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A model analysis of climate and CO$_2$ controls on tree growth and carbon allocation in a semi-arid woodland

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Abstract

Many studies have failed to show an increase in the radial growth of trees in response to increasing atmospheric CO$_2$ concentration [CO$_2$] despite the expected enhancement of photosynthetic rates and water-use efficiency at high [CO$_2$]. A global light use efficiency model of photosynthesis, coupled with a generic carbon allocation and tree-growth model based on mass balance and tree geometry principals, was used to simulate annual ring-width variations for the gymnosperm Callitris columellaris in the semi-arid Great Western Woodlands, Western Australia, over the past 100 years. Parameter values for the tree-growth model were derived from independent observations except for sapwood specific
respiration rate, fine-root turnover time, fine-root specific respiration rate and the ratio of
fine-root mass to foliage area (ζ), which were calibrated to the ring-width measurements by
approximate Bayesian calibration. This procedure imposed a strong constraint on ζ.
Modelled and observed ring-widths showed quantitatively similar, positive responses to
total annual photosynthetically active radiation and soil moisture, and similar negative
responses to vapour pressure deficit. The model also produced enhanced radial growth in
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
values of ζ, including an increase by ca 12% since the 1960s, and eliminated the [CO₂]-
induced increase in radial growth. The potential effect of CO₂ on ring-width was thus shown
to be small compared to effects of climate variability even in this semi-arid climate. It could
be counteracted in the model by a modest allocation shift, as has been observed in field
experiments with raised [CO₂].

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

Introduction
Atmospheric CO₂ concentration [CO₂] has direct impacts on the photosynthesis and water-
use 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 well-
watered temperate and tropical regions have failed to show increases that might be
attributed to increasing [CO₂] (Kienast and Luxmoore, 1988; Gedalof and Berg, 2010;
Moreover, tree-growth modelling (Boucher et al., 2014; Li et al., 2014) has suggested that the expected radial growth enhancement due to the recent [CO$_2$] increase is quite small, compared to the effects of climate variability. A stronger response to enhanced [CO$_2$] might be expected a priori in water-limited regions (Field et al., 1983; Hyvönen et al., 2007), because stomatal conductance is reduced when [CO$_2$] is higher. This is a common empirical observation, 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 [CO$_2$] as [CO$_2$] increases – while the rate of increase of photosynthesis with [CO$_2$] declines. Failure to sample water-limited environments might thus conceivably explain the apparent lack of increased stem growth in response to increasing [CO$_2$].

An alternative explanation could be that increased primary production due to increased [CO$_2$] has not led to increased stem growth due to a shift in carbon allocation away from stems. There is some experimental evidence that changing [CO$_2$] results in changes in carbon allocation between above-ground (leaf, stem) and below-ground (root) biomass pools. Observations of the response to high [CO$_2$] in Free-Air Carbon dioxide Enrichment (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 Ridge FACE: Norby et al., 2004; DUKE-FACE: DeLucia et al., 1999; Pritchard et al., 2008; Rhinelander ASPEN-FACE: King et al., 2001; EUROFACE: Calfapietra et al., 2003; Lukac et al., 2003; Bangor FACE: Smith et al., 2013). In some sites, this increase is clearly at the expense of stem growth (Battipaglia et al., 2013). However, monitoring of below-ground carbon dynamics is challenging and there are no direct, long-term observations of the response of below-ground allocation to gradually increasing [CO$_2$] 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 [CO$_2$] on ring-width, in addition to effects of climate variability.

2 Methods

2.1 The study area

The GWW, with an area of about 160,000 km$^2$, is the largest remaining area of intact mediterranean woodland on Earth (Watson, 2008; Lee et al., 2013). The region is unique 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 GWW is dominated by open eucalypt woodlands, with patches of heathland, mallee and grassland. The climate is characterized by winter rainfall and summer drought, although 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 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 the GWW, with a mean annual rainfall ca 270 mm. The area around the GWW SuperSite is 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.

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

### 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*
**columellaris** was the only woody species present, for sampling. Although the basic measurements required to characterize tree growth (see 2.4) were made on all the trees in the plot (146 individuals), tree-ring cores were obtained from only ten of these trees (Fig. 1). The sampling was carried out in August 2013. The selected trees were canopy trees, with a 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 sign of disturbance. Other environmental conditions (topography, soil type, soil depth) showed no visible variation among the sampled trees. Multiple cores were obtained from each tree, taking care to sample each of the individual stems of each tree. A total of 32 tree ring cores were obtained.

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

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

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.
Nevertheless, there is reasonable coherency between the records from the individual cores and individual trees (Table 1).

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.

2.3 The tree-growth model

We used a generic light-use efficiency model (the P model, Wang et al., 2014) to simulate gross primary production (GPP). Wang et al. (2014) demonstrated the model’s ability to reproduce global geographic and seasonal patterns in GPP derived from flux measurements. Potential GPP (the GPP that would be predicted if all incident PAR were absorbed) is calculated in the model from latitude, elevation, [CO2], and monthly temperature, precipitation, and fractional cloud cover. It depends on the PAR incident on 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 photorespiration and substrate limitation at subsaturating [CO2] represented as a function of 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 al., 2014) as a function of atmospheric aridity (expressed as ΔE, the climatic moisture
deficit: difference between annual (estimated) actual evapotranspiration ($E_a$) and 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 been found empirically to account for the reduction in the light use efficiency of GPP at very low soil moisture content, observed in flux measurements from regions with an intense dry season. The P model produces a seasonal cycle of simulated potential GPP at GWW with a 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 Credo flux station (C. Macfarlane, S. Prober, pers. comm. 2014; data processing by T.W. 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 consistent with flux-derived GPP, ca 0.15 mol m$^{-2}$ day$^{-1}$.

Modelled potential GPP was used as input to a species-based carbon allocation and functional geometric tree-growth model (the T model: Li et al., 2014) to simulate tree growth. In the T model, the fraction of incident PAR absorbed by the canopy (fAPAR) is estimated from the leaf area index within the canopy and used to convert potential to actual GPP using Beer’s law (Jarvis and Leverenz, 1983). Annual net primary production (NPP) is then derived from annual GPP, corrected for foliage respiration, by deducting growth respiration (proportional to NPP) and the maintenance respiration of sapwood and fine roots. NPP is allocated to stem, foliage and fine-root increments, foliage turnover and fine-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 asymptotic height-diameter trajectories (Thomas, 1996; Ishii et al., 2000; Falster and 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.

### 2.4 Derivation of model parameter values

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 could be obtained from measurements made at the sampling site, or from the literature (Table 2). Stem basal diameter, tree height and crown area were measured on 146 trees at the site. The measurements were made on all *Callitris* trees within the 500 m x 500 m plot. Parameter values for the initial slope of the height–diameter relationship (a: 41.35), the initial ratio of crown area to stem cross-sectional area (c: 626.92), and maximum tree height (Hₘ: 9.58 m) were estimated using non-linear regression applied to the effective basal diameter (D), tree height (H), and crown area (A₉) measurements on these 146 trees. Values for sapwood density (ρₛ) and specific leaf area (σ) were derived from five measurements made at the sampling site (Table 2). We used generic values for the extinction coefficient (k) for photosynthetically active radiation (PAR) and yield factor (γ), from the literature (Table 2). Leaf area index within the crown (L) and foliage turnover time (τᵢ) were estimated from published measurements on *Callitris* species in other regions of Australia.
No measurements were available for fine-root turnover time ($\tau_r$), fine-root specific respiration rate ($r_f$), sapwood-specific respiration rate ($r_s$), and ratio of fine-root mass to foliage area ($\zeta$) in *Callitris*, and these were not measured in the field. But their values can have a substantial impact on simulated radial growth, and on the shape of the simulated ontogenetic ageing curve (Li et al., 2014). We used approximate Bayesian parameter calibration (van der Vaart et al., 2015) to derive mutually consistent values of these four parameters. The calibration target was mean ring-width during the period 1950-2012 and the posterior was constructed by sampling the joint parameter distribution 1,000,000 times and retaining the values of the 1000 samples that most closely matched the calibration target (van der Vaart et al., 2015). A constraint was imposed to ensure that there were no negative growth rates of any model component. Calibration was performed using simulations in which climate and $[\text{CO}_2]$ varied realistically. $[\text{CO}_2]$ data were obtained by splicing ice-core records for the interval from 1901 to 1957 (Etheridge et al., 1996; MacFarling Meure et al., 2006) with the annual average of direct atmospheric measurements from Mauna Loa and the South Pole stations from 1958 to 2013:

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 ($\tau_r$), fine-root specific respiration rate ($r_f$), and sapwood-specific respiration rate ($r_s$). However, the ratio of fine-root mass to foliage area ($\zeta$) 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 $\zeta$. The final parameter
values used for all four variables lie within the range of measurements that have been
made on other gymnosperms (Table 2).

2.5 Climate inputs

The P model requires inputs of daily temperature, precipitation, and fractional cloud cover,
which are generally obtained by linear interpolation of monthly values of these variables
(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
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
temperature, precipitation, and cloud cover fraction for the interval 1920 onwards from the
CRU TS v3.22 data set (Harris et al., 2014), using values of these variables for the single
grid cell (30.25°S, 120.75°E) from CRU TS v3.22 in which the sampling site lies. The CRU
climate is derived using a distance-weighted interpolation from all available meteorological
records and has been homogenized to remove any impacts from using information for
individual climate variables from different stations or from different numbers of stations
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
overlapping intervals for each variable; in the case of solar radiation/cloud cover this was
very short (post-1990 only). There is generally good agreement between the gridded
monthly (and annual) temperature and precipitation data and meteorological station data
with respect to long-term means, interannual variability and trends. The correlation between
the gridded and observed values of interannual variability in temperature at Kalgoorlie post-
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 ($p < 0.001$).

### 2.6 Definition of the effective growing season

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

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 ($\text{PAR}_0$), VPD, and the ratio of actual to potential evapotranspiration ($\alpha$) as independent variables in the regression and mean tree-ring width during the period from 1950-2013 as the dependent variable. ($\text{PAR}_0$ 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
PAR; we use the notation PAR\(_0\) for consistency with other work using the P and T models.)

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 period from January to December in the current growth year, and then extended the interval by six-month steps for a period up to three years. In these latter analyses, each six-month period contributes equally to the carbon available for growth. The goodness-of-fit of each 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.

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

### 2.7 Application of the Model

Each tree was initialized with its actual effective single-stemmed basal diameter in the first 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.

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 [CO$_2$]. 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 ($\zeta$) 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 [CO$_2$] and climate for each window.

3 Results

3.1 Baseline simulation of ring-width versus observations

The T model generally captured the amplitude of Callitris tree growth variations (Fig. 2b). The mean simulated ring-width for the period 1950-2012 was 0.840 mm, compared to an observed value of 0.753 mm. The standard deviation (SD) in mean ring-width (0.197 mm) was underestimated compared to the observed SD (0.215 mm). This difference probably reflects the impact of local variability in environmental conditions on individual tree growth, not accounted for in the model. Regression analysis (Fig. 3, Table 4) showed that tree growth has a strongly positive, independent response to both PAR$_0$ and soil moisture availability (indexed by $\alpha$) and a negative response to VPD ($p < 0.01$). (Similar relationships are obtained using a linear mixed-effect model to account for autocorrelation between
replicates and temporally: Table 4). These relationships are captured in the simulations. Although there is more scatter in the observations, the slopes of the observed and simulated responses to PAR0, α and VPD are statistically identical in the model and in the data. The positive relationship with PAR0 reflects the universal control of photosynthesis by light availability, and the positive relationship with α is consistent with observations that the growth of Callitris is strongly influenced by precipitation variability (Ash, 1983; Cullen and Grierson, 2009). VPD affects stomatal conductance such that increasing VPD leads to stomatal closure, with a correspondingly negative impact on photosynthesis and hence 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.

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 0.00 for PAR. The second principal component explains a further 44% of the variance and is related primarily to PAR (-0.87) and secondarily to α (0.36) and VPD (-0.35). The changes in PAR, however, are small (ca 2%) and thus the impact of increasing moisture 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 \((r = 0.60, p < 0.001)\) with the tree-ring observations (Fig. 5), avoiding the systematic overestimation of ring-widths in recent years compared to observations that is seen in the simulation with observed [CO₂] and fixed ζ (Fig. 2b). The RMSE of the modelled ring-widths was reduced from 0.28 to 0.17 mm by allowing variation in ζ. The remaining discrepancies between simulated and observed ring widths probably reflect simplifications in the modelling approach, most particularly with respect to carbon carryover between years and the use of an average value for wood density. However, the progressive nature of the changes in below-ground allocation coupled with the overall improvement in the simulations both indicate that it is plausible that changes in allocation play a role in the response to increasing [CO₂].

4 Discussion and Conclusions

The dependencies of Callitris columellaris radial growth on climate at GWW could be simulated by coupling a generic model of GPP (P) with a model of carbon allocation and functional geometric tree growth (T), using species-specific parameter values in T. Model performance was not adversely affected by the reduction in winter precipitation, and the shift to less frequent but more intense precipitation events, that occurred in latter part of the
Radial growth was positively related to PAR₀ and α, and negatively correlated with VPD, with similar quantitative dependencies shown in the data and in the model.

The response to VPD can be explained as a consequence of the atmospheric control on stomatal conductance and hence photosynthesis. Thus, both atmospheric and soil moisture deficits (the former indexed by VPD, the latter by α) separately influence radial growth. 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 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 observed response to VPD and further support our use of a two-year period contributing to carbon accumulation and growth.

The radial growth of Callitris columellaris in the GWW has not responded to the [CO₂] increase of recent decades. The lack of a response to [CO₂] has been a feature of other quantitative studies of tree growth (e.g. Kienast and Luxmoore, 1988; Archer et al., 1995; 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 efficiency, yet no stimulation of radial growth due to CO₂ fertilization over the past 150 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 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
the production of fine roots, as implied by increasing $\zeta$) would be sufficient to reconcile the
modelled increase in GPP with the lack of any observed increase in ring-width.

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

 Appropriately analysed, tree-ring records worldwide should yield consistent information
about the diverse responses of tree growth and allocation to environmental change. Here,
with the use of a simple process-based model of tree growth, we have explored the
potential for changes in the proportion of above- and below-ground allocation to explain the
lack of evidence for increased radial growth in response to recent increases in [CO₂]. A noteworthy feature of our study is that a relatively minor change in the relative allocation of 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 real world, then the observed stability in radial growth in recent decades does not mean that GPP or NPP is unresponsive to [CO₂] (whether through nutrient limitation, sink limitation or any other mechanism). There are a number of potential sources of uncertainty in our modelling approach, including the representation of aging trends and of the importance of the carry-over of non-structural carbohydrates between growing seasons. Nevertheless, our results support the idea that above-ground biomass production and radial growth are sensitive to environmental effects on carbon allocation. This is important because the influence of environmental conditions on allocation are neglected by most current ecosystem models (De Kauwe et al., 2014).

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Table and Figure Captions

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.

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.

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.
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.

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 functions for fine-root turnover time (τᵣ), fine-root specific respiration rate (rᵣ), sapwood-specific respiration rate (rₛ); 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.

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 (PAR\textsubscript{0}), vapour pressure deficit (VPD), the ratio of actual to potential evapotranspiration (\(\alpha\)), and monthly [CO\textsubscript{2}].

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

Figure 5. Simulation of radial growth in response to changing climate and observed [CO\textsubscript{2}], 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.
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.

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

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Symbol</th>
<th>Uncertainty or range of values from literature</th>
<th>Source of information</th>
<th>Prior value</th>
<th>Posterior value</th>
<th>Accepted value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>initial slope of height-diameter relationship (--)</td>
<td>$a$</td>
<td>$41.35 \pm 2.58$</td>
<td>observation</td>
<td>-</td>
<td>-</td>
<td>41.35</td>
<td>-</td>
</tr>
<tr>
<td>initial ratio of crown area to stem cross-sectional area (--)</td>
<td>$c$</td>
<td>$626.92 \pm 20.03$</td>
<td>observation</td>
<td>-</td>
<td>-</td>
<td>626.92</td>
<td>-</td>
</tr>
<tr>
<td>maximum tree height (m)</td>
<td>$H_u$</td>
<td>$9.58 \pm 1.11$</td>
<td>observation</td>
<td>-</td>
<td>-</td>
<td>9.58</td>
<td>-</td>
</tr>
<tr>
<td>sapwood density (kg C m-3)</td>
<td>$\rho_s$</td>
<td>$406 \pm 32$</td>
<td>observation</td>
<td>-</td>
<td>-</td>
<td>406</td>
<td>-</td>
</tr>
<tr>
<td>specific leaf area (m2 kg-1 C)</td>
<td>$\sigma$</td>
<td>$5.16 \pm 0.32$</td>
<td>observation</td>
<td>-</td>
<td>-</td>
<td>5.16</td>
<td>-</td>
</tr>
<tr>
<td>leaf area index within the crown (--)</td>
<td>$L$</td>
<td>$1.87 \pm 0.18$</td>
<td>species-specific literature value</td>
<td>-</td>
<td>-</td>
<td>1.87</td>
<td>Fieber et al., 2014</td>
</tr>
<tr>
<td>foliage turnover time (yr)</td>
<td>$\tau_f$</td>
<td>$2.58$</td>
<td>species-specific literature value</td>
<td>-</td>
<td>-</td>
<td>2.58</td>
<td>Wright and Westoby, 2002</td>
</tr>
<tr>
<td>PAR turnover coefficient (--)</td>
<td>$k$</td>
<td>$0.48-0.58$</td>
<td>generic value</td>
<td>-</td>
<td>-</td>
<td>0.5</td>
<td>Pierce and Running, 1988</td>
</tr>
<tr>
<td>yield factor (--)</td>
<td>$\gamma$</td>
<td>$0.5-0.7$</td>
<td>generic value</td>
<td>-</td>
<td>-</td>
<td>0.6</td>
<td>Zhang et al., 2009</td>
</tr>
<tr>
<td>fine-root turnover time (yr)</td>
<td>$\tau_r$</td>
<td>$0.76 \pm 0.06$</td>
<td>Bayesian parameter optimization</td>
<td>$0.75 \pm 0.5$</td>
<td>$1.00 \pm 0.40$</td>
<td>1.00</td>
<td>Yuan and Chen, 2010 (estimation for evergreen needleleaf trees)</td>
</tr>
<tr>
<td>fine-root specific respiration rate (yr-1)</td>
<td>$r_{r_f}$</td>
<td>$1.36$</td>
<td>Bayesian parameter optimization</td>
<td>$1.36 \pm 1$</td>
<td>$1.23 \pm 0.74$</td>
<td>1.23</td>
<td>Burton and Frigiter, 2002 (estimation from one-seeded Juniper)</td>
</tr>
<tr>
<td>sapwood specific respiration rate (yr-1)</td>
<td>$r_s$</td>
<td>$0.5-10.20$ nmol mol$^{-1}$ s$^{-1}$</td>
<td>Bayesian parameter optimization</td>
<td>$1 \pm 0.75$ nmol mol$^{-1}$ s$^{-1}$</td>
<td>$1.16 \pm 0.66$ nmol mol$^{-1}$ s$^{-1}$</td>
<td>$1.16$ nmol mol$^{-1}$ s$^{-1}$ (0.034 yr$^{-1}$)</td>
<td>Landsberg and Sands, 2010</td>
</tr>
<tr>
<td>ratio of fine-root mass to foliage area (kgC m-2)</td>
<td>$\zeta$</td>
<td>$1.0; 0.17$</td>
<td>Bayesian parameter optimization</td>
<td>$0.6 \pm 0.5$</td>
<td>$0.150 \pm 0.052$</td>
<td>$0.150$</td>
<td>Burrows et al., 2001 (estimation for Calitris); White et al. (2000) (estimation for evergreen needleleaf tree)</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Formation year</th>
<th>PAR₀ (mm (kmol photon m⁻²)⁻¹)</th>
<th>VPD (mm hPa⁻¹)</th>
<th>α (mm)</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Estimation</td>
<td>0.48</td>
<td>−0.11</td>
<td>0.8</td>
<td>0.184</td>
</tr>
<tr>
<td>Standard error</td>
<td>± 0.20</td>
<td>± 0.04</td>
<td>± 0.4</td>
<td></td>
</tr>
<tr>
<td>p value</td>
<td>0.020</td>
<td>0.016</td>
<td>0.069</td>
<td></td>
</tr>
<tr>
<td>Calendar year</td>
<td>Estimation</td>
<td>0.43</td>
<td>−0.06</td>
<td>0.6</td>
</tr>
<tr>
<td>Standard error</td>
<td>± 0.20</td>
<td>± 0.04</td>
<td>± 0.6</td>
<td></td>
</tr>
<tr>
<td>p value</td>
<td>0.039</td>
<td>0.171</td>
<td>0.266</td>
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</tr>
<tr>
<td>1.5 Calendar years</td>
<td>Estimation</td>
<td>0.68</td>
<td>−0.14</td>
<td>1.4</td>
</tr>
<tr>
<td>Standard error</td>
<td>± 0.22</td>
<td>± 0.05</td>
<td>± 0.5</td>
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<tr>
<td>p value</td>
<td>0.004</td>
<td>0.007</td>
<td>0.009</td>
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<tr>
<td>2 Calendar years</td>
<td>Estimation</td>
<td>0.70</td>
<td>−0.17</td>
<td>1.7</td>
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<tr>
<td>Standard error</td>
<td>± 0.24</td>
<td>± 0.05</td>
<td>± 0.5</td>
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<tr>
<td>p value</td>
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<td>0.002</td>
<td>0.003</td>
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<tr>
<td>2.5 Calendar years</td>
<td>Estimation</td>
<td>0.67</td>
<td>−0.16</td>
<td>1.7</td>
</tr>
<tr>
<td>Standard error</td>
<td>± 0.27</td>
<td>± 0.06</td>
<td>± 0.6</td>
<td></td>
</tr>
<tr>
<td>p value</td>
<td>0.017</td>
<td>0.010</td>
<td>0.009</td>
<td></td>
</tr>
<tr>
<td>3 Calendar years</td>
<td>Estimation</td>
<td>0.94</td>
<td>−0.20</td>
<td>2.0</td>
</tr>
<tr>
<td>Standard error</td>
<td>± 0.29</td>
<td>± 0.07</td>
<td>± 0.7</td>
<td></td>
</tr>
<tr>
<td>p value</td>
<td>0.002</td>
<td>0.004</td>
<td>0.004</td>
<td></td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Untransformed linear model</th>
<th>PAR₀ (mm (kmol photon m⁻²)⁻¹)</th>
<th>α (mm)</th>
<th>VPD (mm hPa⁻¹)</th>
<th>CO₂ (mm ppm⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Observation</td>
<td>Estimation</td>
<td>0.709</td>
<td>1.734</td>
<td>-0.164</td>
</tr>
<tr>
<td></td>
<td>Standard error</td>
<td>±0.246</td>
<td>±0.572</td>
<td>±0.059</td>
</tr>
<tr>
<td></td>
<td>p value</td>
<td>0.006</td>
<td>0.004</td>
<td>0.008</td>
</tr>
<tr>
<td>Simulation with actual CO₂</td>
<td>Estimation</td>
<td>0.762</td>
<td>2.308</td>
<td>-0.096</td>
</tr>
<tr>
<td></td>
<td>Standard error</td>
<td>±0.059</td>
<td>±0.137</td>
<td>±0.014</td>
</tr>
<tr>
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<td>p value</td>
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<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Simulation with time-dependent ζ and actual CO₂</td>
<td>Estimation</td>
<td>0.622</td>
<td>2.221</td>
<td>-0.060</td>
</tr>
<tr>
<td></td>
<td>Standard error</td>
<td>±0.102</td>
<td>±0.224</td>
<td>±0.023</td>
</tr>
<tr>
<td></td>
<td>p value</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.014</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Standardized linear model</th>
<th>PAR₀</th>
<th>α</th>
<th>VPD</th>
<th>CO₂</th>
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</thead>
<tbody>
<tr>
<td>Observation</td>
<td>Estimation</td>
<td>0.095</td>
<td>0.085</td>
<td>-0.099</td>
</tr>
<tr>
<td></td>
<td>Standard error</td>
<td>±0.033</td>
<td>±0.028</td>
<td>±0.036</td>
</tr>
<tr>
<td></td>
<td>p value</td>
<td>0.006</td>
<td>0.004</td>
<td>0.008</td>
</tr>
<tr>
<td>Simulation with actual CO₂</td>
<td>Estimation</td>
<td>0.102</td>
<td>0.113</td>
<td>-0.058</td>
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<tr>
<td></td>
<td>Standard error</td>
<td>±0.008</td>
<td>±0.007</td>
<td>±0.008</td>
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<td>p value</td>
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<td>&lt;0.001</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Simulation with time-dependent ζ and actual CO₂</td>
<td>Estimation</td>
<td>0.088</td>
<td>0.110</td>
<td>-0.034</td>
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<tr>
<td></td>
<td>Standard error</td>
<td>±0.014</td>
<td>±0.011</td>
<td>±0.013</td>
</tr>
<tr>
<td></td>
<td>p value</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.014</td>
</tr>
<tr>
<td>Standardized linear mixed model</td>
<td>PAR_0</td>
<td>α</td>
<td>VPD</td>
<td>CO₂</td>
</tr>
<tr>
<td>---------------------------------</td>
<td>-------</td>
<td>------</td>
<td>------</td>
<td>-------</td>
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<tr>
<td><strong>Observation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estimation</td>
<td>0.096</td>
<td>0.089</td>
<td>−0.095</td>
<td>−0.013</td>
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<tr>
<td>Standard error</td>
<td>±0.034</td>
<td>±0.039</td>
<td>±0.039</td>
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<td>p value</td>
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<td>0.010</td>
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<td>0.825</td>
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<td><strong>Simulation with actual CO₂</strong></td>
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</tr>
<tr>
<td>Estimation</td>
<td>0.090</td>
<td>0.110</td>
<td>−0.057</td>
<td>0.029</td>
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<td>Standard error</td>
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<td>±0.006</td>
<td>±0.008</td>
<td>±0.008</td>
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<tr>
<td>p value</td>
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<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>0.019</td>
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<tr>
<td><strong>Simulation with</strong></td>
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<tr>
<td>time-dependent ζ and actual CO₂</td>
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<td></td>
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<tr>
<td>Estimation</td>
<td>0.085</td>
<td>0.103</td>
<td>−0.050</td>
<td>−0.001</td>
</tr>
<tr>
<td>Standard error</td>
<td>±0.009</td>
<td>±0.005</td>
<td>±0.007</td>
<td>±0.001</td>
</tr>
<tr>
<td>p value</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
<td>&lt;0.001</td>
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</table>
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 ($\tau_r$), fine-root specific respiration rate ($r_r$), sapwood-specific respiration rate ($r_s$); ratio of fine-root mass to foliage area ($\zeta$). b) Comparison between simulated and observed tree-ring widths, for the period 1920 to the present, using varying climate and [CO$_2$]. The black line is the mean of the observations, and the grey bars are
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Figure 3. Simulated and observed responses of tree radial growth to climate variables and [CO$_2$]: 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 (PAR$_0$), vapour pressure deficit (VPD), the ratio of actual to potential evapotranspiration ($\alpha$), and monthly [CO$_2$].
Figure 4. Time-dependent variation of the ratio of fine-root mass to foliage area ($\zeta$) estimated by approximate Bayesian calibration. The graph shows the percentage change to the mean value of $\zeta$ for 30-year moving windows since 1920 (red), using the appropriate [CO$_2$] and $\alpha$ for each window. Values on the $x$-axis are plotted against the middle year of each 30-year window. Also shown are [CO$_2$] (grey) and the first principal component of the multidecadal variability in climate ($\alpha$, VPD, PAR$_0$) (blue).
Figure 5. Simulation of radial growth in response to changing climate and observed [CO$_2$], 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.