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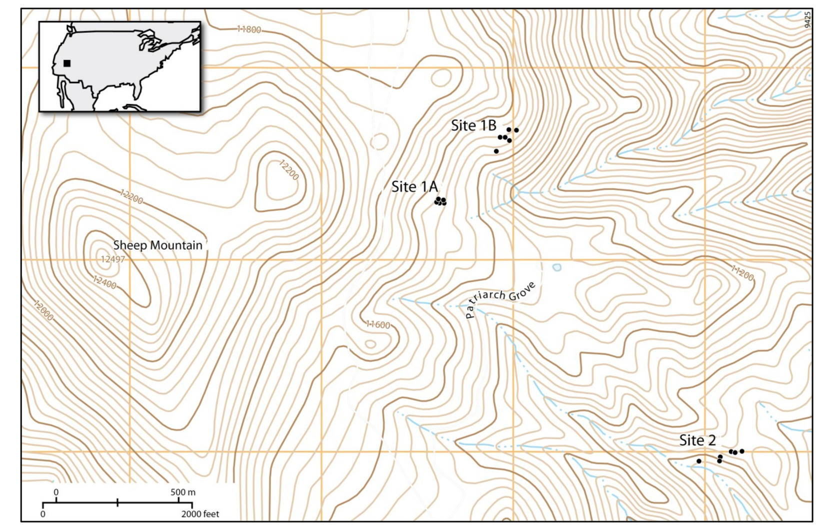

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Isotope evidence for temperature-dependent hydraulic constraints to growth of bristlecone pine

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Introduction

Altitudinally separated bristlecone pine populations in the White Mountains (California, USA) exhibit differential growth responses to 20th century climate variability. These populations provide a natural experiment to explore the physiological responses of this unique and ancient tree species to climate variability and atmospheric CO_2.

We developed annually resolved chronologies of tree ring width, and cellulose stable carbon and oxygen isotopes from bristlecone pine growing at the tree line (~3500 m) and approximately 200 m below for the period AD 1700-2010. Isotope signals were interpreted with a dual-isotope model and a leaf gas exchange model. Method details are provided in **Table 1**.

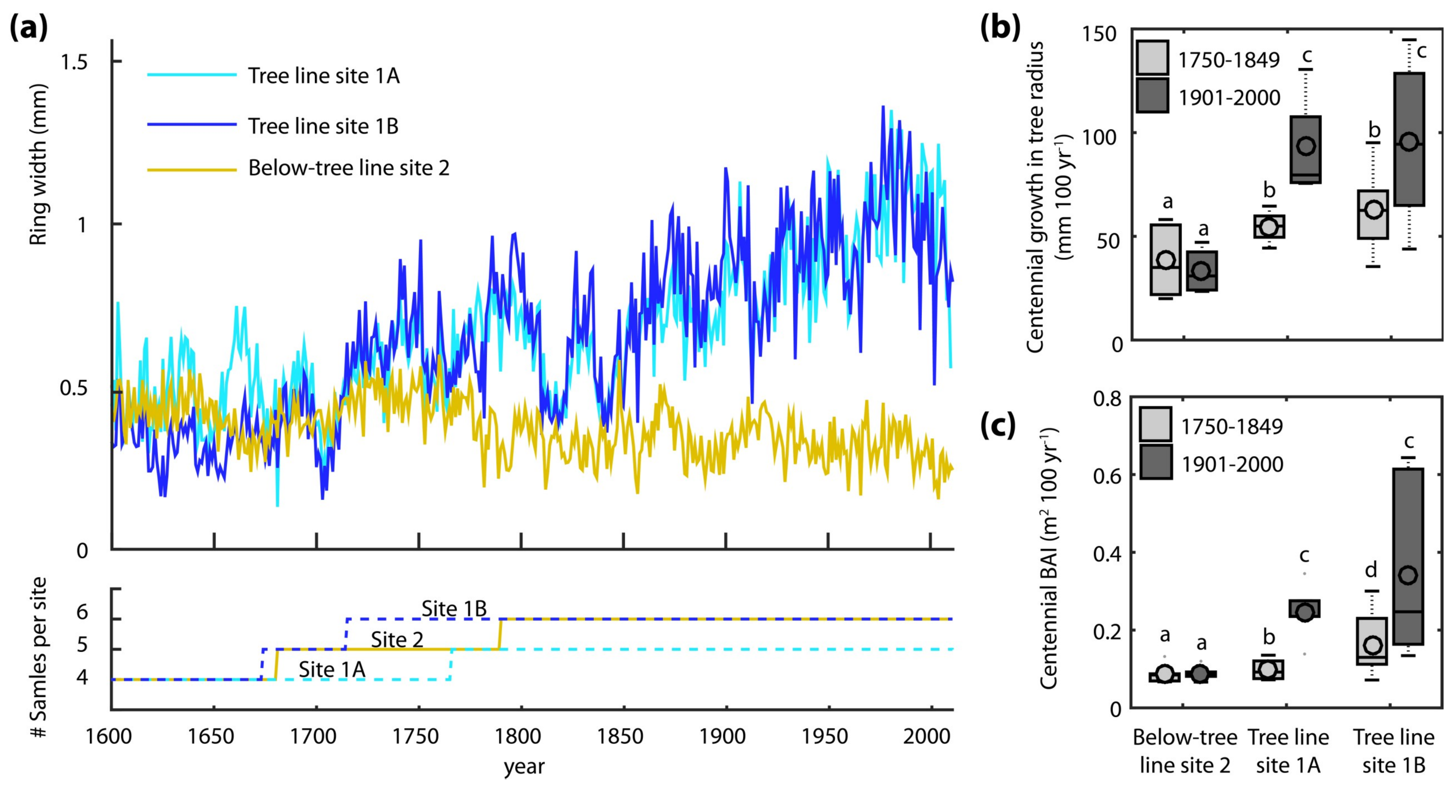

Figure 1: 20th century growth anomalies in bristlecone pine growing in localities at the modern tree line (sites 1A and 1B) and approximately 200 m lower (site 2). (**a**) Site average annual ring width (mm) and the number of trees sampled per growth locality. (**b**) Pre-industrial (1750-1849) and 20th century (1901-2000) average radial growth (mm century^{-1}) at the three growth localities. (**C**) Pre-industrial and 20th century average Basal Area Increment (BAI; m^2 century^{-1}) at the three growth localities.

Results

Ring width chronologies show increased growth at the tree line and reduced growth at lower elevations during the 20th century **(Fig. 1)**. The stable carbon and oxygen isotope records indicate that, in response to measured 20th century warming and atmospheric drying, stomatal conductance and transpiration increased at the tree line, whereas stomatal conductance declined and transpiration remained relatively constant at lower elevations **(Fig. 2)**. These results are supported by the leaf gas exchange model **(Fig. 3)**. The model also shows that rising atmospheric CO_2 levels stimulate leaf-level photosynthesis regardless of elevation.

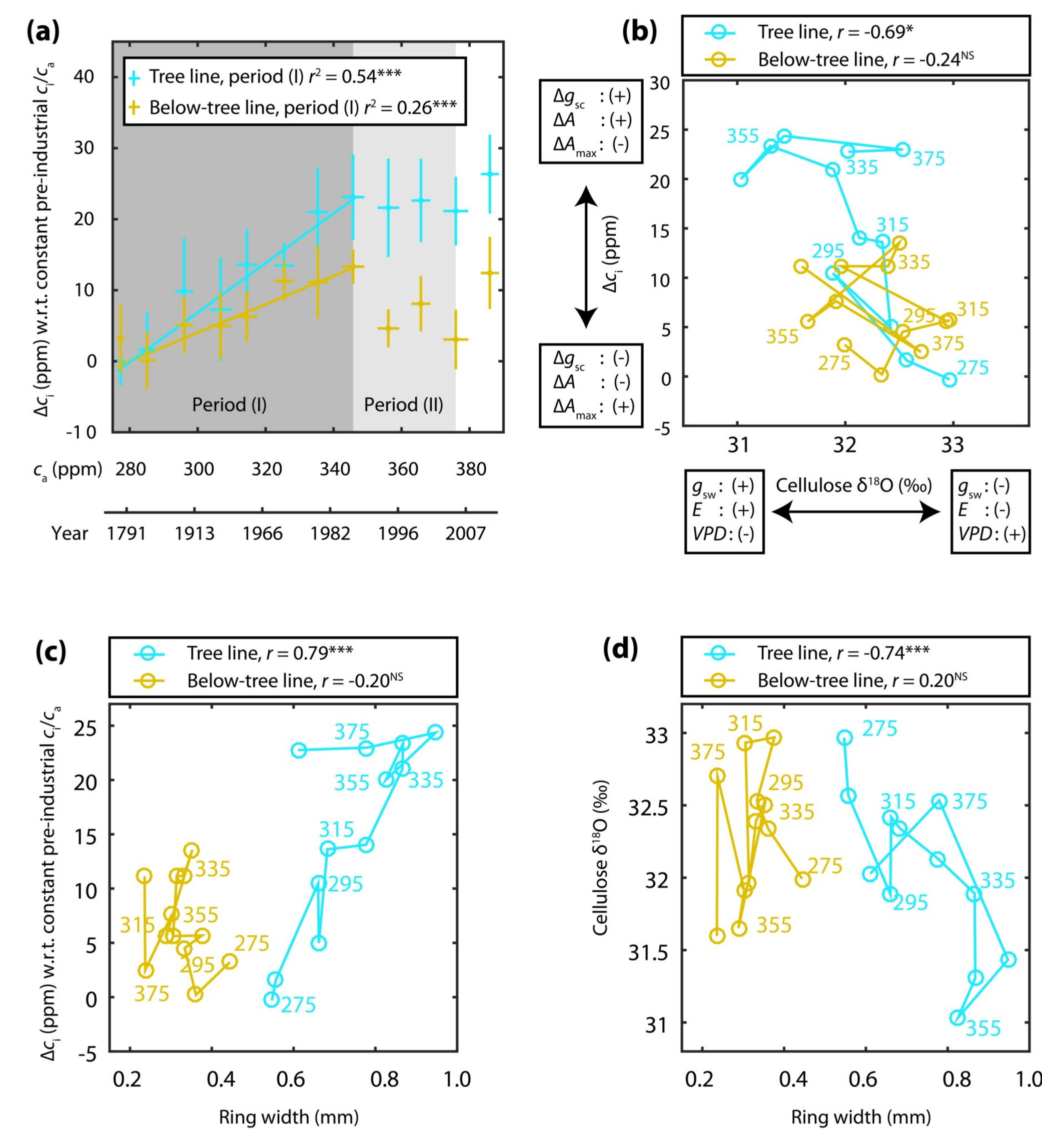

Figure 2: Interpretation of signals conveyed in the records of α-cellulose δ13C and δ18O according to the adapted dual-isotope model. (**a**) Relationship between c_a and the deviation in δ13C-derived c_i from the 'active' (constant c_i/c_a) response of δ13C to c_a, termed Δc_i. Significant positive responses of Δc_i to c_a were observed in period (I), whereas in period (II) a shift to non-significant or negative responses was observed. (**b**) Relationship between α-cellulose δ18O and Δc_i. The black boxes near the axes extremes indicate the interpretation of the adjusted dual-isotope model in terms of changes in stomatal conductance to water vapour (g_{sw}), transpiration (E) and vapour pressure deficit (VPD), and relative changes in stomatal conductance to CO_2 (Δg_{sc}), photosynthesis (ΔA) and photosynthetic capacity (ΔA_{max}). (**c**) Correlation between annual average ring width and Δc_i. (**d**) Correlation between annual average ring width and δ18O.

Table 1: Materials and methods

Materials and Methods

Population selection	• Cellulose core samples from 17 *Pinus longaeva* D. K. Bailey (bristlecone pine) individuals • Samples were taken from three sites. Trees in sites 1A (N=5) and 1B (N=6) are situated at elevations between 3482 m and 3523 m (modern tree line), trees in site 2 (N=6) grow at slightly lower elevations between 3293 m and 3338 m (see map)
Measurements	• Tree ring width and BAI (AD 1700-2010) • α-cellulose δ13C and δ18O at population level • Ecophysiological and morphological traits of needles (LMA, leaf nitrogen, needle size)
Analyses and modelling	• Interpretation of signals in α-cellulose δ13C and δ18O based on an adaptation of the dual-isotope model (*e.g.* Barbour *et al.*, 2004) • Modelling δ13C-derived leaf gas exchange following De Boer *et al.*, 2016

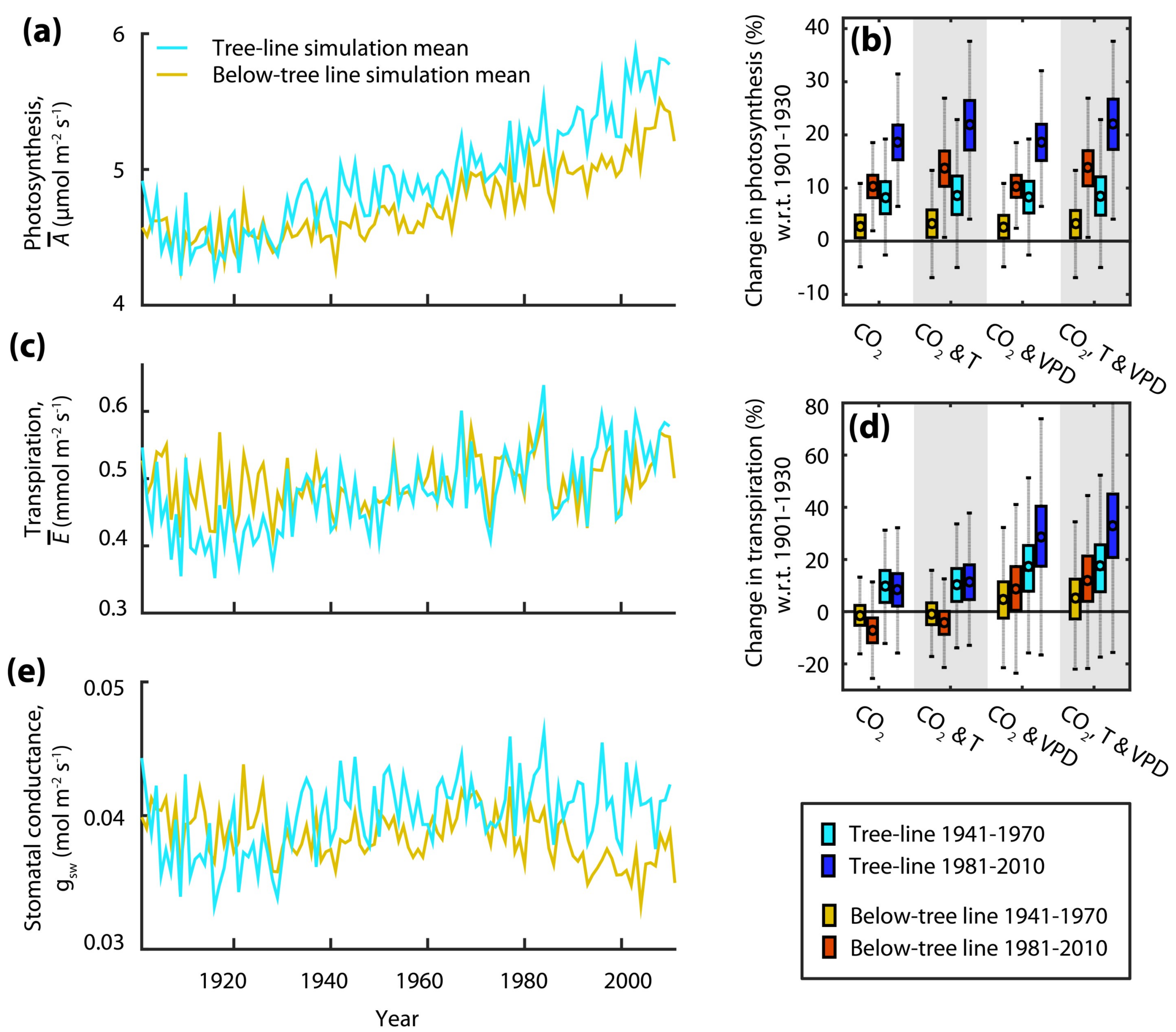

Figure 3: Modelled responses of leaf gas exchange to 20th century changes in atmospheric CO_2, growing season temperature and VPD. **(a)** Leaf-level time-integrated photosynthesis (A) as modelled in the baseline 'CO_2, T and VPD' simulation. **(b)** Modelled changes in A expressed as percentage (%) with respect to the period 1901-1930. The 'CO_2', 'CO_2 & T', 'CO_2 & VPD', and 'CO_2, T & VPD' simulations used different combinations of boundary conditions that represent 20th century changes in each variable. **(c)** Leaf-level time-integrated transpiration (E) as modelled in baseline simulation. **(d)** Modelled changes in E expressed as % with respect to the period 1901-1930. **(e)** Leaf-level stomatal conductance to water vapour (g_{sw}) as modelled in the baseline simulation. Solid lines in panels **(a)**, **(c)** and **(e)** reflect the average of 10.000 Monte-Carlo type simulations using PRISM-based ranges climate boundary conditions. Boxes indicate the uncertainty in each simulation owing to the variability in boundary conditions.

Discussion

Our tree ring chronologies from altitudinally separated bristlecone pine populations corroborate previous work on nearby populations that reflect waning temperature limitation near the tree line and moisture limitation at lower elevations (LaMarche & Stockton, 1974; Hughes & Funkhouser, 2003; Salzer *et al.*, 2009).

We propose that the differential growth responses are indicative of constraints on tree hydraulics; warming alleviates temperature constraints on xylogenesis at the tree line (Petit *et al.*, 2011), while the associated atmospheric drying increases transpiration beyond the tree hydraulic capacity at lower elevations (Meinzer *et al.*, 2009; Carnicer *et al.*, 2013).

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