



## **13C-derived water use efficiency in Mediterranean pines across a precipitation gradient are related to differential moisture-dependant Ci-regulation responses.**

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Persistent predictions of warming and drying in the entire Mediterranean and other regions motivate investigation of terrestrial ecosystem responses to such change. We have used 30 year (1974-2003) records of tree-ring derived growth measures (basal area increment, BAI) and cellulose  $^{13}\text{C}$  isotopic composition from three sites across a geographical rainfall gradient to explore the temporal behaviour and physiological responses to variations in climatic (rainfall, temperature) and atmospheric ( $[\text{CO}_2]$ ,  $\text{Ca}$ ) drivers in *Pinus halepensis* trees. Potential juvenile effects on the cellulose  $^{13}\text{C}$  record were negligible in the two even-aged low density stands and excluded from the mixed-aged natural stand. Agreement between estimates of intrinsic water use efficiency ( $W_i$ ) from cellulose  $^{13}\text{C}$  values and leaf-scale gas exchange measurements, consistency across the sites in the  $W_i$  response to soil water content and an observed insensitivity to known thinning events at the dry site give us confidence that leaf-level physiological responses, and not age and density effects, dominate the  $^{13}\text{C}$  isotopic record in these trees.

Site-level differences and inter-annual variations in the earlywood (EW, associated with the wet and productive period)  $^{13}\text{C}$ -derived estimates of  $W_i$  were related to annual precipitation in a common, site-independent manner, with reduced sensitivity to annual rainfall above  $\sim 600\text{mm}$ . Rainfall was also the predominant driver in inter-annual variations in BAI. While there were no trends in rainfall amount over this period, there were clear trends of increasing  $W_i$  in both the EW and latewood (LW) that ranged between ca. 5 and 20% increase over the study period. These trends were better correlated with the increase in  $\text{Ca}$  than a temperature increase ( $\sim 0.04^\circ\text{C y}^{-1}$ ) that was also observed across the sites.

The different sensitivities of  $W_i$  to  $\text{Ca}$  ( $dW_i/d\text{Ca}$  of 0.1 to 0.5  $\mu\text{mol mol}^{-1} \text{ppm}^{-1}$ ) represented shifting  $\text{C}_i$ -regulation ( $\text{C}_i$ , leaf internal  $\text{CO}_2$  concentration) responses associated with the hydrological conditions and operational limits of  $\text{C}_i$  or  $\text{C}_i/\text{Ca}$  set-points. A constant  $\text{C}_i/\text{Ca}$  was observed under the most favourable conditions (mesic site EW), indicating active regulation to maintain  $\text{C}_i/\text{Ca}$  at an apparent optimum ( $0.62 \pm 0.01$ ) with increasing  $\text{Ca}$ . Consequently,  $W_i$  increased appreciably over time ( $dW_i/d\text{Ca} = 0.26$ ). With increasing moisture deficits, i.e. at the drier sites in the wet season and the drier LW period at the wet site, average  $\text{C}_i$  (and  $\text{C}_i/\text{Ca}$ ) was lower, and attributed to lower average stomatal conductance. However, with the increasing aridity there was an increasingly passive response in  $\text{C}_i$  regulation with increasing  $\text{Ca}$  ( $d\text{C}_i/d\text{Ca} = 0.7$  at the intermediate site and 1.0 at the dry site), resulting in an increase in  $\text{C}_i/\text{Ca}$  towards the apparent optimum and mild increases in  $W_i$ . Consequently, while average  $W_i$  increased, sensitivity of  $W_i$  to  $\text{Ca}$  decreased with aridity. At the arid extreme of the analysis (latewood in the dry site), a different strategy was observed. Here  $\text{C}_i$  was lowest (190 ppm), but was also maintained relatively constant over the period, resulting in the sharpest increase in  $W_i$  observed with the increase in  $\text{Ca}$ . This low  $\text{C}_i$  possibly represents a lower functional  $\text{C}_i$  limit for this species, and the change in strategy (from passive  $\text{C}_i$  regulation and increasing  $\text{C}_i/\text{Ca}$  to active  $\text{C}_i$  control and decreasing  $\text{C}_i/\text{Ca}$ ) served to maximise the increase in  $W_i$  under the driest conditions, within the constraint of this minimum  $\text{C}_i$ . Overall, the results contribute to our understanding of the range of adjustments forest ecosystems may make to the dry conditions anticipated in the future.