



## Tree rings in context: linking annual growth, intra-annual water relations, and forest structure in a density experiment

Eva Meijers<sup>1</sup>, Jorad de Vries<sup>1</sup>, Gert-Jan Nabuurs<sup>1,2</sup>, and Frank Sterck<sup>1</sup>

<sup>1</sup>Wageningen University, Environmental Sciences, Forest Ecology & Forest Management, Netherlands (eva.meijers@wur.nl)

<sup>2</sup>Wageningen Research, Environmental Sciences, Sustainable forest ecosystems group

Tree-ring studies commonly rely on stand-level chronologies derived from ten or more trees and interpret growth responses at the annual scale. While this approach has been highly successful for detecting broad climate signals, it obscures individual-level variability and collapses intra-annual processes that regulate tree growth and water relations. Yet key physiological responses to forest density—particularly those related to water stress—operate at the scale of individual trees and days to weeks rather than years. Providing physiological context to annual tree-ring records may therefore be essential for assessing whether intermediate density reductions translate into greater tree hydraulic safety.

Here, we investigate how forest density affects tree growth and water relations by combining annual tree-ring data with intra-annual and spatially explicit structural measurements in a forest density experiment established in 2019 on nutrient-poor sandy soils in the Netherlands. The experiment comprises four density treatments (control, high thinning ~20% removal, shelterwood ~80% removal, and clearcut) across three temperate tree species (*Fagus sylvatica*, *Pseudotsuga menziesii*, and *Pinus sylvestris*). Our structural measurements (as captured by terrestrial laser scanning) reveal that local tree density varies strongly within treatments, with intra-treatment variability reaching up to 50%. This heterogeneity allows us to construct a continuous density gradient at the individual-tree level rather than relying solely on treatment- or stand-level averages, which commonly mask divergent individual responses in aggregated tree-ring chronologies.

Tree-ring analyses show a consistent increase in annual growth with decreasing stand density. However, high-frequency dendrometer measurements indicate that this enhanced growth is not necessarily accompanied by improved tree water status, suggesting that reduced competition does not automatically translate into greater hydraulic safety. We propose that this decoupling arises from compensating mechanisms such as increased evaporative demand under more open canopies and higher water uptake by understory vegetation. Overall, our results demonstrate that integrating annual tree-ring records with intra-annual physiological measurements and high-resolution forest structural data provides essential context for interpreting growth responses to forest density. They further indicate that tree water and density relations are more complex than commonly assumed, with multiple compensating processes potentially masking density effects.

This multi-scale perspective enables a shift from purely correlative inference toward a more process-oriented understanding of how forest density shapes tree growth under increasing drought stress.