

A model analysis of climate and CO2 controls on tree growth and carbon allocation in a semi-arid woodland

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1	A model analysis of climate and CO ₂ controls on tree growth
2	and carbon allocation in a semi-arid woodland
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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 CO2 concentration [CO2] despite the expected enhancement of
17	photosynthetic rates and water-use efficiency at high [CO2]. 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

22 growth model were derived from independent observations except for sapwood specific

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Woodlands, Western Australia, over the past 100 years. Parameter values for the tree-

23 respiration rate, fine-root turnover time, fine-root specific respiration rate and the ratio of 24 fine-root mass to foliage area (ζ), which were calibrated to the ring-width measurements by 25 approximate Bayesian calibration. This procedure imposed a strong constraint on ζ . 26 Modelled and observed ring-widths showed quantitatively similar, positive responses to total annual photosynthetically active radiation and soil moisture, and similar negative 27 responses to vapour pressure deficit. The model also produced enhanced radial growth in 28 29 response to increasing [CO₂] during recent decades, but the data do not show this. Recalibration in moving 30-year time windows produced temporal shifts in the estimated 30 values of ζ , including an increase by ca 12% since the 1960s, and eliminated the [CO₂]-31 induced increase in radial growth. The potential effect of CO₂ on ring-width was thus shown 32 to be small compared to effects of climate variability even in this semi-arid climate. It could 33 34 be counteracted in the model by a modest allocation shift, as has been observed in field experiments with raised [CO₂]. 35

36

37 Keywords

Tree growth modelling, Tree rings, CO₂ fertilisation, Carbon allocation, Response to climate
 change, Water-use efficiency.

40

41 Introduction

Atmospheric CO₂ concentration [CO₂] has direct impacts on the photosynthesis and wateruse efficiency of C₃ plants (Drake et al., 1997; Ainsworth and Long, 2005; Norby and Zak, 2011; De Kauwe et al., 2013). However, several studies of tree radial growth in wellwatered temperate and tropical regions have failed to show increases that might be attributed to increasing [CO₂] (Kienast and Luxmoore, 1988; Gedalof and Berg, 2010;

47 Girardin et al., 2011; Peñuelas et al., 2011; van der Sleen et al., 2015). Moreover, treegrowth modelling (Boucher et al., 2014; Li et al., 2014) has suggested that the expected 48 49 radial growth enhancement due to the recent [CO₂] increase is guite small, compared to the 50 effects of climate variability. A stronger response to enhanced [CO2] might be expected a 51 priori in water-limited regions (Field et al., 1983; Hyvönen et al., 2007), because stomatal conductance is reduced when [CO₂] is higher. This is a common empirical observation, 52 53 consistent with the least-cost hypothesis (Wright et al., 2003; Prentice et al., 2014), which predicts a near-constant ratio of leaf-internal to ambient [CO₂] as [CO₂] increases – while 54 55 the rate of increase of photosynthesis with [CO₂] declines. Failure to sample water-limited environments might thus conceivably explain the apparent lack of increased stem growth in 56 57 response to increasing [CO₂].

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59 An alternative explanation could be that increased primary production due to increased 60 [CO₂] has not led to increased stem growth due to a shift in carbon allocation away from stems. There is some experimental evidence that changing [CO₂] results in changes in 61 carbon allocation between above-ground (leaf, stem) and below-ground (root) biomass 62 63 pools. Observations of the response to high [CO₂] in Free-Air Carbon dioxide Enrichment 64 (FACE) experiments show that trees commonly increase total carbon allocation below ground, in the form of increased root production and/or exudation of labile substrates (Oak 65 Ridge FACE: Norby et al., 2004; DUKE-FACE: DeLucia et al., 1999; Pritchard et al., 2008; 66 Rhinelander ASPEN-FACE: King et al., 2001; EUROFACE: Calfapietra et al., 2003; Lukac 67 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 [CO₂] under natural conditions.

Process-based model experiments provide a way of comparing the consequences of alternative hypotheses. Here we used a global light-use efficiency model of photosynthesis coupled with a dynamic allocation and tree-growth model to simulate the radial growth of the gymnosperm *Callitris columellaris* growing in the water-limited environment of the Great Western Woodlands (GWW), Western Australia. We specifically examined whether we could detect an effect of [CO₂] on ring-width, in addition to effects of climate variability.

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81 2 Methods

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83 2.1 The study area

The GWW, with an area of about 160,000 km², is the largest remaining area of intact 84 mediterranean woodland on Earth (Watson, 2008; Lee et al., 2013). The region is unique 85 86 because of the abundance and diversity of trees that grow there, despite the dry climate and nutrient-poor sandy soils (Watson, 2008; Prober et al., 2012). The vegetation of the 87 GWW is dominated by open eucalypt woodlands, with patches of heathland, mallee and 88 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 occasional heavy rains in summer (Sturman and Tapper, 1996). The sampling site lies near 91 92 the GWW SuperSite (GWW SuperSite, Credo, 30.1°S, 120.7°E, 400m a.s.l.; http://www.tern-supersites.net.au/supersites/gwwl) in the northernmost and driest part of 93 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), associated with *Acacia* and the multi-stemmed gymnosperm *Callitris columellaris*, with
 Atriplex in the understory. However, *Callitris columellaris* was the only woody species at the
 sampling site itself. Human impact around the site is minimal.

99

The coastal southwestern region of Western Australia has experienced a multidecadal 100 101 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 summer storms. The number of rain days decreased, especially after 1960 (-6.2 106 107 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° /decade (p < 0.001) and vapour pressure deficit (VPD) also 111 increased, while soil moisture (as indexed by α , 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**

The genus *Callitris* has provided good records of annual tree growth in a variety of climates across Australia and is known to be sensitive to changing water availability (Ash, 1983; Cullen and Grierson, 2007; Baker et al., 2008; Cullen et al., 2008; Cullen and Grierson, 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 because they appeared to be the oldest trees on the plot. The sampling plot showed no 125 126 sign of disturbance. Other environmental conditions (topography, soil type, soil depth) showed no visible variation among the sampled trees. Multiple cores were obtained from 127 128 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 (δ_i) and individual-stem 138 diameter increments $(d(\delta_i)/dt)$ by:

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

The effective annual growth measured at the site is shown in Fig. 1. Note that, in contrast with traditional tree-ring studies, the ring-width series were not detrended to account for ageing because ageing effects are explicitly simulated by our model.. Furthermore, we 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 cores145 and individual trees (Table 1).

146

Tree-ring series from the Southern Hemisphere are conventionally presented with annual increments attributed to the calendar year in which tree growth was initiated (Schulman, 1956). Although the longest record obtained dates from 1870 (Fig. 1), only three trees have pre-1920 records. Some early changes such as the step-like decrease and increase before 1920 are likely to be artifacts because of the small number of long records. For this reason, and because the climate data are also less reliable in the early decades of the 20th century, 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, [CO₂], 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 intrinsic quantum efficiency of photosynthesis (Collatz et al., 1998), and the effects of 163 164 photorespiration and substrate limitation at subsaturating [CO₂] represented as a function of 165 the leaf-internal [CO₂] and the photorespiratory compensation point. Leaf-internal [CO₂] is estimated from ambient [CO₂] via the least-cost hypothesis (Wright et al., 2003; Prentice et 166 167 al., 2014) as a function of atmospheric aridity (expressed as ΔE , the climatic moisture 168 deficit: difference between annual (estimated) actual evapotranspiration (Ea) and 169 equilibrium evapotranspiration (E_q)), air temperature and elevation. In the version used here, GPP is further multiplied by $\alpha^{1/4}$ (Cramer and Prentice, 1988). This correction has 170 been found empirically to account for the reduction in the light use efficiency of GPP at very 171 172 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 (Eucalyptus-dominated) vegetation as calculated from measurements made at the nearby 175 Credo flux station (C. Macfarlane, S. Prober, pers. comm. 2014: data processing by T.W. 176 177 Davis, pers. comm. 2014). The fractional cover of vegetation (trees, shrubs, grasses) is about 0.1, thus the simulated potential GPP of ca 1.5 mol m⁻² day⁻¹ at the peak is 178 179 consistent with flux-derived GPP, ca 0.15 mol m⁻² day⁻¹.

180

Modelled potential GPP was used as input to a species-based carbon allocation and 181 182 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 functional or geometric relationships between different dimensions of the tree, including 190 asymptotic height-diameter trajectories (Thomas, 1996; Ishii et al., 2000; Falster and 191 192 Westoby, 2005).

A full description of the coupled (PT) model is given in Li et al. (2014). The model was used to simulate the growth of *Pinus koraiensis* in a temperate, relatively moist site in the Changbai Mountains, China. Tree growth there is primarily constrained by growing-season PAR, which in turn is strongly influenced by cloud cover. When driven by local climate data and changing atmospheric [CO₂], the model produced a good representation of interannual 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 C₃ photosynthesis and has no adjustable parameters. The T model, in contrast, is species-specific and requires values for 13 parameters. Most of these 203 204 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 $(H_m: 9.58 \text{ m})$ were estimated using non-linear regression applied to the effective basal 210 diameter (D), tree height (H), and crown area ($A_{\rm C}$) measurements on these 146 trees. 211 Values for sapwood density ($\rho_{\rm S}$) and specific leaf area (σ) 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 (τ) were estimated from published measurements on *Callitris* species in other regions of 216 Australia.

218 No measurements were available for fine-root turnover time (τ r), fine-root specific 219 respiration rate $(r_{\rm f})$, sapwood-specific respiration rate $(r_{\rm S})$, and ratio of fine-root mass to 220 foliage area (ζ) 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 $[CO_2]$ varied realistically. $[CO_2]$ 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.

We examined correlations among the posterior parameter values using both Pearson correlation coefficients and principal components analysis. These analyses showed no correlation among estimates of fine-root turnover time (τ_r), fine-root specific respiration rate (r_r), and sapwood-specific respiration rate (r_s). However, the ratio of fine-root mass to foliage area (ζ) was correlated with fine root turnover time (0.69) and fine root respiration rate (-0.70). The calibration produced a shift in the median value for all four parameters (Fig. 2a) and a substantial reduction in uncertainty was obtained for ζ . The final parameter values used for all four variables lie within the range of measurements that have been made on other gymnosperms (Table 2).

243

244 **2.5 Climate inputs**

The P model requires inputs of daily temperature, precipitation, and fractional cloud cover, 245 246 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, Menzies) within 100 km of the GWW site, but none has records for all three variables 248 249 covering the whole interval sampled by the tree-ring series (i.e. 1920-2013). Thus, none of these local records can be used to drive the simulations. We therefore used monthly 250 251 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 gridded climate values with observed values from the three meteorological stations for all 258 259 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

values of interannual variability in precipitation at Menzies between 1901 and 2008 is 0.905 (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

We investigated the optimal interval influencing carbon accumulation and tree growth using ordinary least-squares multiple linear regression. Based on likely physiological constraints in a drought-controlled environment, we used total annual photosynthetically active radiation (PAR₀), VPD, and the ratio of actual to potential evapotranspiration (α) as independent variables in the regression and mean tree-ring width during the period from 1950-2013 as the dependent variable. (PAR₀ is defined as total incident PAR during the period with temperatures > 0°C, but for GWW this is the same as the total annual incident

289 PAR; we use the notation PAR₀ 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 derive the target mean tree-ring width. We defined the effective growing season as the 291 292 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 variable (p value) and the R^2 of the overall model. 296

297

The results from ordinary least-squares multiple linear regression analysis (Table 3) 298 showed that the best prediction of tree-ring width is obtained using an effective growing 299 300 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

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

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The model was run initially using values of the four poorly-known parameters calibrated to reproduce the mean ring-width for the period 1950-2012, with varying climate and [CO₂]. As a test of whether carbon allocation might plausibly have varied, we ran a second simulation in which the ratio of fine-root mass to foliage area (ζ) was calibrated using a spline fit to the mean ring-width during successive 30-year windows between 1920-2012, with a step of five years between windows and using appropriate [CO₂] 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 PAR₀ and soil moisture 335 availability (indexed by α) 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 PAR₀, α and VPD are statistically identical in the model and in the 340 data. The positive relationship with PAR₀ reflects the universal control of photosynthesis by 341 light availability, and the positive relationship with α 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 stomatal closure, with a correspondingly negative impact on photosynthesis and hence 344 345 carbon assimilation and growth.

Whereas the responses of modelled and measured ring-width to climate variables are quantitatively similar, there is a discrepancy in the response to [CO₂]. The data show no significant response (-0.0006 ± 0.0015 mm ppm⁻¹, p = 0.687) while the model shows a small but significant positive response (0.0011 ± 0.0004 mm ppm⁻¹, p = 0.004). The correlation between simulated and observed interannual variability (Fig. 2b) is not significant (r = 0.06, p = 0.571), reflecting an unrealistic simulated increase during recent decades. The root mean squared error (RMSE) of this simulation was 0.28 mm.

353

354 **3.2 Effects of increasing [CO₂] on tree-ring width and carbon allocation strategy**

Time-dependent calibration produced values of ζ that decreased by *ca* 6% from the beginning of the simulation to the 30-year interval centred on 1965, and subsequently increased by *ca* 12% by the 30-year interval centred on 1995 (Fig. 4). In other words, the values of ζ required to match the observations increased through the period when [CO₂] increased the most (*ca* 40 ppm, as compared to *ca* 12 ppm before 1965). GWW climate has also varied systematically during this period. The first principal component of multidecadal variability (based on 30-year means of standardized values of α , VPD and

PAR₀) explains 55% of the overall variance with loadings of -0.71 for both α and VPD and 362 363 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 α (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 ζ (Fig. 4). The simulation with time-varying values of ζ produced improved correlation (*r* = 0.60, *p* < 0.001) 367 368 with the tree-ring observations (Fig. 5), avoiding the systematic overestimation of ringwidths in recent years compared to observations that is seen in the simulation with 369 370 observed [CO₂] and fixed ζ (Fig. 2b). The RMSE of the modelled ring-widths was reduced 371 from 0.28 to 0.17 mm by allowing variation in ζ . 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 [CO₂].

378

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 record. Radial growth was positively related to PAR_0 and α , and negatively correlated with 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 α) separately influence radial growth. 391 Previous studies have shown that the growth of Callitris in southwestern Australia is controlled by precipitation (Sgherza et al., 2010), but there is only a weak correlation 392 393 between stable carbon isotope measurements and precipitation of the current year because Callitris has a strong water-conservation strategy. These findings are consistent with the 394 395 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 [CO₂] 399 increase of recent decades. The lack of a response to [CO₂] 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 growth of tropical trees (van der Sleen et al., 2015) showed an increase in water-use 402 403 efficiency, yet no stimulation of radial growth due to CO₂ fertilization over the past 150 404 years. The modelled response of ring-width to [CO₂] in our analysis was small compared with the responses to α , VPD and PAR₀ – as can be seen by comparing standardized 405 406 regression coefficients for the modelled ring-widths, which are three to six times smaller for [CO₂] than for the climate variables (Table 4). A modest shift in carbon allocation (towards 407

408 the production of fine roots, as implied by increasing ζ) 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 [CO₂] 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 in ζ might come about as a consequence of increased [CO₂]. FACE experiments are 415 416 equivocal about the impact of enhanced [CO₂] 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 [CO₂]. Our results do not support this reasoning, however, suggesting instead that the trees 423 may be allocating more below ground as [CO₂] 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 the T model. 426

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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 [CO₂]. 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 response to increasing [CO₂] in the simulations. If such changes in allocation occur in the 435 436 real world, then the observed stability in radial growth in recent decades does not mean that 437 GPP or NPP is unresponsive to [CO₂] (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).

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644 **Table and Figure Captions**

645

Table 1. Standard summary statistics for the tree-ring series. Values are given both for the period 1920-2012 and for the period post-1950, because there are only a limited number of 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 values were obtained from field measurements, or are generic. For those values estimated 650 651 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 measurements of sapwood specific respiration rate and for ratio of fine-root mass to foliage 657 658 area and we therefore give the individual measurements rather than a range for these 659 parameters.

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Table 3. Regression analysis of relationship between ring-width and climate parameters using different definitions of the effective growing season, based on the interval from 1950 to present. The dependent variable is mean ring-width. The independent variables are the total incident photosynthetically active radiation (PAR₀), vapour pressure deficit (VPD), and the ratio of actual to potential evapotranspiration (α). This analysis indicates that the optimum period contributing to tree growth is two years.

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Table 4. Regression analyses of simulated and observed response of tree growth to climate variables and CO₂. The dependent variable is mean radial growth series of the ten trees (from 1950 to 2012). The independent variables are the total incident photosynthetically active radiation (PAR₀), the ratio of actual to potential evapotranspiration (α), vapour pressure deficit (VPD) and monthly [CO₂]. Above: analysis based on untransformed variables. Middle: analysis based on standardized variables. Below: linear mixed model analysis based on standardized variables.

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

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Figure 2. a) Prior (dashed line) and posterior (solid line) probability distribution functions for fine-root turnover time (r_r), fine-root specific respiration rate (r_r), sapwood-specific respiration rate (r_s); ratio of fine-root mass to foliage area (ζ). b) Comparison between simulated and observed tree-ring widths, for the period 1920 to the present, using varying climate and [CO₂]. The black line is the mean of the observations, and the grey bars are the standard deviation (SD) among the ten individual trees sampled. The blue line and bars are the mean and standard deviation for the ten simulated individual trees.

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Figure 3. Simulated and observed response of tree radial growth to major climate variables
 and [CO₂]: partial residual plots based on the regression analysis, obtained using the *visreg*

package in R, are shown. The dependent variable is mean ring-width (from 1950 to 2012). The predictor variables are total incident photosynthetically active radiation (PAR₀), vapour pressure deficit (VPD), the ratio of actual to potential evapotranspiration (α), and monthly [CO₂].

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Figure 4. Time-dependent variation of the ratio of fine-root mass to foliage area (ζ) estimated by approximate Bayesian calibration. The graph shows the percentage change to the mean value of ζ for 30-year moving windows since 1920 (red), using the appropriate [CO₂] and α for each window. Values on the *x*-axis are plotted against the middle year of each 30-year window. Also shown are [CO₂] (grey) and the first principal component of the multidecadal variability in climate (α , VPD, PAR₀) (blue).

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Figure 5. Simulation of radial growth in response to changing climate and observed [CO₂], allowing for the effect of changing allocation to fine roots. The black line is the mean of the observations, and the grey bars are the standard deviation (SD) among the ten individual trees sampled. The blue line and bars are the mean and standard deviation for the ten simulated individual trees.

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

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

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

Parameter	Symbol	Uncertainty or range of values from literature	Source of information	Prior value	Posterior value	Accepted value	Reference
initial slope of height-diameter relationship (-)	а	41.35 ± 2.58	observation	-	-	41.35	-
initial ratio of crown area to stem cross-sectional area (-)	с	626.92 ± 20.03	observation	-	-	626.92	-
maximum tree height (m)	H_m	9.58 ± 1.11	observation	-	-	9.58	-
sapwood density (kg C m-3)	$ ho_s$	406 ± 32	observation	-	-	406	-
specific leaf area (m2 kg-1 C)	σ	5.16 ± 0.32	observation	-	-	5.16	-
leaf area index within the crown (–)	L	1.87 ± 0.18	species-specific literature value	-	-	1.87	Fieber et al., 2014
foliage turnover time (yr)	$ au_{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)	$ au_r$	0.76 ± 0.06	Bayesian parameter optimization	0.75 ± 0.5	1.00 ± 0.40	1.00	Yuan and Chen, 2010 (estimation for evergreen needleleaf trees)
fine-root specific respiration rate (yr-1)	r_r	1.36	Bayesian parameter optimization	1.36±1	1.23 ± 0.74	1.23	Burton and Prigitzer, 2002 (estimation from one- seeded Juniper)
sapwood specific respiration rate (yr-1)	r _s	0.5-10, 20 nmol mol–1 s–1	Bayesian parameter optimization	1 ± 0.75 nmol mol -1 s -1	$\begin{array}{c} 1.16 \pm 0.66 \\ nmol \ mol-1 \ s-1 \end{array}$	1.16 nmol mol-1 s-1 (0.034 yr-1)	Landsberg and Sands, 2010
ratio of fine-root mass to foliage area (kgC m-2)	ζ	1.0; 0.17	Bayesian parameter optimization	0.6 ± 0.5	0.150 ± 0.052	0.150	Burrows et al., 2001 (estimation for Callitris); White et al. (2000) (estimation for evergreen needleleaf tree)

Table 3. Regression analysis of relationship between ring-width and climate parameters using different definitions of the effective growing season, based on the interval from 1950 to present. The dependent variable is mean ring-width. The independent variables are the total incident photosynthetically active radiation (PAR₀), vapour pressure deficit (VPD), and the ratio of actual to potential evapotranspiration (α). This analysis indicates that the optimum period contributing to tree growth is two years.

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

731 Table 4. Regression analyses of simulated and observed response of tree growth to 732 climate variables and CO₂. The dependent variable is mean radial growth series of the ten trees (from 1950 to 2012). The independent variables are the total incident 733 734 photosynthetically active radiation (PAR₀), the ratio of actual to potential evapotranspiration (α), vapour pressure deficit (VPD) and monthly [CO₂]. Above: analysis 735 based on untransformed variables. Middle: analysis based on standardized variables. 736 737 Below: linear mixed model analysis based on standardized variables.

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		PAR ₀	a	VPD	CO ₂
Untransformed linear model		(mm (kmol	(mm)	(mm	(mm
		photon m ⁻²) ⁻¹)		hPa⁻¹)	ppm⁻¹)
	Estimation	0.709	1.734	-0.164	-0.001
Observation	Standard error	±0.246	±0.572	±0.059	±0.001
	<i>p</i> value	0.006	0.004	0.008	0.687
Simulation with	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	Estimation	0.622	2.221	-0.060	-0.001
time-dependent ζ	Standard error	±0.102	±0.224	±0.023	±0.001
and actual CO2	<i>p</i> value	<0.001	<0.001	0.014	0.113

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Standardized linear model		PAR ₀	α	VPD	CO ₂
	Estimation	0.095	0.085	-0.099	-0.011
Observation	Standard error	±0.033	±0.028	±0.036	±0.027
	<i>p</i> value	0.006	0.004	0.008	0.687
Simulation with	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	Estimation	0.088	0.110	-0.034	-0.017
time-dependent ζ	Standard error	±0.014	±0.011	±0.013	±0.011
and actual CO2	<i>p</i> value	<0.001	<0.001	0.014	0.113

Standardized linear mixed model		PAR ₀	α	VPD	CO ₂
	Estimation	0.096	0.089	-0.095	-0.013
Observation	Standard error	±0.034	±0.039	±0.039	±0.057
	<i>p</i> value	0.005	0.010	0.029	0.825
Simulation with	Estimation	0.090	0.110	-0.057	0.029
	Standard error	±0.006	±0.006	±0.008	±0.008
	<i>p</i> value	<0.001	<0.001	<0.001	0.019
Simulation with	Estimation	0.085	0.103	-0.050	-0.001
time-dependent ζ	Standard error	±0.009	±0.005	±0.007	±0.001
and actual CO2	<i>p</i> value	<0.001	<0.001	<0.001	1



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



Figure 2. a) Prior (dashed line) and posterior (solid line) probability distribution function for fine-root turnover time (τ_r), fine-root specific respiration rate (r_r), sapwood-specific respiration rate (r_s); ratio of fine-root mass to foliage area (ζ). b) Comparison between simulated and observed tree-ring widths, for the period 1920 to the present, using varying climate and [CO₂]. The black line is the mean of the observations, and the grey bars are

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



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Figure 3. Simulated and observed responses of tree radial growth to climate variables and [CO₂]: partial residual plots based on the regression analysis, obtained using the *visreg* package in R, are shown. The dependent variable is mean ring-width (from 1950 to 2012). The predictor variables are annual incident photosynthetically active radiation (PAR₀), vapour pressure deficit (VPD), the ratio of actual to potential evapotranspiration (α), and monthly [CO₂].



Figure 4. Time-dependent variation of the ratio of fine-root mass to foliage area (ζ) estimated by approximate Bayesian calibration. The graph shows the percentage change to the mean value of ζ for 30-year moving windows since 1920 (red), using the appropriate [CO₂] and α for each window. Values on the *x*-axis are plotted against the middle year of each 30-year window. Also shown are [CO₂] (grey) and the first principal component of the multidecadal variability in climate (α , VPD, PAR₀) (blue).



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Figure 5. Simulation of radial growth in response to changing climate and observed [CO₂], allowing for the effect of changing allocation to fine roots. The black line is the mean of the observations, and the grey bars are the standard deviation (SD) among the ten individual trees sampled. The blue line and bars are the mean and standard deviation for the ten simulated individual trees.