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Long-term growth trajectories in a changing climate: disentangling age from size effects in old Fagus trees from contrasting bioclimates

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Understanding the drivers promoting exceptional longevity in trees and how their growth performances vary approaching maximum lifespan still represent intriguing challenges not only for tree biology, but also for modelling the long-term forest ecosystem functioning under a changing environment.
Tree growth rate is expected to increase with increasing stem size, but higher risk of hydraulic failure and mortality can affect larger trees under increasingly dry conditions. In turn, very old trees are characterized by slow growth and smaller size, factors able to confer advantages against biotic and abiotic disturbances. Rising evidences that very old trees are negligibly affected by the progressive deterioration of physiological functions associated with age support the idea that size, not age, is the main constrain to tree lifespan, so that negative senescence has been proposed as a frequent phenomenon in trees. Additional empirical knowledge is needed to thoroughly assess how complex, uneven-aged old-growth forests cope under climate change in order to define their role in terrestrial carbon cycle.
We used a tree-ring network of 8 European beech (Fagus sylvatica L.) old-growth forests containing several of the oldest crossdated broadleaf trees of the Northern Hemisphere (400-600 years old) to analyse how their growth rates vary along age/size development. We sampled advanced old-growth stands, where canopy tree mortality is naturally occurring, divided among contrasting bioclimatic conditions: eastern Alps and central Apennines (rainy vs. dry summer). To disentangle the long-term effects of size and age on long-term tree growth history, we reconstructed Basal Area Increment (BAI) along size (DBH) development, grouping growth trajectories in different age classes.
On average, BAI increased continuously as stem size increased, regardless of bioclimatic region and age class. Old trees grew the slowest and kept increasing BAI trends. In turn, especially on the drier Apennines, fast-growing young trees showed a precocious slow-down of their increments, following their fast size/crown development. On the Alps, wetter climatic conditions seemed to afford the widespread maintenance of positive increments along size development.
At the individual level, high growth variability exists among canopy trees in old-growth forests. In some cases, old trees showed recent BAI values comparable to young ones. However, increasing patterns are not necessarily the norm, especially in the Apennines. In a recent, common period marked by warmer/drier conditions, 55-60% displayed no significant BAI trend. In the drought-prone Apennines, BAI declined in 28% of trees. Size matters when assessing climate impact on Apennines growth trends: among larger trees (DBH $\geq$ 65 cm), most trends were insignificant and negative, and oldest trees showed the strongest declines.
At the southern range edge of beech, the recurrent and intense droughts of the last decades have caused important growth declines, probably accompanied by synchronous mortality pulses among large trees. Bioclimatic conditions, climate variation and stem age interact with size to explain the complexity of tree growth performance, and all these factors should be taken into account when modelling long-term forest functioning.