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Tree-ring anatomy and carbon isotope ratio reveal direct and legacy effects of climate on xylem formation in Mediterranean Pinus pinea

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The Mediterranean region is considered a hot spot of climate change, displaying a rapid shift towards warmer and drier conditions. Understanding how climate affects tree growth and functioning is therefore particularly urgent. However, compared to boreal and temperate regions, mechanisms of Mediterranean tree growth response to climate are less known. In fact, tree growth patterns are more complicated here than at northern latitudes. While in cold and temperate environments radial growth is restricted to one season, under Mediterranean climate there are usually two favourable seasons within the year. Accordingly, secondary growth occurs twice a year, in spring and in autumn (bimodal temporal growth pattern) in some tree species. The classical tree-ring approach, which considers one ring corresponding to one growing season, is not fully suitable. Investigation of growth patterns in Mediterranean trees therefore requires intra-ring analyses.

In this study, we aim to provide a comprehensive and temporally detailed understanding of climate influence on xylem formation in Mediterranean Pinus pinea L. (Italian stone pine or umbrella pine). Analyses were conducted along tree-ring series at intra-ring resolution to assess intra-annual xylem formation processes and responses to climate. We used two approaches: first, we investigated tree-ring anatomical traits, to infer the climate influence on xylem morphogenesis processes. Second, we assessed 13C /12C isotope ratios in the earlywood and latewood of tree rings to get information on the climate influence on seasonal water use of trees, and on how carbon reserves are used for wood formation in different periods of the growing season.

Xylem anatomy was strongly related to environmental conditions occurring a few months before and during the growing season. In particular, the lumen diameter of the first earlywood tracheids was related to winter precipitation, whereas the size of earlywood tracheids produced later was influenced by mid-spring precipitation. Lumen diameter of latewood tracheids was associated with precipitation in mid-autumn. No tracheid feature was affected by summer drought, suggesting a complete break of xylogenesis. Carbon isotope composition in the earlywood was associated to spring climate conditions, suggesting that earlywood is formed using both recently and formerly assimilated carbon. In contrast, latewood carbon isotope composition was related to temperature many months before xylogenesis, likely because xylem formation in autumn mainly relies on stored carbon pools of different ages.

Our integrated approach provided new evidence on the short-term and carry-over effects of climate on the bimodal temporal xylem formation in P. pinea. We demonstrate that investigations on different variables and time scales are necessary to disentangle the complex climate influence on tree growth processes under Mediterranean conditions.