is some experimental evidence that changing [CO<sub>2</sub>] results in changes in  
62 carbon allocation between above-ground (leaf, stem) and below-ground (root) biomass  
63 pools. Observations of the response to high [CO<sub>2</sub>] in Free-Air Carbon dioxide Enrichment  
64 (FACE) experiments show that trees commonly increase total carbon allocation below  
65 ground, in the form of increased root production and/or exudation of labile substrates (Oak  
66 Ridge FACE: Norby et al., 2004; DUKE-FACE: DeLucia et al., 1999; Pritchard et al., 2008;  
67 Rhinelander ASPEN-FACE: King et al., 2001; EUROFACE: Calfapietra et al., 2003; Lukac  
68 et al., 2003; Bangor FACE: Smith et al., 2013). In some sites, this increase is clearly at the  
69 expense of stem growth (Battipaglia et al., 2013). However, monitoring of below-ground  
70 carbon dynamics is challenging and there are no direct, long-term observations of the  
71 response of below-ground allocation to gradually increasing [CO<sub>2</sub>] under natural conditions.

72

73 Process-based model experiments provide a way of comparing the consequences of  
74 alternative hypotheses. Here we used a global light-use efficiency model of photosynthesis  
75 coupled with a dynamic allocation and tree-growth model to simulate the radial growth of  
76 the gymnosperm *Callitris columellaris* growing in the water-limited environment of the Great  
77 Western Woodlands (GWW), Western Australia. We specifically examined whether we  
78 could detect an effect of [CO<sub>2</sub>] on ring-width, in addition to effects of climate variability.

79

80

## 81 **2 Methods**

82

### 83 **2.1 The study area**

84 The GWW, with an area of about 160,000 km<sup>2</sup>, is the largest remaining area of intact  
85 mediterranean woodland on Earth (Watson, 2008; Lee et al., 2013). The region is unique  
86 because of the abundance and diversity of trees that grow there, despite the dry climate  
87 and nutrient-poor sandy soils (Watson, 2008; Prober et al., 2012). The vegetation of the  
88 GWW is dominated by open eucalypt woodlands, with patches of heathland, mallee and  
89 grassland. The climate is characterized by winter rainfall and summer drought, although  
90 storms associated with monsoonal penetration into the continental interior can also bring  
91 occasional heavy rains in summer (Sturman and Tapper, 1996). The sampling site lies near  
92 the GWW SuperSite (GWW SuperSite, Credo, 30.1°S, 120.7°E, 400m a.s.l.;  
93 <http://www.tern-supersites.net.au/supersites/gww/>) in the northernmost and driest part of  
94 the GWW, with a mean annual rainfall *ca* 270 mm. The area around the GWW SuperSite is  
95 dominated by naturally regenerating eucalypts (*Eucalyptus salmonophloia* and *E. salubris*),

96 associated with *Acacia* and the multi-stemmed gymnosperm *Callitris columellaris*, with  
97 *Atriplex* in the understory. However, *Callitris columellaris* was the only woody species at the  
98 sampling site itself. Human impact around the site is minimal.

99

100 The coastal southwestern region of Western Australia has experienced a multidecadal  
101 drought that began in the mid-1970s (Ansell et al., 2000; Cai and Cowan, 2006; Hope et al.,  
102 2006; Cullen and Grierson, 2009; Van Ommen and Morgan, 2010), characterized by a large  
103 reduction in winter rainfall. The CRU TS v3.22 climate data (Harris et al., 2014) for the  
104 GWW show abruptly reduced winter rainfall from around 1990 but total annual precipitation  
105 has increased, by about 7 mm/decade over the century ( $p = 0.015$ ), due to enhanced  
106 summer storms. The number of rain days decreased, especially after 1960 ( $-6.2$   
107 day/decade,  $p < 0.001$ ) while the mean precipitation on rain days (precipitation intensity)  
108 increased (0.38 mm/decade,  $p < 0.001$ ). These trends are superimposed on large  
109 interannual variability, with annual rainfall ranging from ca 100 to > 400 mm. Mean annual  
110 temperature increased by  $0.16^{\circ}$ /decade ( $p < 0.001$ ) and vapour pressure deficit (VPD) also  
111 increased, while soil moisture (as indexed by  $\alpha$ , the ratio of modelled actual to potential  
112 evapotranspiration: Cramer and Prentice, 1988) showed an initially increasing trend that  
113 flattened off after 1960.

114

## 115 **2.2 Tree ring data**

116 The genus *Callitris* has provided good records of annual tree growth in a variety of climates  
117 across Australia and is known to be sensitive to changing water availability (Ash, 1983;  
118 Cullen and Grierson, 2007; Baker et al., 2008; Cullen et al., 2008; Cullen and Grierson,  
119 2009). We selected a 500 x 500 m plot near the GWW SuperSite, where *Callitris*

120 *columellaris* was the only woody species present, for sampling. Although the basic  
121 measurements required to characterize tree growth (see 2.4) were made on all the trees in  
122 the plot (146 individuals), tree-ring cores were obtained from only ten of these trees (Fig. 1).  
123 The sampling was carried out in August 2013. The selected trees were canopy trees, with a  
124 mean height of 4.2 meters, not overshadowed by other individuals, and were chosen  
125 because they appeared to be the oldest trees on the plot. The sampling plot showed no  
126 sign of disturbance. Other environmental conditions (topography, soil type, soil depth)  
127 showed no visible variation among the sampled trees. Multiple cores were obtained from  
128 each tree, taking care to sample each of the individual stems of each tree. A total of 32 tree  
129 ring cores were obtained.

130

131 Annual growth was measured on each core. The cores were cross-dated visually, based on  
132 pointing-year identification and ring-width pattern matching, and the final measuring  
133 accuracy was checked with the cross-dating software COFECHA (Holmes, 1983). The  
134 measurements of tree growth on individual stems were aggregated to produce an estimate  
135 of the total radial growth of each tree for comparison with model outputs. The “effective”  
136 single-stemmed basal diameter ( $D$ ) and “effective” single-stemmed diameter increment  
137 ( $dD/dt$ ) were obtained from observed multi-stemmed basal diameter ( $\delta_i$ ) and individual-stem  
138 diameter increments ( $d(\delta_i)/dt$ ) by:

139 
$$D = \sqrt{\sum_{i=1}^n \delta_i^2}, \text{ and } dD/dt = \frac{1}{D} \sum_{i=1}^n (\delta_i \cdot d\delta_i/dt)$$

140 The effective annual growth measured at the site is shown in Fig. 1. Note that, in contrast  
141 with traditional tree-ring studies, the ring-width series were not detrended to account for  
142 ageing because ageing effects are explicitly simulated by our model.. Furthermore, we  
143 simulate each of the ten sampled trees individually rather than creating a composite series.



144 Nevertheless, there is reasonable coherency between the records from the individual cores  
145 and individual trees ([Table 1](#)).

146

147 Tree-ring series from the Southern Hemisphere are conventionally presented with annual  
148 increments attributed to the calendar year in which tree growth was initiated (Schulman,  
149 1956). Although the longest record obtained dates from 1870 ([Fig. 1](#)), only three trees have  
150 pre-1920 records. Some early changes such as the step-like decrease and increase before  
151 1920 are likely to be artifacts because of the small number of long records. For this reason,  
152 and because the climate data are also less reliable in the early decades of the 20<sup>th</sup> century,  
153 we focus our analysis on the years since 1920.

154

### 155 **2.3 The tree-growth model**

156 We used a generic light-use efficiency model (the P model, Wang et al., 2014) to simulate  
157 gross primary production (GPP). Wang et al. (2014) demonstrated the model's ability to  
158 reproduce global geographic and seasonal patterns in GPP derived from flux  
159 measurements. Potential GPP (the GPP that would be predicted if all incident PAR were  
160 absorbed) is calculated in the model from latitude, elevation, [CO<sub>2</sub>], and monthly  
161 temperature, precipitation, and fractional cloud cover. It depends on the PAR incident on  
162 the vegetation canopy during the growing season (with temperatures above 0°C), the  
163 intrinsic quantum efficiency of photosynthesis (Collatz et al., 1998), and the effects of  
164 photorespiration and substrate limitation at subsaturating [CO<sub>2</sub>] represented as a function of  
165 the leaf-internal [CO<sub>2</sub>] and the photorespiratory compensation point. Leaf-internal [CO<sub>2</sub>] is  
166 estimated from ambient [CO<sub>2</sub>] via the least-cost hypothesis (Wright et al., 2003; Prentice et  
167 al., 2014) as a function of atmospheric aridity (expressed as  $\Delta E$ , the climatic moisture

168 deficit: difference between annual (estimated) actual evapotranspiration ( $E_a$ ) and  
169 equilibrium evapotranspiration ( $E_q$ ), air temperature and elevation. In the version used  
170 here, GPP is further multiplied by  $\alpha^{1/4}$  (Cramer and Prentice, 1988). This correction has  
171 been found empirically to account for the reduction in the light use efficiency of GPP at very  
172 low soil moisture content, observed in flux measurements from regions with an intense dry  
173 season. The P model produces a seasonal cycle of simulated potential GPP at GWW with a  
174 peak in austral summer, similar to the seasonal cycle of GPP in the predominant  
175 (*Eucalyptus*-dominated) vegetation as calculated from measurements made at the nearby  
176 Credo flux station (C. Macfarlane, S. Prober, pers. comm. 2014; data processing by T.W.  
177 Davis, pers. comm. 2014). The fractional cover of vegetation (trees, shrubs, grasses) is  
178 about 0.1, thus the simulated potential GPP of *ca*  $1.5 \text{ mol m}^{-2} \text{ day}^{-1}$  at the peak is  
179 consistent with flux-derived GPP, *ca*  $0.15 \text{ mol m}^{-2} \text{ day}^{-1}$ .

180

181 Modelled potential GPP was used as input to a species-based carbon allocation and  
182 functional geometric tree-growth model (the T model: Li et al., 2014) to simulate tree  
183 growth. In the T model, the fraction of incident PAR absorbed by the canopy (fAPAR) is  
184 estimated from the leaf area index within the canopy and used to convert potential to actual  
185 GPP using Beer's law (Jarvis and Leverenz, 1983). Annual net primary production (NPP) is  
186 then derived from annual GPP, corrected for foliage respiration, by deducting growth  
187 respiration (proportional to NPP) and the maintenance respiration of sapwood and fine  
188 roots. NPP is allocated to stem, foliage and fine-root increments, foliage turnover and fine-  
189 root turnover. Carbon is allocated to different tissues within the constraint of the basic  
190 functional or geometric relationships between different dimensions of the tree, including  
191 asymptotic height-diameter trajectories (Thomas, 1996; Ishii et al., 2000; Falster and  
192 Westoby, 2005).

193

194 A full description of the coupled (PT) model is given in Li et al. (2014). The model was used  
195 to simulate the growth of *Pinus koraiensis* in a temperate, relatively moist site in the  
196 Changbai Mountains, China. Tree growth there is primarily constrained by growing-season  
197 PAR, which in turn is strongly influenced by cloud cover. When driven by local climate data  
198 and changing atmospheric [CO<sub>2</sub>], the model produced a good representation of interannual  
199 variability in *Pinus koraiensis* growth over the past 50 years.

200

#### 201 **2.4 Derivation of model parameter values**

202 The P model is generic for C<sub>3</sub> photosynthesis and has no adjustable parameters. The T  
203 model, in contrast, is species-specific and requires values for 13 parameters. Most of these  
204 could be obtained from measurements made at the sampling site, or from the literature  
205 (Table 2). Stem basal diameter, tree height and crown area were measured on 146 trees at  
206 the site. The measurements were made on all *Callitris* trees within the 500 m x 500 m plot.  
207 Parameter values for the initial slope of the height–diameter relationship ( $a$ : 41.35), the  
208 initial ratio of crown area to stem cross-sectional area ( $c$ : 626.92), and maximum tree height  
209 ( $H_m$ : 9.58 m) were estimated using non-linear regression applied to the effective basal  
210 diameter ( $D$ ), tree height ( $H$ ), and crown area ( $A_C$ ) measurements on these 146 trees.  
211 Values for sapwood density ( $\rho_S$ ) and specific leaf area ( $\sigma$ ) were derived from five  
212 measurements made at the sampling site (Table 2). We used generic values for the  
213 extinction coefficient ( $k$ ) for photosynthetically active radiation (PAR) and yield factor ( $y$ ),  
214 from the literature (Table 2). Leaf area index within the crown ( $L$ ) and foliage turnover time  
215 ( $\tau_f$ ) were estimated from published measurements on *Callitris* species in other regions of  
216 Australia.

217

218 No measurements were available for fine-root turnover time ( $\tau_r$ ), fine-root specific  
219 respiration rate ( $r_r$ ), sapwood-specific respiration rate ( $r_s$ ), and ratio of fine-root mass to  
220 foliage area ( $\zeta$ ) in *Callitris*, and these were not measured in the field. But their values can  
221 have a substantial impact on simulated radial growth, and on the shape of the simulated  
222 ontogenetic ageing curve (Li et al., 2014). We used approximate Bayesian parameter  
223 calibration (van der Vaart et al., 2015) to derive mutually consistent values of these four  
224 parameters. The calibration target was mean ring-width during the period 1950-2012 and  
225 the posterior was constructed by sampling the joint parameter distribution 1,000,000 times  
226 and retaining the values of the 1000 samples that most closely matched the calibration  
227 target (van der Vaart et al., 2015). A constraint was imposed to ensure that there were no  
228 negative growth rates of any model component. Calibration was performed using  
229 simulations in which climate and [CO<sub>2</sub>] varied realistically. [CO<sub>2</sub>] data were obtained by  
230 splicing ice-core records for the interval from 1901 to 1957 (Etheridge et al., 1996;  
231 MacFarling Meure et al., 2006) with the annual average of direct atmospheric  
232 measurements from Mauna Loa and the South Pole stations from 1958 to 2013:

233 [http://scrippsco2.ucsd.edu/data/merged\\_ice\\_core/merged\\_ice\\_core\\_yearly.csv](http://scrippsco2.ucsd.edu/data/merged_ice_core/merged_ice_core_yearly.csv).

234 We examined correlations among the posterior parameter values using both Pearson  
235 correlation coefficients and principal components analysis. These analyses showed no  
236 correlation among estimates of fine-root turnover time ( $\tau_r$ ), fine-root specific respiration rate  
237 ( $r_r$ ), and sapwood-specific respiration rate ( $r_s$ ). However, the ratio of fine-root mass to  
238 foliage area ( $\zeta$ ) was correlated with fine root turnover time (0.69) and fine root respiration  
239 rate (-0.70). The calibration produced a shift in the median value for all four parameters  
240 (Fig. 2a) and a substantial reduction in uncertainty was obtained for  $\zeta$ . The final parameter

241 values used for all four variables lie within the range of measurements that have been  
242 made on other gymnosperms (Table 2).

243

## 244 **2.5 Climate inputs**

245 The P model requires inputs of daily temperature, precipitation, and fractional cloud cover,  
246 which are generally obtained by linear interpolation of monthly values of these variables  
247 (Wang et al., 2014). There are four meteorological stations (Credo, Kalgoorlie, Ora Banda,  
248 Menzies) within 100 km of the GWW site, but none has records for all three variables  
249 covering the whole interval sampled by the tree-ring series (i.e. 1920-2013). Thus, none of  
250 these local records can be used to drive the simulations. We therefore used monthly  
251 temperature, precipitation, and cloud cover fraction for the interval 1920 onwards from the  
252 CRU TS v3.22 data set (Harris et al., 2014), using values of these variables for the single  
253 grid cell (30.25°S, 120.75°E) from CRU TS v3.22 in which the sampling site lies. The CRU  
254 climate is derived using a distance-weighted interpolation from all available meteorological  
255 records and has been homogenized to remove any impacts from using information for  
256 individual climate variables from different stations or from different numbers of stations  
257 through time. Nevertheless, we examined the reliability of this approach by comparing the  
258 gridded climate values with observed values from the three meteorological stations for all  
259 overlapping intervals for each variable; in the case of solar radiation/cloud cover this was  
260 very short (post-1990 only). There is generally good agreement between the gridded  
261 monthly (and annual) temperature and precipitation data and meteorological station data  
262 with respect to long-term means, interannual variability and trends. The correlation between  
263 the gridded and observed values of interannual variability in temperature at Kalgoorlie post-  
264 1911 is 0.907 ( $p < 0.001$ ). Similarly, the correlation between the gridded and observed

265 values of interannual variability in precipitation at Menzies between 1901 and 2008 is 0.905  
266 ( $p < 0.001$ ).

267

## 268 **2.6 Definition of the effective growing season**

269 The GWW is characterized by strong precipitation seasonality, while temperature variations  
270 are modest. In climates with cold winters there is always a distinct growing season, even for  
271 evergreen trees. Carbon that is assimilated after maximum leaf-out in any year is normally  
272 stored and contributes to tree growth in the subsequent growing season (Michelot et al.,  
273 2012). Thus the effective growing season for tree growth in seasonally cold climates can be  
274 defined as from mid-summer in one year until mid-summer in the subsequent year (Li et al.,  
275 2014). It is less obvious how to define the effective growing season in moisture-limited  
276 regions. However, several studies have indicated that radial growth in *Callitris* is affected  
277 not only by seasonal precipitation during the year when tree-ring growth is initiated, but also  
278 by precipitation during the wet season in previous years (Baker et al., 2008; Cullen and  
279 Grierson, 2009), suggesting that it is necessary to consider an effective growing season for  
280 carbon accumulation that is longer than the current growth year.

281

282 We investigated the optimal interval influencing carbon accumulation and tree growth using  
283 ordinary least-squares multiple linear regression. Based on likely physiological constraints  
284 in a drought-controlled environment, we used total annual photosynthetically active  
285 radiation ( $PAR_0$ ), VPD, and the ratio of actual to potential evapotranspiration ( $\alpha$ ) as  
286 independent variables in the regression and mean tree-ring width during the period from  
287 1950-2013 as the dependent variable. ( $PAR_0$  is defined as total incident PAR during the  
288 period with temperatures  $> 0^\circ\text{C}$ , but for GWW this is the same as the total annual incident

289 PAR; we use the notation  $PAR_0$  for consistency with other work using the P and T models.)  
290 The post-1950 interval was used for this analysis in order to use all ten tree-ring records to  
291 derive the target mean tree-ring width. We defined the effective growing season as the  
292 period from January to December in the current growth year, and then extended the interval  
293 by six-month steps for a period up to three years. In these latter analyses, each six-month  
294 period contributes equally to the carbon available for growth. The goodness-of-fit of each  
295 model was judged based on the significance of the slope coefficient of each independent  
296 variable ( $p$  value) and the  $R^2$  of the overall model.

297

298 The results from ordinary least-squares multiple linear regression analysis (Table 3)  
299 showed that the best prediction of tree-ring width is obtained using an effective growing  
300 season of two years (from January in the previous year to December in the year of the tree-  
301 ring formation). This interval also produced significant  $p$  values for each of the predictor  
302 variables (Table 3). The overall relationship, and the significance of each climate variable,  
303 deteriorated when the effective growing season was defined as longer than two years.  
304 Thus, in the subsequent application of the model, we used a carbon-accumulation period of  
305 two years (equally-weighted mean of the two years) to drive simulated growth rates. This is  
306 consistent with the observation that radial growth of *Callitris* is influenced by precipitation in  
307 the previous rainy season as well as the present one (Baker et al., 2008; Cullen and  
308 Grierson, 2009).

309

## 310 **2.7 Application of the Model**

311 Each tree was initialized with its actual effective single-stemmed basal diameter in the first  
312 year of growth, except that trees that started growing before 1901 were initialized using the

313 actual effective single-stemmed basal diameter in 1901. The availability of climate data  
314 determined the earliest start date of the simulations (1901). The initial basal diameter was  
315 calculated from the measured diameter in August 2013 (which varied between 11.9 and  
316 28.2 cm) and measured radial growth between the starting date and sampling date.

317

318 The model was run initially using values of the four poorly-known parameters calibrated to  
319 reproduce the mean ring-width for the period 1950-2012, with varying climate and [CO<sub>2</sub>]. As  
320 a test of whether carbon allocation might plausibly have varied, we ran a second simulation  
321 in which the ratio of fine-root mass to foliage area ( $\zeta$ ) was calibrated using a spline fit to the  
322 mean ring-width during successive 30-year windows between 1920-2012, with a step of five  
323 years between windows and using appropriate [CO<sub>2</sub>] and climate for each window.

324

## 325 **3 Results**

326

### 327 **3.1 Baseline simulation of ring-width versus observations**

328 The T model generally captured the amplitude of *Callitris* tree growth variations (Fig. 2b).  
329 The mean simulated ring-width for the period 1950-2012 was 0.840 mm, compared to an  
330 observed value of 0.753 mm. The standard deviation (SD) in mean ring-width (0.197 mm)  
331 was underestimated compared to the observed SD (0.215 mm). This difference probably  
332 reflects the impact of local variability in environmental conditions on individual tree growth,  
333 not accounted for in the model. Regression analysis (Fig. 3, Table 4) showed that tree  
334 growth has a strongly positive, independent response to both PAR<sub>0</sub> and soil moisture  
335 availability (indexed by  $\alpha$ ) and a negative response to VPD ( $p < 0.01$ ). (Similar relationships  
336 are obtained using a linear mixed-effect model to account for autocorrelation between



337 replicates and temporally: Table 4). These relationships are captured in the simulations.  
338 Although there is more scatter in the observations, the slopes of the observed and  
339 simulated responses to  $PAR_0$ ,  $\alpha$  and VPD are statistically identical in the model and in the  
340 data. The positive relationship with  $PAR_0$  reflects the universal control of photosynthesis by  
341 light availability, and the positive relationship with  $\alpha$  is consistent with observations that the  
342 growth of *Callitris* is strongly influenced by precipitation variability (Ash, 1983; Cullen and  
343 Grierson, 2009). VPD affects stomatal conductance such that increasing VPD leads to  
344 stomatal closure, with a correspondingly negative impact on photosynthesis and hence  
345 carbon assimilation and growth.

346 Whereas the responses of modelled and measured ring-width to climate variables are  
347 quantitatively similar, there is a discrepancy in the response to  $[CO_2]$ . The data show no  
348 significant response ( $-0.0006 \pm 0.0015$  mm ppm<sup>-1</sup>,  $p = 0.687$ ) while the model shows a  
349 small but significant positive response ( $0.0011 \pm 0.0004$  mm ppm<sup>-1</sup>,  $p = 0.004$ ). The  
350 correlation between simulated and observed interannual variability (Fig. 2b) is not  
351 significant ( $r = 0.06$ ,  $p = 0.571$ ), reflecting an unrealistic simulated increase during recent  
352 decades. The root mean squared error (RMSE) of this simulation was 0.28 mm.

353

### 354 **3.2 Effects of increasing $[CO_2]$ on tree-ring width and carbon allocation strategy**

355 Time-dependent calibration produced values of  $\zeta$  that decreased by ca 6% from the  
356 beginning of the simulation to the 30-year interval centred on 1965, and subsequently  
357 increased by ca 12% by the 30-year interval centred on 1995 (Fig. 4). In other words, the  
358 values of  $\zeta$  required to match the observations increased through the period when  $[CO_2]$   
359 increased the most (ca 40 ppm, as compared to ca 12 ppm before 1965). GWW climate  
360 has also varied systematically during this period. The first principal component of  
361 multidecadal variability (based on 30-year means of standardized values of  $\alpha$ , VPD and

362 PAR<sub>0</sub>) explains 55% of the overall variance with loadings of -0.71 for both  $\alpha$  and VPD and  
363 0.00 for PAR. The second principal component explains a further 44% of the variance and  
364 is related primarily to PAR (-0.87) and secondarily to  $\alpha$  (0.36) and VPD (-0.35). The  
365 changes in PAR, however, are small (ca 2%) and thus the impact of increasing moisture  
366 availability during the first half of the period could explain the initial decline in  $\zeta$  (Fig. 4). The  
367 simulation with time-varying values of  $\zeta$  produced improved correlation ( $r = 0.60$ ,  $p < 0.001$ )  
368 with the tree-ring observations (Fig. 5), avoiding the systematic overestimation of ring-  
369 widths in recent years compared to observations that is seen in the simulation with  
370 observed [CO<sub>2</sub>] and fixed  $\zeta$  (Fig. 2b). The RMSE of the modelled ring-widths was reduced  
371 from 0.28 to 0.17 mm by allowing variation in  $\zeta$ . The remaining discrepancies between  
372 simulated and observed ring widths probably reflect simplifications in the modelling  
373 approach, most particularly with respect to carbon carryover between years and the use of  
374 an average value for wood density. However, the progressive nature of the changes in  
375 below-ground allocation coupled with the overall improvement in the simulations both  
376 indicate that it is plausible that changes in allocation play a role in the response to  
377 increasing [CO<sub>2</sub>].

378

## 379 **4 Discussion and Conclusions**

380 The dependencies of *Callitris columellaris* radial growth on climate at GWW could be  
381 simulated by coupling a generic model of GPP (P) with a model of carbon allocation and  
382 functional geometric tree growth (T), using species-specific parameter values in T. Model  
383 performance was not adversely affected by the reduction in winter precipitation, and the  
384 shift to less frequent but more intense precipitation events, that occurred in latter part of the

385 record. Radial growth was positively related to  $PAR_0$  and  $\alpha$ , and negatively correlated with  
386 VPD, with similar quantitative dependencies shown in the data and in the model.

387

388 The response to VPD can be explained as a consequence of the atmospheric control on  
389 stomatal conductance and hence photosynthesis. Thus, both atmospheric and soil moisture  
390 deficits (the former indexed by VPD, the latter by  $\alpha$ ) separately influence radial growth.  
391 Previous studies have shown that the growth of *Callitris* in southwestern Australia is  
392 controlled by precipitation (Sgherza et al., 2010), but there is only a weak correlation  
393 between stable carbon isotope measurements and precipitation of the current year because  
394 *Callitris* has a strong water-conservation strategy. These findings are consistent with the  
395 observed response to VPD and further support our use of a two-year period contributing to  
396 carbon accumulation and growth.

397

398 The radial growth of *Callitris columellaris* in the GWW has not responded to the  $[CO_2]$   
399 increase of recent decades. The lack of a response to  $[CO_2]$  has been a feature of other  
400 quantitative studies of tree growth (e.g. Kienast and Luxmoore, 1988; Archer et al., 1995;  
401 Gedalof and Berg, 2010; Peñuelas et al., 2011). Analyses of stable carbon isotopes and  
402 growth of tropical trees (van der Sleen et al., 2015) showed an increase in water-use  
403 efficiency, yet no stimulation of radial growth due to  $CO_2$  fertilization over the past 150  
404 years. The modelled response of ring-width to  $[CO_2]$  in our analysis was small compared  
405 with the responses to  $\alpha$ , VPD and  $PAR_0$  – as can be seen by comparing standardized  
406 regression coefficients for the modelled ring-widths, which are three to six times smaller for  
407  $[CO_2]$  than for the climate variables (Table 4). A modest shift in carbon allocation (towards

408 the production of fine roots, as implied by increasing  $\zeta$ ) would be sufficient to reconcile the  
409 modelled increase in GPP with the lack of any observed increase in ring-width.

410

411 Although the data presented here do not allow us to statistically disentangle potential  
412 effects of climate variability and  $[\text{CO}_2]$  on carbon allocation patterns, we note that an  
413 increase in fine-root production has been observed at the majority of Free Air Carbon  
414 dioxide Enrichment (FACE) sites. Therefore, it is reasonable to speculate that an increase  
415 in  $\zeta$  might come about as a consequence of increased  $[\text{CO}_2]$ . FACE experiments are  
416 equivocal about the impact of enhanced  $[\text{CO}_2]$  on tree growth, but the shift in allocation is a  
417 common feature. The Swiss Canopy Crane site is an outlier, with decreased below-ground  
418 allocation (Bader et al., 2009). We might expect *a priori* that trees at sites experiencing  
419 strong nutrient limitation would show this kind of response because of the need to extract  
420 more nutrients to support increased NPP, whereas trees at sites experiencing strong water  
421 limitation might show the opposite response due to enhanced water use efficiency at high  
422  $[\text{CO}_2]$ . Our results do not support this reasoning, however, suggesting instead that the trees  
423 may be allocating more below ground as  $[\text{CO}_2]$  increases even in the strongly water-limited  
424 environment of the GWW. Increased below-ground allocation could in part represent carbon  
425 export to mycorrhizae or the rhizosphere (Godbold et al., 2015), which is not considered in  
426 the T model.

427

428 Appropriately analysed, tree-ring records worldwide should yield consistent information  
429 about the diverse responses of tree growth and allocation to environmental change. Here,  
430 with the use of a simple process-based model of tree growth, we have explored the  
431 potential for changes in the proportion of above- and below-ground allocation to explain the

432 lack of evidence for increased radial growth in response to recent increases in [CO<sub>2</sub>]. A  
433 noteworthy feature of our study is that a relatively minor change in the relative allocation of  
434 carbon to fine roots *versus* leaves is sufficient to suppress an increase in radial growth in  
435 response to increasing [CO<sub>2</sub>] in the simulations. If such changes in allocation occur in the  
436 real world, then the observed stability in radial growth in recent decades does not mean that  
437 GPP or NPP is unresponsive to [CO<sub>2</sub>] (whether through nutrient limitation, sink limitation or  
438 any other mechanism). There are a number of potential sources of uncertainty in our  
439 modelling approach, including the representation of aging trends and of the importance of  
440 the carry-over of non-structural carbohydrates between growing seasons. Nevertheless, our  
441 results support the idea that above-ground biomass production and radial growth are  
442 sensitive to environmental effects on carbon allocation. This is important because the  
443 influence of environmental conditions on allocation are neglected by most current  
444 ecosystem models (De Kauwe et al., 2014).

445

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454

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642

643

644 **Table and Figure Captions**

645

646 Table 1. Standard summary statistics for the tree-ring series. Values are given both for the  
647 period 1920-2012 and for the period post-1950, because there are only a limited number of  
648 individual trees represented in the first 30 year period.

649 Table 2. Definition of T model parameters and derivation of parameter values. Most of the  
650 values were obtained from field measurements, or are generic. For those values estimated  
651 using Bayesian calibration, we show the range of values given for *Callitris* (or related  
652 species) in the literature, the prior values used in the calibration, the posterior values and  
653 uncertainties, and the value used in the final model. The units are defined in the parameter  
654 column, except in the case of sapwood specific respiration where the measurements are in  
655 a different unit from the model parameter (and therefore specified explicitly). Values for  
656 most parameters fall in well-behaved ranges, but there are large differences in the available  
657 measurements of sapwood specific respiration rate and for ratio of fine-root mass to foliage  
658 area and we therefore give the individual measurements rather than a range for these  
659 parameters.

660

661 Table 3. Regression analysis of relationship between ring-width and climate parameters  
662 using different definitions of the effective growing season, based on the interval from 1950  
663 to present. The dependent variable is mean ring-width. The independent variables are the  
664 total incident photosynthetically active radiation ( $PAR_0$ ), vapour pressure deficit (VPD), and  
665 the ratio of actual to potential evapotranspiration ( $\alpha$ ). This analysis indicates that the  
666 optimum period contributing to tree growth is two years.

667

668 Table 4. Regression analyses of simulated and observed response of tree growth to climate  
669 variables and CO<sub>2</sub>. The dependent variable is mean radial growth series of the ten trees  
670 (from 1950 to 2012). The independent variables are the total incident photosynthetically  
671 active radiation (PAR<sub>0</sub>), the ratio of actual to potential evapotranspiration ( $\alpha$ ), vapour  
672 pressure deficit (VPD) and monthly [CO<sub>2</sub>]. Above: analysis based on untransformed  
673 variables. Middle: analysis based on standardized variables. Below: linear mixed model  
674 analysis based on standardized variables.

675

676 Figure 1. Interannual variability in tree-ring widths of *Callitris columellaris* from the Great  
677 Western Woodlands, Western Australia. In the top panel, the black line is the mean of the  
678 observations, and the grey bars show the standard deviation (SD) of the individual sampled  
679 trees. The blue line in the bottom panel shows the number of trees sampled for each  
680 interval.

681

682 Figure 2. a) Prior (dashed line) and posterior (solid line) probability distribution functions for  
683 fine-root turnover time ( $\tau_f$ ), fine-root specific respiration rate ( $r_f$ ), sapwood-specific  
684 respiration rate ( $r_s$ ); ratio of fine-root mass to foliage area ( $\zeta$ ). b) Comparison between  
685 simulated and observed tree-ring widths, for the period 1920 to the present, using varying  
686 climate and [CO<sub>2</sub>]. The black line is the mean of the observations, and the grey bars are the  
687 standard deviation (SD) among the ten individual trees sampled. The blue line and bars are  
688 the mean and standard deviation for the ten simulated individual trees.

689

690 Figure 3. Simulated and observed response of tree radial growth to major climate variables  
691 and [CO<sub>2</sub>]: partial residual plots based on the regression analysis, obtained using the *visreg*



692 package in R, are shown. The dependent variable is mean ring-width (from 1950 to 2012).  
693 The predictor variables are total incident photosynthetically active radiation ( $PAR_0$ ), vapour  
694 pressure deficit (VPD), the ratio of actual to potential evapotranspiration ( $\alpha$ ), and monthly  
695  $[CO_2]$ .

696

697 Figure 4. Time-dependent variation of the ratio of fine-root mass to foliage area ( $\zeta$ )  
698 estimated by approximate Bayesian calibration. The graph shows the percentage change to  
699 the mean value of  $\zeta$  for 30-year moving windows since 1920 (red), using the appropriate  
700  $[CO_2]$  and  $\alpha$  for each window. Values on the x-axis are plotted against the middle year of  
701 each 30-year window. Also shown are  $[CO_2]$  (grey) and the first principal component of the  
702 multidecadal variability in climate ( $\alpha$ , VPD,  $PAR_0$ ) (blue).

703

704 Figure 5. Simulation of radial growth in response to changing climate and observed  $[CO_2]$ ,  
705 allowing for the effect of changing allocation to fine roots. The black line is the mean of the  
706 observations, and the grey bars are the standard deviation (SD) among the ten individual  
707 trees sampled. The blue line and bars are the mean and standard deviation for the ten  
708 simulated individual trees.

709

710 Table 1. Standard summary statistics for the tree-ring series. Values are given both for the  
 711 period 1920-2012 and for the period post-1950, because there are only a limited number of  
 712 individual trees represented in the first 30-year period.

713

Interval	1920-2012	1950-2012
Mean	0.482	0.4825
Standard deviation	0.321875	0.324125
First order autocorrelation	0.20521875	0.19253125
Mean correlation among all radii	0.137	0.147
Mean correlation between trees	0.128	0.136
Mean correlation within trees	0.237	0.259
Signal-to-noise ratio	2.912	3.3
Expressed population signal	0.744	0.767

714

715 Table 2. Definition of T model parameters and derivation of parameter values. Most of the values were obtained from field measurements,  
716 or are generic. For those values estimated using Bayesian calibration, we show the range of values given for *Callitris* (or related species)  
717 in the literature, the prior values used in the calibration, the posterior values and uncertainties, and the value used in the final model. The  
718 units are defined in the parameter column, except in the case of sapwood specific respiration where the measurements are in a different  
719 unit from the model parameter (and therefore specified explicitly). Values for most parameters fall in well-behaved ranges, but there are  
720 large differences in the available measurements of sapwood specific respiration rate and for ratio of fine-root mass to foliage area and we  
721 therefore give the individual measurements rather than a range for these parameters.

Parameter	<i>Symbol</i>	Uncertainty or range of values from literature	Source of information	Prior value	Posterior value	Accepted value	Reference
initial slope of height-diameter relationship (-)	$a$	$41.35 \pm 2.58$	observation	-	-	41.35	-
initial ratio of crown area to stem cross-sectional area (-)	$c$	$626.92 \pm 20.03$	observation	-	-	626.92	-
maximum tree height (m)	$H_m$	$9.58 \pm 1.11$	observation	-	-	9.58	-
sapwood density (kg C m <sup>-3</sup> )	$\rho_s$	$406 \pm 32$	observation	-	-	406	-
specific leaf area (m <sup>2</sup> kg <sup>-1</sup> C)	$\sigma$	$5.16 \pm 0.32$	observation	-	-	5.16	-
leaf area index within the crown (-)	$L$	$1.87 \pm 0.18$	species-specific literature value	-	-	1.87	Fieber et al., 2014
foliage turnover time (yr)	$\tau_f$	2.58	species-specific literature value	-	-	2.58	Wright and Westoby, 2002
PAR extinction coefficient (-)	$k$	0.48-0.58	generic value	-	-	0.5	Pierce and Running, 1988
yield factor (-)	$Y$	0.5-0.7	generic value	-	-	0.6	Zhang et al., 2009
fine-root turnover time (yr)	$\tau_r$	$0.76 \pm 0.06$	Bayesian parameter optimization	$0.75 \pm 0.5$	$1.00 \pm 0.40$	1.00	Yuan and Chen, 2010 (estimation for evergreen needleleaf trees)
fine-root specific respiration rate (yr <sup>-1</sup> )	$r_r$	1.36	Bayesian parameter optimization	$1.36 \pm 1$	$1.23 \pm 0.74$	1.23	Burton and Prigitzer, 2002 (estimation from one-seeded Juniper)
sapwood specific respiration rate (yr <sup>-1</sup> )	$r_s$	0.5-10, 20 nmol mol <sup>-1</sup> s <sup>-1</sup>	Bayesian parameter optimization	$1 \pm 0.75$ nmol mol <sup>-1</sup> s <sup>-1</sup>	$1.16 \pm 0.66$ nmol mol <sup>-1</sup> s <sup>-1</sup>	1.16 nmol mol <sup>-1</sup> s <sup>-1</sup> (0.034 yr <sup>-1</sup> )	Landsberg and Sands, 2010
ratio of fine-root mass to foliage area (kgC m <sup>-2</sup> )	$\zeta$	1.0; 0.17	Bayesian parameter optimization	$0.6 \pm 0.5$	$0.150 \pm 0.052$	0.150	Burrows et al., 2001 (estimation for <i>Callitris</i> ); White et al. (2000) (estimation for evergreen needleleaf tree)

722

723 Table 3. Regression analysis of relationship between ring-width and climate parameters  
 724 using different definitions of the effective growing season, based on the interval from 1950  
 725 to present. The dependent variable is mean ring-width. The independent variables are the  
 726 total incident photosynthetically active radiation (PAR<sub>0</sub>), vapour pressure deficit (VPD), and  
 727 the ratio of actual to potential evapotranspiration ( $\alpha$ ). This analysis indicates that the  
 728 optimum period contributing to tree growth is two years.

729

		PAR <sub>0</sub> (mm (kmol photon m <sup>-2</sup> )- <sup>-1</sup> )	VPD (mm hPa <sup>-1</sup> )	$\alpha$ (mm)	<i>R</i> <sup>2</sup>
Formation year	Estimation	0.48	-0.11	0.8	0.184
	Standard error	± 0.20	± 0.04	± 0.4	
	<i>p</i> value	0.020	0.016	0.069	
Calendar year	Estimation	0.43	-0.06	0.6	0.094
	Standard error	± 0.20	± 0.04	± 0.6	
	<i>p</i> value	0.039	0.171	0.266	
1.5 Calendar years	Estimation	0.68	-0.14	1.4	0.286
	Standard error	± 0.22	± 0.05	± 0.5	
	<i>p</i> value	0.004	0.007	0.009	
2 Calendar years	Estimation	0.70	-0.17	1.7	0.345
	Standard error	± 0.24	± 0.05	± 0.5	
	<i>p</i> value	0.006	0.002	0.003	
2.5 Calendar years	Estimation	0.67	-0.16	1.7	0.269
	Standard error	± 0.27	± 0.06	± 0.6	
	<i>p</i> value	0.017	0.010	0.009	
3 Calendar years	Estimation	0.94	-0.20	2.0	0.293
	Standard error	± 0.29	± 0.07	± 0.7	
	<i>p</i> value	0.002	0.004	0.004	

730

731 Table 4. Regression analyses of simulated and observed response of tree growth to  
 732 climate variables and CO<sub>2</sub>. The dependent variable is mean radial growth series of the ten  
 733 trees (from 1950 to 2012). The independent variables are the total incident  
 734 photosynthetically active radiation (PAR<sub>0</sub>), the ratio of actual to potential  
 735 evapotranspiration ( $\alpha$ ), vapour pressure deficit (VPD) and monthly [CO<sub>2</sub>]. Above: analysis  
 736 based on untransformed variables. Middle: analysis based on standardized variables.  
 737 Below: linear mixed model analysis based on standardized variables.  
 738

Untransformed linear model		PAR <sub>0</sub> (mm (kmol photon m <sup>-2</sup> ) <sup>-1</sup> )	$\alpha$ (mm)	VPD (mm hPa <sup>-1</sup> )	CO <sub>2</sub> (mm ppm <sup>-1</sup> )
Observation	Estimation	0.709	1.734	-0.164	-0.001
	Standard error	±0.246	±0.572	±0.059	±0.001
	<i>p</i> value	0.006	0.004	0.008	0.687
Simulation with actual CO <sub>2</sub>	Estimation	0.762	2.308	-0.096	0.001
	Standard error	±0.059	±0.137	±0.014	±0.000
	<i>p</i> value	<0.001	<0.001	<0.001	0.004
Simulation with time-dependent $\zeta$ and actual CO <sub>2</sub>	Estimation	0.622	2.221	-0.060	-0.001
	Standard error	±0.102	±0.224	±0.023	±0.001
	<i>p</i> value	<0.001	<0.001	0.014	0.113

739

740

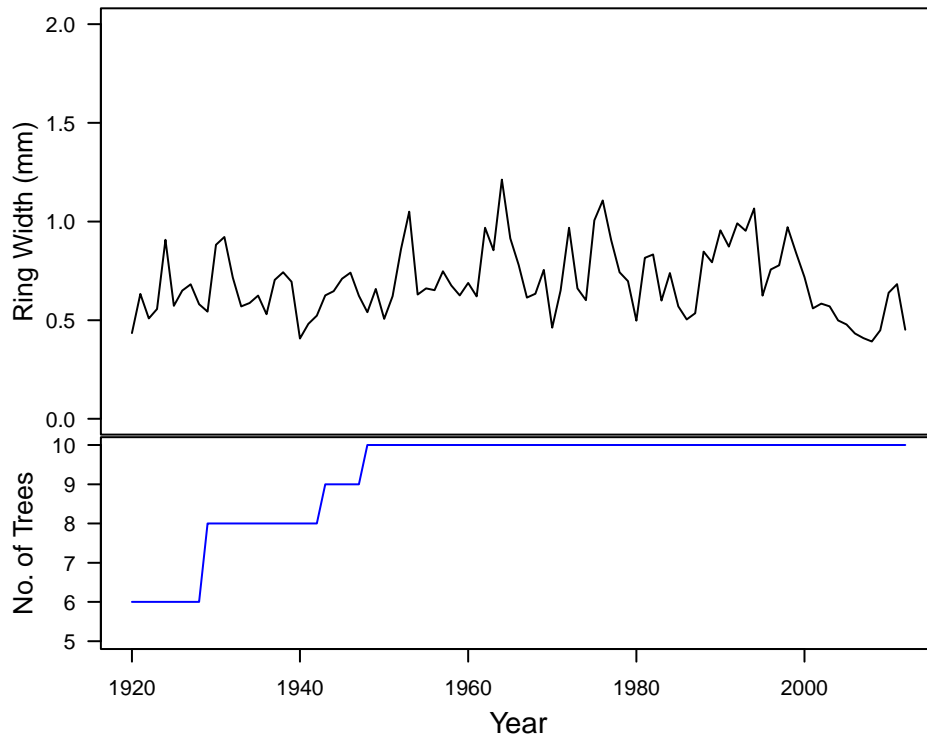
Standardized linear model		PAR <sub>0</sub>	$\alpha$	VPD	CO <sub>2</sub>
Observation	Estimation	0.095	0.085	-0.099	-0.011
	Standard error	±0.033	±0.028	±0.036	±0.027
	<i>p</i> value	0.006	0.004	0.008	0.687
Simulation with actual CO <sub>2</sub>	Estimation	0.102	0.113	-0.058	0.020
	Standard error	±0.008	±0.007	±0.008	±0.007
	<i>p</i> value	<0.001	<0.001	<0.001	0.004
Simulation with time-dependent $\zeta$ and actual CO <sub>2</sub>	Estimation	0.088	0.110	-0.034	-0.017
	Standard error	±0.014	±0.011	±0.013	±0.011
	<i>p</i> value	<0.001	<0.001	0.014	0.113

741

Standardized linear mixed model		PAR <sub>0</sub>	$\alpha$	VPD	CO <sub>2</sub>
Observation	Estimation	0.096	0.089	-0.095	-0.013
	Standard error	$\pm 0.034$	$\pm 0.039$	$\pm 0.039$	$\pm 0.057$
	<i>p</i> value	0.005	0.010	0.029	0.825
Simulation with actual CO <sub>2</sub>	Estimation	0.090	0.110	-0.057	0.029
	Standard error	$\pm 0.006$	$\pm 0.006$	$\pm 0.008$	$\pm 0.008$
	<i>p</i> value	<0.001	<0.001	<0.001	0.019
Simulation with time-dependent $\zeta$ and actual CO <sub>2</sub>	Estimation	0.085	0.103	-0.050	-0.001
	Standard error	$\pm 0.009$	$\pm 0.005$	$\pm 0.007$	$\pm 0.001$
	<i>p</i> value	<0.001	<0.001	<0.001	1

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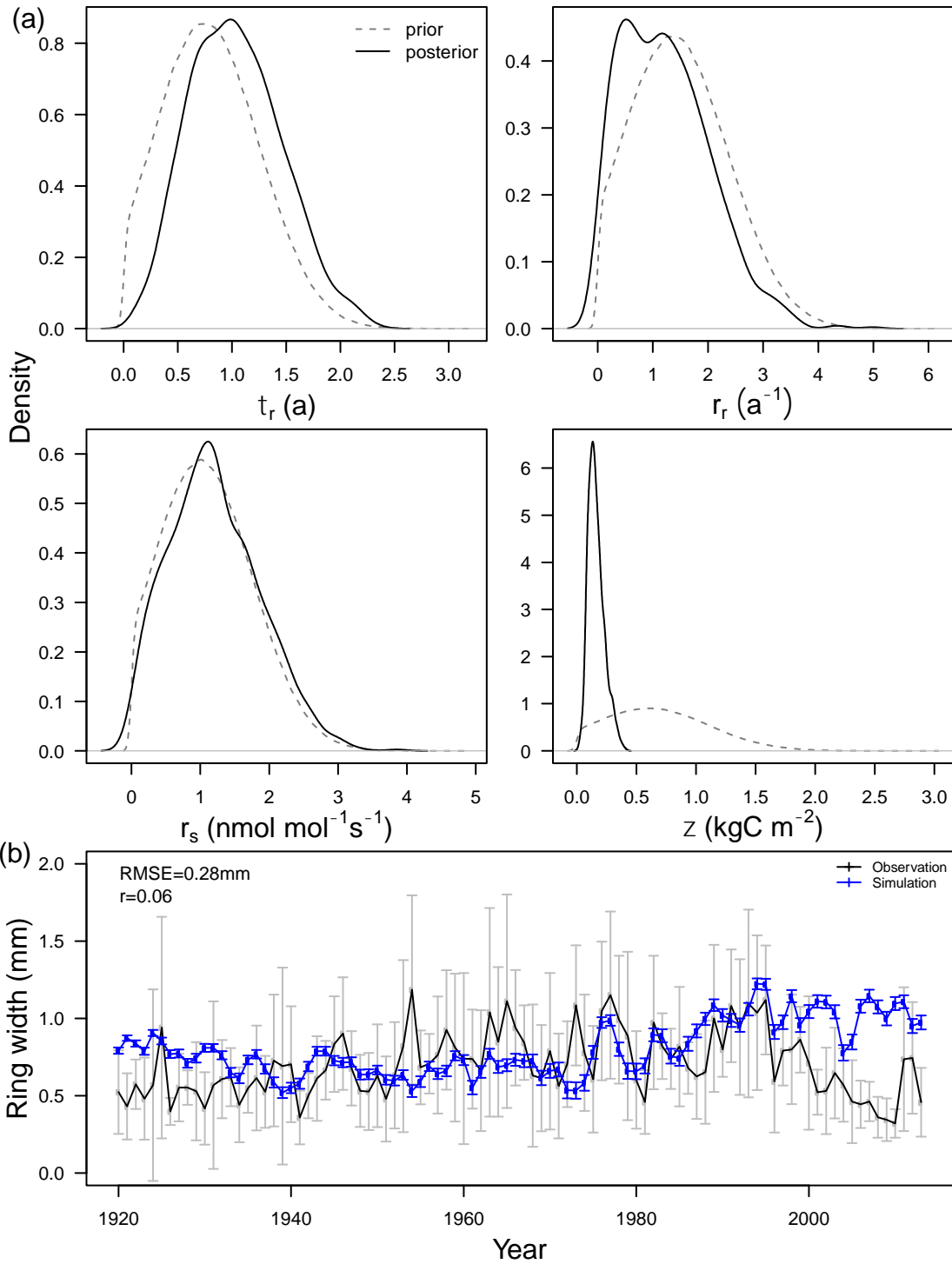
743



744

745 Figure 1. Interannual variability in tree-ring widths of *Callitris columellaris* from the Great  
 746 Western Woodlands, Western Australia. In the top panel, the black line is the mean of the  
 747 observations, and the grey bars show the standard deviation (SD) of the individual  
 748 sampled trees. The blue line in the bottom panel shows the number of trees sampled for  
 749 each interval.

750



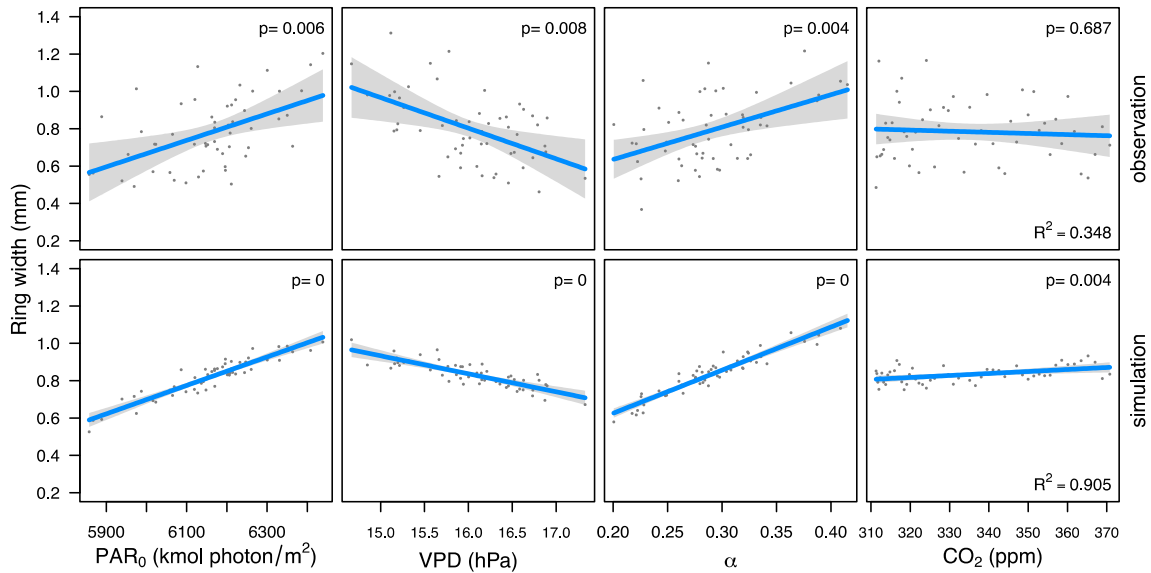
751

752 Figure 2. a) Prior (dashed line) and posterior (solid line) probability distribution function for  
 753 fine-root turnover time ( $\tau_r$ ), fine-root specific respiration rate ( $r_r$ ), sapwood-specific  
 754 respiration rate ( $r_s$ ); ratio of fine-root mass to foliage area ( $\zeta$ ). b) Comparison between  
 755 simulated and observed tree-ring widths, for the period 1920 to the present, using varying  
 756 climate and  $[CO_2]$ . The black line is the mean of the observations, and the grey bars are



757 the standard deviation (SD) among the ten individual trees sampled. The blue line and  
758 bars are the mean and standard deviation for the ten simulated individual trees.

759

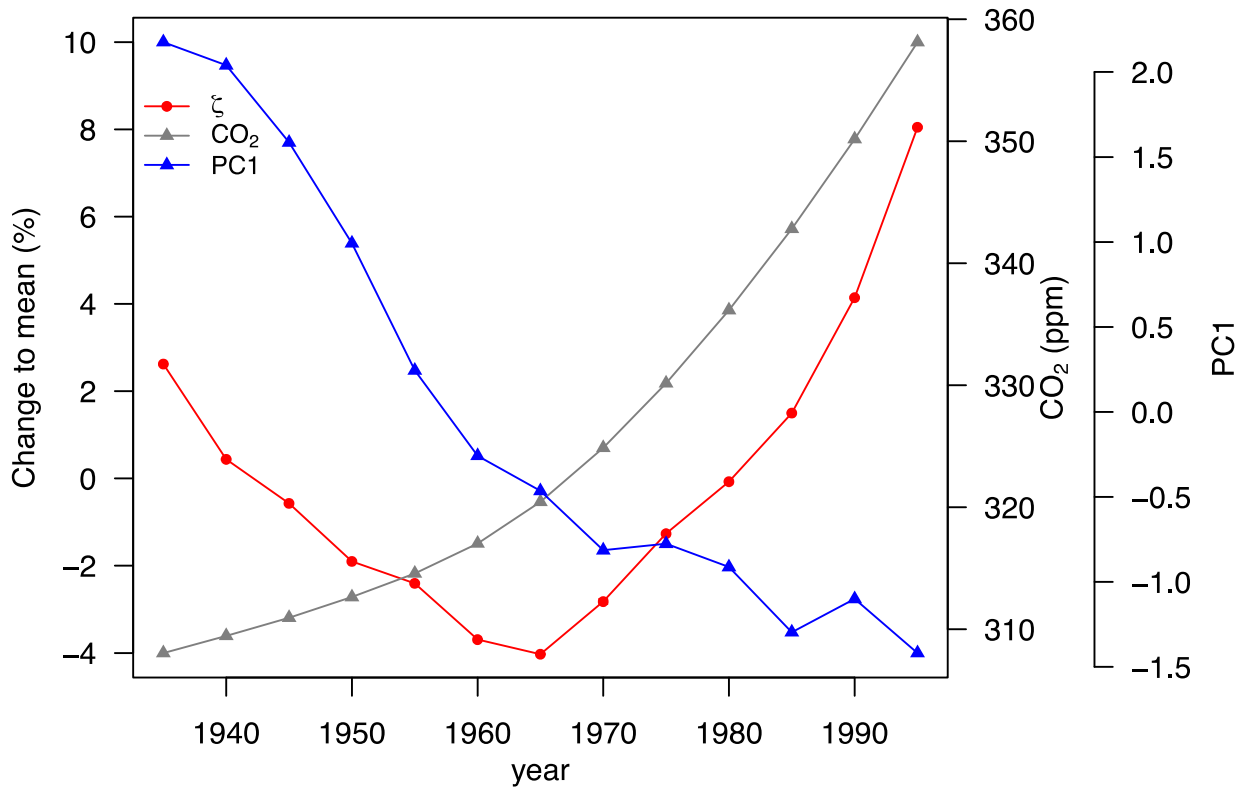


760

761 Figure 3. Simulated and observed responses of tree radial growth to climate variables and  
762 [CO<sub>2</sub>]: partial residual plots based on the regression analysis, obtained using the *visreg*  
763 package in R, are shown. The dependent variable is mean ring-width (from 1950 to 2012).  
764 The predictor variables are annual incident photosynthetically active radiation (PAR<sub>0</sub>),  
765 vapour pressure deficit (VPD), the ratio of actual to potential evapotranspiration (α), and  
766 monthly [CO<sub>2</sub>].

767

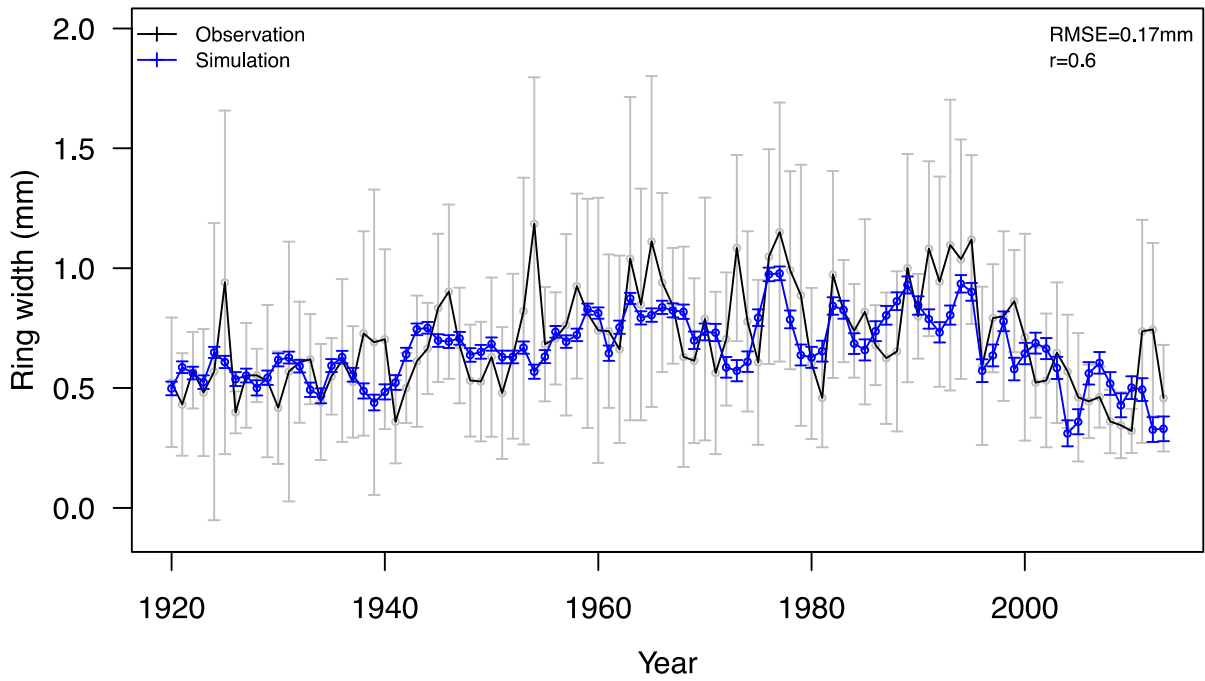
768



769

770 Figure 4. Time-dependent variation of the ratio of fine-root mass to foliage area ( $\zeta$ )  
 771 estimated by approximate Bayesian calibration. The graph shows the percentage change  
 772 to the mean value of  $\zeta$  for 30-year moving windows since 1920 (red), using the appropriate  
 773 [CO<sub>2</sub>] and  $\alpha$  for each window. Values on the x-axis are plotted against the middle year of  
 774 each 30-year window. Also shown are [CO<sub>2</sub>] (grey) and the first principal component of the  
 775 multidecadal variability in climate ( $\alpha$ , VPD, PAR<sub>0</sub>) (blue).

776



777

778 Figure 5. Simulation of radial growth in response to changing climate and observed [CO<sub>2</sub>],  
 779 allowing for the effect of changing allocation to fine roots. The black line is the mean of the  
 780 observations, and the grey bars are the standard deviation (SD) among the ten individual  
 781 trees sampled. The blue line and bars are the mean and standard deviation for the ten  
 782 simulated individual trees.

783