EGU21-10443
https://doi.org/10.5194/egusphere-egu21-10443
EGU General Assembly 2021

Predicted and observed multidecadal variations of tree physiological responses to climate and rising CO_2: insights from tree-ring carbon isotopes in temperate forests.

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Increasing water-use efficiency (WUE), the ratio of carbon gain to water loss, is a key mechanism that enhances carbon uptake by terrestrial vegetation under rising atmospheric CO_2 (c_a). Existing theory and empirical evidence suggest a proportional increase of WUE in response to rising c_a as plants maintain a relatively constant ratio between the leaf internal (c_i) and ambient (c_a) partial CO_2 pressure (c_i/c_a). This has been hypothesized as the main driver of the strengthening of the terrestrial carbon sink over the recent decades. However, proportionality may not characterize CO_2 effects on WUE on longer time-scales and the role of climate in modulating these effects is uncertain. We evaluated the long-term WUE responses to c_a and climate from 1901-2012 CE by reconstructing intrinsic WUE (iWUE, the ratio of photosynthesis to stomatal conductance) using carbon isotopes in tree rings across temperate forests in the northeastern USA. We further replicated iWUE reconstructions at eight additional sites for the 1992-2012 period-overlapping with the common period of the longest flux-tower record at Harvard Forest to evaluate the spatial coherence of recent iWUE variation across the region. Finally, we compared tree-ring based and modelled c_i/c_a over the 1901-2012 period to examine whether temporal patterns of c_i/c_a reconstructions are consistent with predictions based on the optimality principle of balancing the costs of water loss and carbon gain.

We found that iWUE increased steadily from 1901 to 1975 CE but remained constant thereafter despite continuously rising c_a. This finding is consistent with a passive physiological response to c_a and coincides with a shift to significantly wetter conditions across the region. Tree physiology was driven by summer moisture at multi-decadal time-scales and did not maintain a constant c_i/c_a in

response to rising c_a indicating that a point was reached where rising CO_2 had a diminishing effect on tree iWUE. The c_i/c_a derived from tree-ring $d^{13}C$ and the predicted values based on the optimality theory model had similar median values over the 1901-2012 CE period, though with a modest agreement ($R^2_{adj} = 0.22$, $p < 0.001$). The reconstructed and predicted c_i/c_a trends were not statistically different from 0 when estimated over the 1901-2012 CE period; however, isotope-based reconstruction of the c_i/c_a trendshowed distinct multidecadal variation while the predicted c_i/c_a remained nearly constant. Our results challenge the mechanism, magnitude, and persistence of CO_2's effect on iWUE with significant implications for projections of terrestrial productivity under a changing climate.