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

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Tree ring archives from the extremely long-lived bristlecone pine (*Pinus longaeva* D. K. Bailey) can provide annually-resolved information on historic growth conditions. However, closely located bristlecone pine populations have shown mixed, and sometimes contrasting growth responses to climate variability over the last century. Hence, a better physiological understanding is required to interpret local growth responses in terms of larger scale climate variability.

Here we explore the hypothesis that differential growth responses of altitudinally separated bristlecone pine populations reflect shifts in xylem hydraulic constraints related to sub-optimal temperatures and excess atmospheric moisture demand. We developed annually resolved chronologies of tree ring width, and cellulose stable carbon (δ^{13}C) and oxygen (δ^{18}O) isotopes from bristlecone pine populations growing near the modern tree line and approximately 200 m below. Combined signals from the carbon and oxygen isotopes were interpreted according to the theoretical principles of the dual-isotope model and a hybrid mechanistic-empirical leaf gas exchange model.

Our tree ring chronologies corroborate previous results that show increased growth near the tree line and reduced growth at lower elevations since the start of the 20^{th} century. The dual-isotope model suggests that the near tree-line population increased stomatal conductance, whereas the below tree-line population decreased stomatal conductance while maintaining relatively constant transpiration. Climate indices available for the growth localities of our bristlecone pine populations indicate that temperature, atmospheric Vapour Pressure Deficit (VPD), and precipitation have increased during the 20^{th} century. Using the observed changes in climate and CO_2 as input, our leaf gas exchange model indicates that the near-tree line population was able to respond to rising VPD by increasing transpiration, whereas the below-tree line population responded by reducing stomatal conductance. Our gas-exchange model further suggests that the influences of warming and rising CO_2 are comparable between the altitudinally separated populations.

As an interpretation of these results, we propose that the reconstructed changes in stomatal conductance and transpiration are symptomatic of differential constraints on xylem hydraulic conductivity; warming near the tree line alleviates the constraint of sub-optimal temperatures on xylem formation and whole-tree water transport, whereas warming and concomitant atmospheric drying at lower elevations increases transpiration beyond the hydraulic capacity of the tree. Our results suggest that the apparent differential climate sensitivity of bristlecone pine growing at different altitudes may be related to hydraulic constraints.