



A model analysis of climate and CO₂ 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 CO₂ concentration [CO₂] despite the expected enhancement of photosynthetic rates and water-use efficiency at high [CO₂]. 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 principles, 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 optimization. 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].

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1. 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; Girardin et al., 2011; Peñuelas et al., 2011; van der Sleen et al., 2015). Moreover, tree-growth modelling (Boucher et al., 2014; Li et al., 2014) has suggested that the expected radial growth enhancement due to the recent [CO₂] increase is quite small, compared to the effects of

climate variability. A stronger response to enhanced [CO₂] might be expected *a priori* in water-limited regions (Field et al., 1983; Hyvönen et al., 2007), because stomatal conductance is reduced when [CO₂] is higher. This is a common empirical observation, consistent with the least-cost hypothesis (Wright et al., 2003; Prentice et al., 2014), which predicts a near-constant ratio of leaf-internal to ambient [CO₂] as [CO₂] increases – while the rate of increase of photosynthesis with [CO₂] declines. Failure to sample water-limited environments might thus conceivably explain the apparent lack of increased stem growth in response to increasing [CO₂].

An alternative explanation could be that increased primary production due to increased [CO₂] has not led to increased stem growth due to a shift in carbon allocation away from stems. There is some experimental evidence that changing [CO₂] results in changes in carbon allocation between above-ground (leaf, stem) and below-ground (root) biomass pools. Observations of the response to high [CO₂] in Free-Air Carbon dioxide Enrichment (FACE) experiments show that trees commonly increase total carbon allocation below

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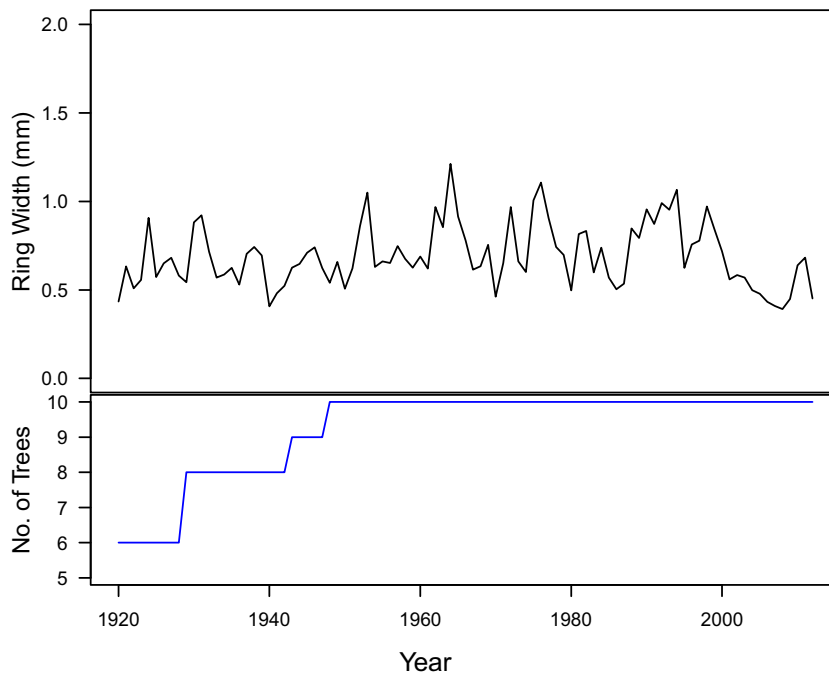


Fig. 1. Interannual variability in tree-ring widths of *Callitris columellaris* from the Great Western Woodlands, Western Australia. In the top panel, the black line is the mean of the observations, and the grey bars show the standard deviation (SD) of the individual sampled trees. The blue line in the bottom panel shows the number of trees sampled for each interval. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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 [CO₂] under natural conditions.

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

2. Methods

2.1. The study area

The GWW, with an area of about 160,000 km², 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, 400 m a.s.l.; <http://www.tern-supersites.net.au/supersites/gww/>)

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 day/decade, $p<0.001$) while the mean precipitation on rain days (precipitation intensity) increased (0.38 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 °C/decade ($p<0.001$) and vapour pressure deficit (VPD) also increased, while soil moisture (as indexed by α , 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, 2009; Baker et al., 2008; Cullen et al., 2008). We selected a 500 × 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

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