

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

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

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Abstract

We used a light-use efficiency model of photosynthesis coupled with a dynamic carbon allocation and tree-growth model to simulate annual growth of the gymnosperm *Callitris columellaris* in the semi-arid Great Western Woodlands, Western Australia, over the past 100 years. Parameter values 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, which were estimated by Bayesian optimization. The model reproduced the general pattern of interannual variability in radial growth (tree-ring width), including the response to the shift in precipitation regimes that occurred in the 1960s. Simulated and observed responses to climate were consistent. Both showed a significant positive response of tree-ring width to total photosynthetically active radiation received and to the ratio of modeled actual to equilibrium evapotranspiration, and a significant negative response to vapour pressure deficit. However, the simulations showed an enhancement of radial growth in response to increasing atmospheric CO₂ concentration (ppm) ([CO₂]) during recent decades that is not present in the observations. The discrepancy disappeared when the model was recalibrated on successive 30-year windows. Then the ratio of fine-root mass to foliage area increases by 14 % (from 0.127 to 0.144 kg C m⁻²) as [CO₂] increased while the other three estimated parameters remained constant. The absence of a signal of increasing [CO₂] has been noted in many tree-ring records, despite the enhancement of photosynthetic rates and water-use efficiency resulting from increasing [CO₂]. Our simulations suggest that this behaviour could be explained as a consequence of a shift towards below-ground carbon allocation.

1 Introduction

The Great Western Woodlands (GWW) in southwestern Western Australia, with an area of about 160 000 km², is the largest remaining area of intact Mediterranean

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woodland on Earth (Watson, 2008; Lee et al., 2013). The GWW region is unique because of the diversity of large trees that grow there, despite the dry climate and nutrient-poor sandy soils (Watson, 2008; Prober et al., 2012).

The southwest region of Western Australia has experienced a multidecadal drought since the mid-1970s (Ansell et al., 2000; Cai and Cowan, 2006; Hope et al., 2006), characterized by a substantial reduction in winter rainfall. This change is consistent with a poleward shift in the mid-latitude storm track (Smith et al., 2000; Frederiksen and Frederiksen, 2007) and a reduction in the frequency of synoptic events and the associated amount of winter precipitation, coupled with an increase in the intensity of individual rainfall events (Hope et al., 2006). These changes are projected to continue under global warming (Yin, 2005; Hope, 2006). They have been variously linked to changes in the Indian Ocean dipole (Smith et al., 2000; England et al., 2006), in Antarctic climate (van Ommen and Morgan, 2010) and ultimately to changes in the Southern Annular Mode (Cai and Cowan, 2006; Hendon et al., 2007; Meneghini et al., 2007; Feng et al., 2010).

These regional changes in climate are also reflected in the GWW. At the GWW Supersite at Credo (30.1° S, 120.7° E), mean annual temperature has increased significantly in the last 100 years (0.139 ± 0.015 °C decade⁻¹, $p < 0.001$). There has been no trend in annual precipitation, but the number of rain days has decreased significantly since the middle of last century, especially after 1960 (-6.16 day decade⁻¹, $p < 0.001$); and the mean precipitation on rain days (i.e. precipitation intensity) has increased (0.38 mm decade⁻¹, $p < 0.001$). The interannual variability of annual precipitation has also increased (72.8 and 81.7 mm for the standard deviation (SD) of annual precipitation before and after 1960 respectively). These changes were expected to have had a significant impact on tree growth in the GWW.

It remains unclear whether the changes in climate in southwestern Western Australia are anthropogenic (Pitman et al., 2004; Cai and Cowan, 2006). However, the observed increase in [CO₂] has direct impacts on photosynthesis and the water-use efficiency of trees (Drake et al., 1997). Model studies have suggested that the impact of [CO₂]

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on the radial stem growth is limited (Boucher et al., 2014; Li et al., 2014) and this is supported by tree-ring studies (Kienast and Luxmoore, 1988; Gedalof and Berg, 2010; van der Sleen et al., 2015). However, the previous modelling studies were conducted in regions where tree growth is limited by temperature, rather than moisture availability and its seasonal distribution. A stronger response to enhanced [CO₂] might be expected a priori in water-limited regions (Field et al., 1983; Hyvönen et al., 2007), such as the GWW, because of the known increase in water-use efficiency caused by rising [CO₂].

In this study, we demonstrate that the radial growth of the gymnosperm *Callitris columellaris* in the GWW can be simulated using a light-use efficiency model of photosynthesis coupled with a dynamic allocation and tree-growth model. We then use this model to explore the impact of changes in climate and [CO₂] on tree growth under water-limited conditions.

2 Methods

2.1 The study area

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 the monsoonal penetration into the continental interior can also bring occasional rains in summer (Sturman et al., 1996). The sampling site (GWW Super Site, Credo, 30.1° S, 120.7° E, 400 m a.s.l.) lies in the northernmost and driest part of the GWW (Fig. 1). This area 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 understorey. Human impact on the landscape is minimal.

2.2 Tree ring data

The genus *Callitris* has been shown to provide a good record of annual tree growth in a wide variety of climates across Australia (Ash, 1983; Cullen and Grierson, 2007, 2009; Baker et al., 2008; Cullen et al., 2008). Tree-ring cores were obtained from ten *Callitris* trees in August 2013. The selected trees were canopy trees and not overshadowed by other individuals. Other environmental conditions (e.g. soil depth) showed no obvious variation between 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. Measurements of annual growth were made on each core. Visual cross-dating and 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 (δ_i) and individual-stem diameter increments ($d(\delta_i)/dt$) by:

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

The effective annual growth measured at the study site is shown in Fig. 2. 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 tree-ring record obtained dates from 1870 (Fig. 2), only three trees have pre-1920 records. We therefore focus on the interval from 1920 to 2013.

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2.3 The tree growth model

We used a light-use efficiency model (the P model: Wang et al., 2014) to simulate gross primary production (GPP), which is then 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. The P model simulates GPP per unit of absorbed PAR using data on latitude, elevation, [CO₂] and monthly temperature, precipitation, and fractional cloud cover (Wang et al., 2014).

The potential GPP per unit of absorbed PAR as predicted by the P model depends on the PAR incident on the vegetation canopy during the growing season (temperature above 0°C), the intrinsic quantum efficiency of photosynthesis, 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 modified by a factor $\alpha^{1/4}$ (α is the ratio of actual to potential evapotranspiration) to account for the reduction in GPP at very low soil moisture content, which has been observed in flux measurements in arid regions. 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 with the help of Beer's law (Jarvis and Leverenz, 1983). Annual net primary production (NPP) is derived from annual GPP, corrected for foliage respiration, by deducting growth respiration (assumed to be 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 model is given in Li et al. (2014). The model has previously been used to simulate the growth of *Pinus koraiensis* in a temperate and relatively moist site in the Changbai Mountains, China. Tree growth in the Changbai Mountains is primarily constrained by 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 all C₃ plants and has no free parameters. The T model requires 15 parameters to be specified. Most of these could be obtained from measurements made at the sampling site, or from the literature (Table 1). Stem basal diameter, tree height and crown area were measured on 150 trees at the sampling site. 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 (H_m : 9.58 m) were estimated using non-linear regression applied to the effective basal diameter (D), tree height (H), and crown area (A_c) measurements on these trees. Values for sapwood density (ρ_s) and specific leaf area (σ) were derived from five measurements made at the sampling site (Table 1).

We used generic values for the quantum efficiency of photosynthesis (ε), PAR extinction coefficient (k) and yield factor (y), from the literature (Table 1). We used estimates of leaf area index within the crown (L) and foliage turnover time (τ_f) measured on *Callitris* species in other regions of Australia. Previous analyses show that the T model is relatively insensitive to these five parameters (Li et al., 2014).

There are no estimates of fine-root turnover time (τ_r), fine-root specific respiration rate (r_r), sapwood-specific respiration rate (r_s), and ratio of fine-root mass to foliage area (ζ) for *Callitris* in the literature and these parameters were not measured in the

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field. However, these parameters have been shown to have a substantial impact on simulated radial growth and the shape of the ontogenetic ageing curve (Li et al., 2014). We used neural-network Bayesian parameter optimization (Jaakkola and Jordan, 2000; Pelikan, 2005), constrained by mean ring width during the period 1950–2012, to derive mutually consistent values of these four parameters. The final optimized parameter values lie within the range of measurements that have been made on other gymnosperms (Table 1).

2.5 Climate inputs

The P model requires daily temperature, precipitation, and fractional cloud cover as an input, which are generally obtained from linear interpolation of monthly values of these variables (Wang et al., 2014). Although three meteorological stations (Credo, Kalgoorlie, Ora Banda, Menzies; Fig. 1) are near to the GWW site, none has records for all three variables covering the whole interval sampled by the tree-ring series (i.e. 1920–2013). 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). We used values for the single grid cell (30.25° S, 120.75° E) in which the GWW site lies (Fig. 3). We examined the reliability of this approach by comparing the gridded climate values with observed values from the four 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 ($p < 0.001$).

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2.6 Definition of the effective growing season

The GWW is characterized by strong precipitation seasonality, while temperature variations are relatively 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 precipitation during the current growing year 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 year.

We investigated the optimal interval influencing carbon accumulation and tree growth using generalized linear modeling (GLM: Nelder and Baker, 1972). We used total annual photosynthetically active radiation (PAR_0), mean annual temperature (MAT), and the ratio of actual to potential evapotranspiration (α) as independent variables in the GLM and mean tree-ring width during the period from 1950–2013 as the dependent variable. 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.

These analyses (Table 2) show that the best overall prediction of tree-ring width ($R^2 = 0.308$) was obtained using an effective growing season of two years (from January in

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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 2). The overall relationship, and the significance of each climate variable, deteriorated when the effective growing season was defined as any longer than two years. Thus, in the subsequent application of the model, we used a carbon-accumulation period of two years to simulate growth rates. This is consistent with the general observation that radial growth of *Callitris* is also influenced by precipitation in the previous rainy season (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 initialised 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 initially run with a fixed [CO₂] of 360 ppm. To examine the impact of changing [CO₂] on tree growth, we made a second simulation using the observed annual [CO₂] between 1901 and 2013 (296–389 ppm; Fig. 3). The CO₂ observations are based on merging ice-core records for the interval from 1901 to 1957 (Etheridge et al., 1996; MacFarling Meure et al., 2006) and the yearly 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).

3 Results

3.1 Simulated ring width vs. observations

The T model captured the amplitude and interannual variability of *Callitris* tree growth in the GWW realistically (Fig. 4). The mean simulated ring width for the period 1950–2012 was 0.722 mm, compared to an observed value of 0.718 mm. There was a highly significant positive correlation ($r = 0.37$, $p < 0.01$) between the simulated and observed mean tree-ring time series. The model underestimated the SD (SD) of the mean ring width series (0.122 mm) compared to the observed SD (0.190 mm). This difference probably reflects the impact of local variability in environmental conditions on individual tree growth, which is not accounted for in our modelling approach.

GLM analysis (Fig. 5a, Table 3) showed that observed tree growth has a strongly positive, independent response to both PAR_0 and soil moisture stress (as measured by α) and a negative response to MAT. These relationships can also be shown in the simulations. Although there is more scatter in the observations, the slopes of the observed and simulated response to PAR_0 and α are similar in the model and the observations. The strength of the observed response to MAT is stronger ($-0.177 \text{ mm } ^\circ\text{C}^{-1}$) than in the model ($-0.079 \text{ mm } ^\circ\text{C}^{-1}$).

The positive relationship with PAR_0 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 determined by precipitation variability (Ash, 1983; Cullen and Grierson, 2009). Since the negative relationship between tree growth and MAT is independent of the impact of increasing temperature on soil moisture availability (α), we hypothesized that this reflects the influence of temperature on atmospheric moisture conditions and specifically vapour pressure deficit (VPD: the difference between saturated and actual vapour pressure). VPD affects stomatal conductance such that increasing VPD leads to stomatal closure, with a correspondingly negative impact on photosynthesis and hence carbon assimilation. To test this hypothesis, we ran the GLM analysis including VPD as a fourth independent variable (Fig. 5b, Table 3).

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In this analysis, tree growth still had a significant positive response to PAR_0 and α , and showed a significant negative response to VPD ($-0.217 \pm 0.125 \text{ mm hPa}^{-1}$) but no longer showed any significant relationship with MAT ($p = 0.704$). This finding indicates that the apparent relationship with MAT reflects the correlation between temperature and increasing VPD, rather than an independent effect of temperature stress.

3.2 Simulations with varying $[CO_2]$

Comparison of the fixed and varying $[CO_2]$ simulations (Fig. 6) shows a positive response of tree ring width to $[CO_2]$: simulated ring widths were smaller in the varying $[CO_2]$ simulation than in the fixed $[CO_2]$ simulation prior to ca 1990 (i.e. when the actual $[CO_2]$ was less than 360 ppm) and larger thereafter. The average difference in simulated ring width in the last decade of the simulation is 0.228 mm. But the positive impact of enhanced $[CO_2]$ is not apparent in the observations. GLM analysis (Fig. 7, Table 3) shows that there is no relationship between $[CO_2]$ and observed tree ring width (slope = $-0.001 \pm 0.001 \text{ mm ppm}^{-1}$, $p = 0.687$). As a result, the simulations using realistic time-varying $[CO_2]$ did not satisfactorily reproduce the observed pattern of variability in ring widths.

While enhanced $[CO_2]$ is expected to have a positive effect on tree growth (Huang et al., 2007; Hyvönen et al., 2007; Donohue et al., 2013) the absence of a response in tree radial growth to elevated $[CO_2]$ has been noted previously (Kienast and Luxmoore, 1988; Gedalof and Berg, 2010). Possible explanations for this are that either the additional carbon is consumed through enhanced respiration or allocated to other parts of the tree – effects that are not taken into account when fixed parameter values are used for respiration and allocation between different pools. As a test of whether parameter values might plausibly have changed in response to varying $[CO_2]$, we ran the Bayesian parameter optimization of fine-root turnover time (τ_r), fine-root specific respiration rate (r_r), sapwood specific respiration rate (r_s) and ratio of fine-root mass to foliage area (ζ) for 30 year moving windows since 1920 using appropriate $[CO_2]$ for

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each window. This resulted in no change in the estimated values for fine-root turnover time, fine-root specific respiration rate, and sapwood-specific respiration rate (Fig. 8). However, the estimated value of the ratio of fine-root mass to foliage area (ζ) increased by about 14 % from 1950 to the end of the period. A simulation with observed $[\text{CO}_2]$ and time-varying values of ζ produced a better agreement ($r = 0.27$) with the tree-ring observations (Fig. 9). In particular, this simulation does not produce an overestimation of ring widths in recent years compared to observations.

4 Discussion and conclusions

We have shown that the radial growth (ring width) of the gymnosperm *Callitris columellaris* over the last century in the seasonally dry environment of the GWW can be realistically simulated by coupling a generic model of GPP with a model of carbon allocation and functional geometric tree growth using species-specific parameter values. Model performance was not adversely affected by the reduction in winter precipitation and the shift towards more variable precipitation that occurred in the mid-1970s, indicating that it successfully captured the climate controls on tree growth during the whole period considered. This conclusion was borne out by GLM analyses, which show that the simulated and observed responses to key climate variables were similar.

The radial growth of *Callitris columellaris* in the GWW is positively correlated with PAR_0 and α , and negatively correlated with MAT. However, we have shown that the relationship with MAT can be explained by the positive correlation between MAT and VPD. When VPD was included in the analyses, we found a strong negative relationship between radial growth and VPD and no additional effect of MAT. 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 represented by VPD, the latter by α) apparently exert independent controls on radial stem growth. In analyses of the climate controls on radial growth of *Pinus koraiensis* in the Changbai Mountains (Li et al., 2014), we attributed the negative

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correlation with MAT as reflecting the fact that the site was at the southern limit of the distribution of *Pinus koraiensis* in China. However, it could be that this relationship was also driven by VPD.

We have shown that the radial growth of *Callitris columellaris* in the GWW has not responded to increasing [CO₂] in recent decades. The lack of a response to [CO₂] has been a feature of several other tree-ring studies (Kienast and Luxmoore, 1988; Archer et al., 1995; Gedalof and Berg, 2010; van der Sleen et al., 2015). Our model experiments suggest that the lack of response in radial growth could be because of changes in allocation to different components of the tree, specifically increased allocation to fine roots. This is consistent with analyses of stable carbon isotopes and growth rings of tropical trees (van der Sleen et al., 2015), which found an increase in water-use efficiency but no stimulation of radial growth from CO₂ fertilisation during the recent 150 years.

Results from free-air carbon enrichment (FACE) experiments are equivocal about the impact of enhanced [CO₂] on tree growth and the allocation to fine roots. However, the majority of sites (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) have shown increased allocation to fine roots as a consequence of enhanced [CO₂]. The Swiss Canopy Crane site is the 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, whereas trees at sites experiencing strong water limitation might show the opposite response due to enhanced water use efficiency at high [CO₂]. Our results do not support this reasoning, suggesting instead that the trees are allocating more below ground as [CO₂] increases even in the strongly water limited environment of the GWW. It is also possible that the shift in precipitation regime has contributed to a shift towards carbon allocation below ground.

Appropriately analyzed, tree-ring records worldwide should yield consistent information about the diverse responses of tree growth and allocation to environmental

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change. A noteworthy feature of our study is that a relatively slight change in the allocation of carbon to fine roots vs. leaves provides a quantitatively consistent explanation of the apparent absence of a growth response to [CO₂]. If this explanation is correct, it does not support the interpretation that tree NPP is not responsive to [CO₂] (whether through nutrient limitation, sink limitation or any other reason). It does however support the idea that above-ground NPP and radial growth are sensitive to environmental effects on the allocation of assimilates to different plant compartments.

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Table 1. Definition of T model parameters and derivation of parameter values. Two values are given for the ratio of fine-root mass to foliage area; the value in brackets is from the Bayesian parameter optimization using variable CO₂.

Parameter	Symbol	Value	Uncertainty or range of value from literature	Value source	Reference
initial slope of height–diameter relationship (–)	a	41.35	41.35 ± 2.58	observation	–
initial ratio of crown area to stem cross-sectional area (–)	c	626.92	626.92 ± 20.03	observation	–
maximum tree height (m)	H_m	9.58	9.58 ± 1.11	observation	–
sapwood density (kg C m ⁻³)	ρ_s	406	406 ± 32	observation	–
specific leaf area (m ² kg ⁻¹ C)	σ	5.16	5.16 ± 0.32	observation	–
leaf area index within the crown (–)	L	1.87	1.87 ± 0.18	species-based parameter value from the literature	Fieber et al. (2014)
foliage turnover time (years)	τ_f	2.58	–	species-based parameter value from the literature	Wright and Westoby (2002)
intrinsic quantum efficiency (mol C (mol photon) ⁻¹)	ε	0.085	–	generic value	Collatz et al. (1998) Wang et al. (2014)
PAR extinction coefficient (–)	k	0.5	0.48–0.58	generic value	Pierce and Running (1988)
yield factor (–)	y	0.6	0.5–0.7	generic value	Zhang et al. (2009)
fine-root turnover time (years)	τ_r	0.82	0.76 ± 0.06	Bayesian parameter optimization	Yuan and Chen (2010) (estimation for evergreen needleleaf trees)
fine-root specific respiration rate (yr ⁻¹)	r_r	1.41	1.36	Bayesian parameter optimization	Burton and Prigitzer (2002) (estimation from one-seeded Juniper)
sapwood specific respiration rate (yr ⁻¹)	r_s	0.035 (1.03 nmol mol ⁻¹ s ⁻¹)	0.5–10, 20 nmol mol ⁻¹ s ⁻¹	Bayesian parameter optimization	Landsberg and Sands (2010)
ratio of fine-root mass to foliage area (kg C m ⁻²)	ζ	0.132 (0.129)	1.0; 0.17	Bayesian parameter optimization	Burrows et al. (2001) (estimation for <i>Callitris</i>) White et al. (2000) (estimation for evergreen needleleaf tree)

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Table 2. GLM 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 annual photosynthetically active radiation (PAR), mean annual temperature (MAT), and the ratio of actual to potential evapotranspiration (α). The coefficients give the change in ring width (mm) per unit change in the climate parameter.

		PAR ₀ (mm (kmol photon m ⁻²) ⁻¹)	MAT (mm °C ⁻¹)	α (mm)	R ²
Formation year	Estimation	0.347	-0.052	0.746	0.076
	Error	± 0.186	± 0.054	± 0.558	
	<i>p</i> value	0.068	0.340	0.187	
Calendar year	Estimation	0.335	-0.093	0.930	0.141
	Error	± 0.185	± 0.051	± 0.436	
	<i>p</i> value	0.076	0.074	0.038	
1.5 Calendar year	Estimation	0.557	-0.148	1.640	0.270
	Error	± 0.207	± 0.057	± 0.510	
	<i>p</i> value	0.010	0.013	0.002	
2 Calendar year	Estimation	0.527	-0.177	2.003	0.308
	Error	± 0.229	± 0.065	± 0.539	
	<i>p</i> value	0.025	0.008	0.000	
2.5 Calendar year	Estimation	0.530	-0.158	2.092	0.236
	Error	± 0.262	± 0.074	± 0.634	
	<i>p</i> value	0.048	0.037	0.002	
3 Calendar year	Estimation	0.774	-0.192	2.434	0.252
	Error	± 0.282	± 0.081	± 0.685	
	<i>p</i> value	0.008	0.022	0.001	

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Table 3. GLM analyses of simulated and observed response of tree growth to climate variables and CO₂. The dependent variable is mean ring width series (dates from 1950 and to 2012). The independent variables are annual photosynthetically active radiation (PAR), mean annual temperature (MAT), the ratio of actual to potential evapotranspiration (α), vapour pressure deficit (VPD) and monthly [CO₂].

		PAR (mm(kmolphoton m ⁻²) ⁻¹)	MAT (mm °C ⁻¹)	α (mm)	VPD (mm hPa ⁻¹)	CO ₂ (mmppm ⁻¹)
Observation	Estimation	0.527	-0.177	2.003		
	Error	± 0.229	± 0.065	± 0.539		
	<i>p</i> value	0.025	0.008	0.000		
Simulation with 360 ppm CO ₂	Estimation	0.771	-0.079	2.704		
	Error	± 0.064	± 0.018	± 0.150		
	<i>p</i> value	< 0.001	< 0.001	< 0.001		
Observation	Estimation	0.713	0.057	1.574	-0.217	
	Error	± 0.248	± 0.148	± 0.583	± 0.125	
	<i>p</i> value	0.006	0.704	0.009	0.088	
Simulation with 360 ppm CO ₂	Estimation	0.827	-0.010	2.576	-0.065	
	Error	± 0.069	± 0.041	± 0.161	± 0.035	
	<i>p</i> value	< 0.001	0.812	< 0.001	< 0.001	
Observation	Estimation	0.709		1.734	-0.164	-0.001
	Error	± 0.246		± 0.572	± 0.059	± 0.001
	<i>p</i> value	0.006		0.004	0.008	0.687
Simulation with real CO ₂	Estimation	0.779		2.322	-0.099	0.008
	Error	± 0.058		± 0.134	± 0.014	± 0.000
	<i>p</i> value	< 0.001		< 0.001	< 0.001	< 0.001

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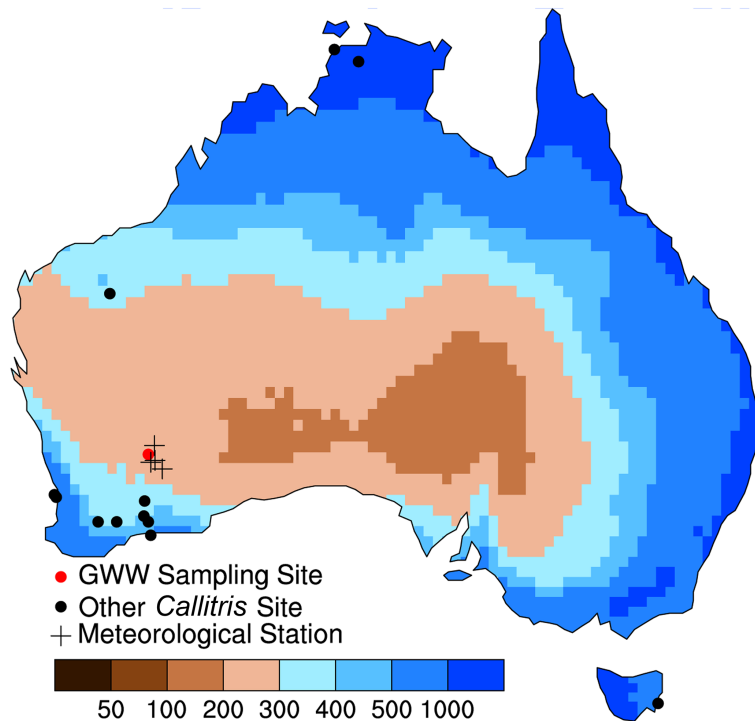


Figure 1. Location of the Great Western Woodlands sampling site, Western Australia. The underlying map shows mean annual precipitation (MAP). We also show the location of other sites across Australia where *Callitris* have been sampled (data from International Tree-Ring Data Bank), and the locations of the nearest meteorological stations to the sampling site.

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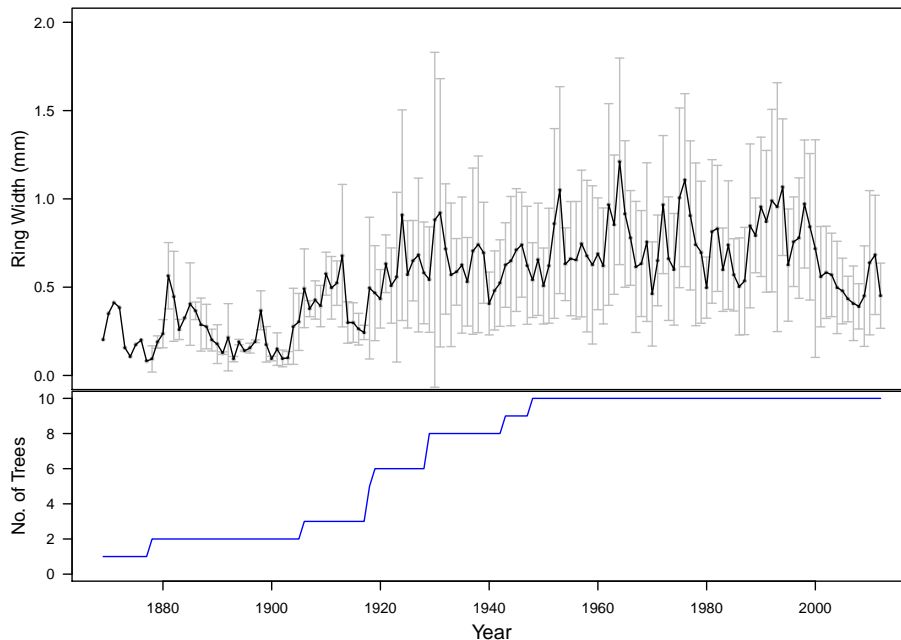


Figure 2. Interannual variability in tree-ring widths of *Callitris columellaris* from the Great Western Woodlands, Western Australia. In the top panel, the black line is the mean of the observations, and the grey bars show the SD of the individual sampled trees. The blue line in the bottom panel shows the number of trees sampled for each interval.

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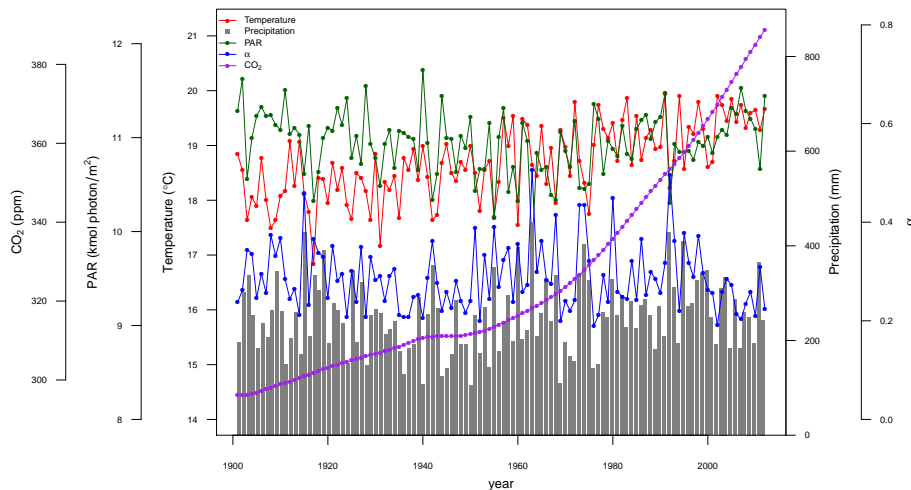


Figure 3. Climate at the Great Western Woodlands site. The plot shows mean annual temperature, precipitation, photosynthetically active radiation (PAR) and the ratio of actual to equilibrium evapotranspiration (α). The observed changes in [CO₂] are shown for comparison.

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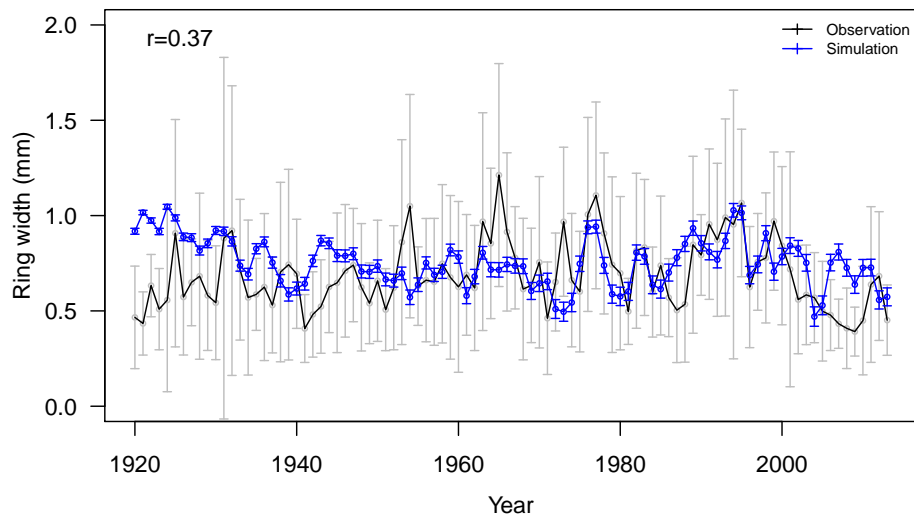


Figure 4. Comparison between simulated and observed tree ring widths, for the period 1920 to the present, with [CO₂] set at 360 ppm. The black line is the mean of observations, and the grey bars are the SD among trees. The blue line and bars are the mean and SD from the simulations.

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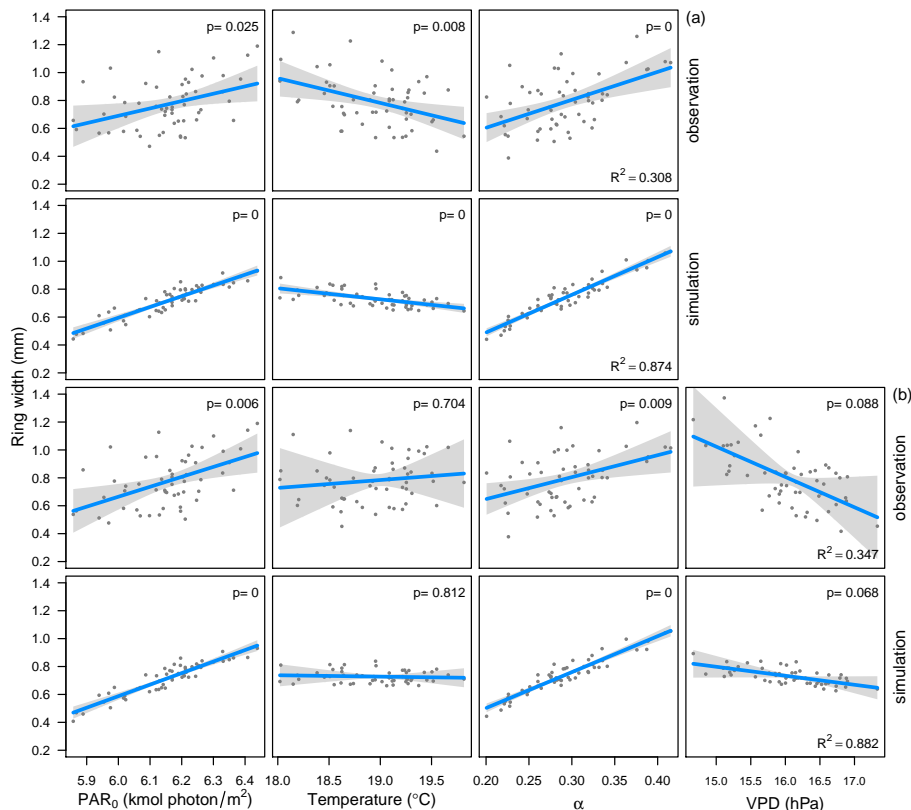


Figure 5. Simulated and observed responses of tree growth to climate: partial residual plots based on the GLM analysis, obtained using the visreg package in R, are shown. The upper plots show results from analyses in which the predictor variables are **(a)** photosynthetically active radiation (PAR₀), the ratio of actual to potential evapotranspiration (α) and mean annual temperature (MAT) and **(b)** PAR₀, α , MAT and vapour pressure deficit (VPD).

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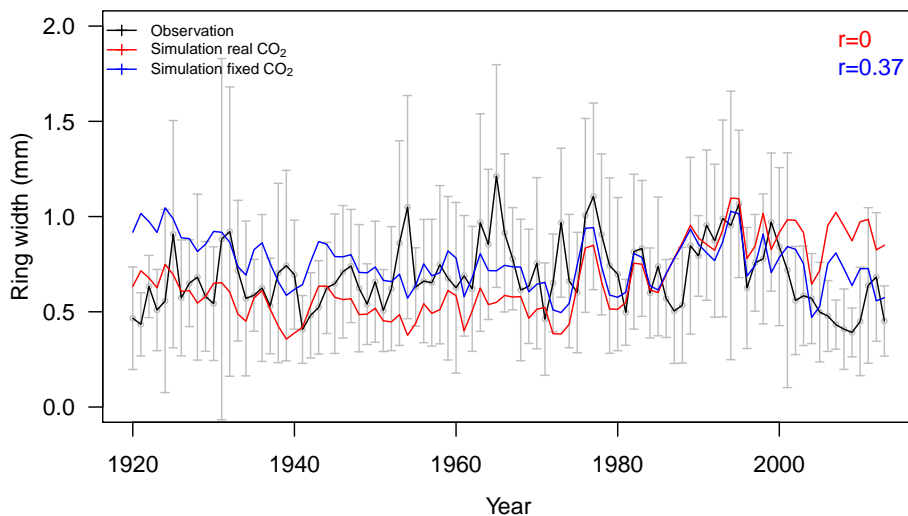


Figure 6. Comparison of simulated ring width in simulations with fixed (blue line) and time-varying (red line) [CO₂]. The black line is the mean of the observed ring widths.

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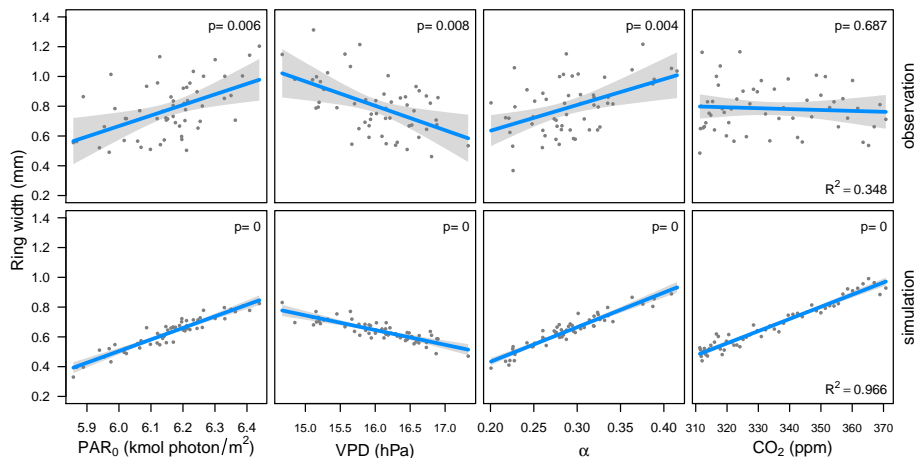


Figure 7. Simulated and observed response of tree radial growth to [CO₂]: partial residual plots based on the GLM analysis, obtained using the visreg package in R, are shown. The dependent variable is mean ring width (from 1950 and to 2012). The predictor variables are annual photosynthetically active radiation (PAR₀), vapour pressure deficit (VPD), the ratio of actual to potential evapotranspiration (α), and monthly [CO₂].

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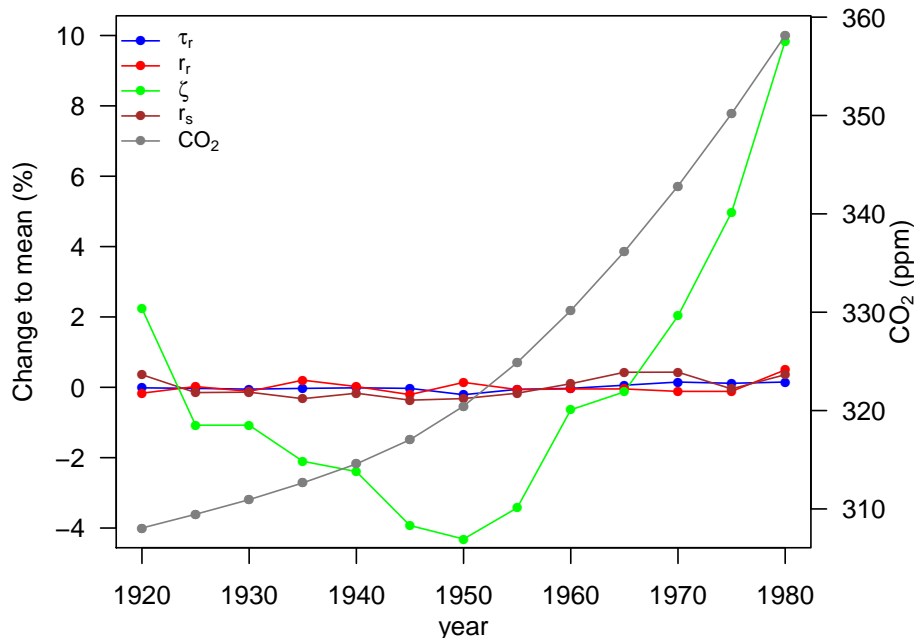


Figure 8. Impact of changing [CO₂] on the values of parameters estimated by Bayesian optimization. The graph shows the percentage change to the mean value of each of the parameters fine-root turnover time (τ_r), fine-root specific respiration rate (r_r), sapwood specific respiration rate (r_s) and ratio of fine-root mass to foliage area (ζ) for 30 year moving windows since 1920, using the appropriate [CO₂] for each window. X axis is the beginning year of each 30 year moving window.

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

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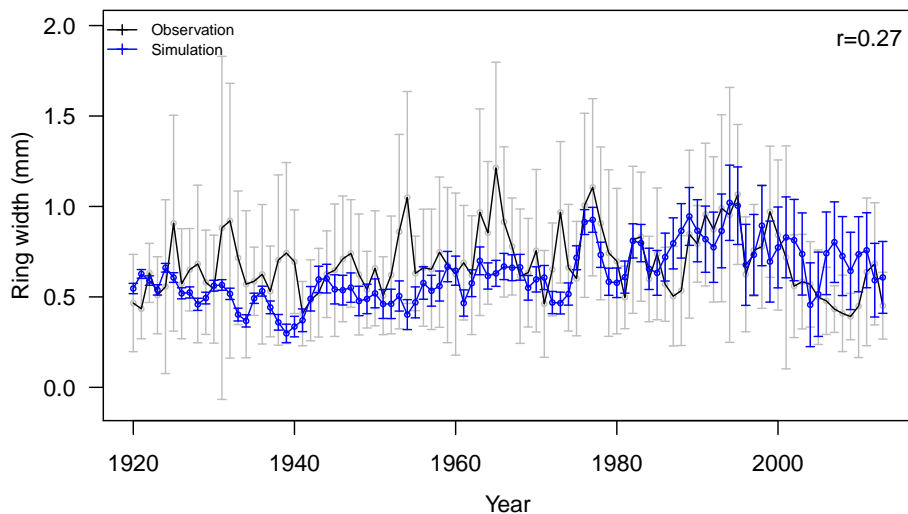


Figure 9. Simulation of radial growth in response to changing climate and observed [CO₂], allowing for the effect of changing allocation to fine roots.

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