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Commentary

Seeing the forest through the trees: how tree-level measurements can help understand forest dynamics

One of the main challenges in forest ecology is to understand and predict forest responses to climate change, climate extremes and disturbances (McDowell *et al.*, 2020). Forest monitoring and remote-sensing studies have shown that these responses can be strong (Phillips *et al.*, 2009) and long lasting (Wigneron *et al.*, 2020), with implications for carbon sequestration (Wigneron *et al.*, 2020) and community composition (Esquivel-Muelbert *et al.*, 2019). However, monitoring studies at the whole-forest level contribute little to understanding the mechanisms driving those responses. Such insights need to be obtained from observations of individual trees, because it is at this level that drought, heat, fire, insect outbreaks and other disturbances affect tree photosynthesis, water transport, growth rate and mortality risk. Forest-level responses to climatic extremes and disturbances emerge from the aggregation of these tree-level effects. Therefore, a better understanding and better predictions of forest responses to changing conditions require individual-tree response studies (Zuidema *et al.*, 2013; Sass-Klaassen *et al.*, 2016). In this issue of *New Phytologist*, Piponiot *et al.* (2022; pp. 1664–1677) take an important step in this direction through the first global analysis of size-dependent contributions of trees to forest biomass dynamics. The authors use millions of tree stem measurements from 25 forest monitoring plots to calculate size distributions of woody biomass, productivity and mortality. A unique and powerful characteristic of their Forest Global Environmental Observatory (ForestGEO) network is that thin trees (1–10 cm stem diameter) are measured in large plots (4–52 ha). The Piponiot *et al.* study proves that this extremely labour-intensive sampling of small trees pays off.

> *'How can studies on individual-tree responses to environmental conditions help in understanding and predicting whole-forest responses to disturbances and climate change?'*

One of the most striking findings in the Piponiot *et al.* study is that, whereas large trees dominate forest biomass, small trees are proportionally more important for productivity. Putting this in numbers: large trees (> 60 cm stem diameter) make up *c.* 40% of forest biomass when averaged across study sites. This is much more than the average biomass share of 5% for trees < 10 cm diameter. However, the contribution of small trees to forest productivity is twice as much as would be expected from their share in forest biomass, therefore 10% on average. This factor two higher productivity for small trees compared with their proportion in forest biomass is markedly constant across forest types and climate zones. Additionally, smaller trees were also found to contribute proportionally more to the loss of biomass through mortality. Therefore, whereas the largest trees store most of the biomass of the world's forests, small trees significantly contribute to forest dynamics. These findings are a clear motivation to continue measuring small trees where this is already done, or consider doing so where this is not the case.

Previous research has shown that small and large trees strongly differ in their responses to climatic extremes and disturbances. Observational and experimental studies found that smaller trees handle droughts better than large trees, both in terms of growth and survival (Van Nieuwstadt & Sheil, 2005; Rowland *et al.*, 2015). This is possibly due to the higher transpiration rates and greater vulnerability to hydraulic stress of large trees (Nepstad *et al.*, 2007). Fire, conversely, tends to be more lethal for smaller trees, because of their thinner bark (Van Nieuwstadt & Sheil, 2005). Other important factors driving forest dynamics – lightning and strong winds – predominantly kill larger trees (Yanoviak *et al.*, 2020) due to their higher exposure. Lastly, tree mortality induced by insect outbreaks, a major biotic driver of forest dynamics, can also be size dependent, albeit in complex ways (Stephenson *et al.*, 2019; Koontz *et al.*, 2021). In short, there are important reasons to incorporate size differences when studying the effects of disturbances and climate change. In addition, taxonomic identity, functional traits and intraspecific variation may also importantly mediate size-dependent growth and mortality responses to disturbances and climatic extremes.

How can studies on individual-tree responses to environmental conditions help in understanding and predicting forest responses to disturbances and climate change? Fig. 1 contains some examples of tree-level measurements and the data they generate. By looking backwards, the study of growth rings in tree stems has greatly contributed to understanding the effects of climatic variability (Babst *et al.*, 2019) and climate extremes (Anderegg *et al.*, 2015) on the annual biomass growth of individual trees (Fig. 1). Recent developments in growth-ring analyses in the tropics have expanded this to all forest biomes (Zuidema *et al.*, 2022), although wet and warm forests remain underrepresented. In addition, the recent rise in dendrometer studies has generated important new insights into the growth dynamics of individual trees in response to within-year climatic variation (Etzold *et al.*, 2022) and climate extremes (Salomón *et al.*, 2022). However, the scale at which these labour-intensive measurements can be implemented is limited. Finally,

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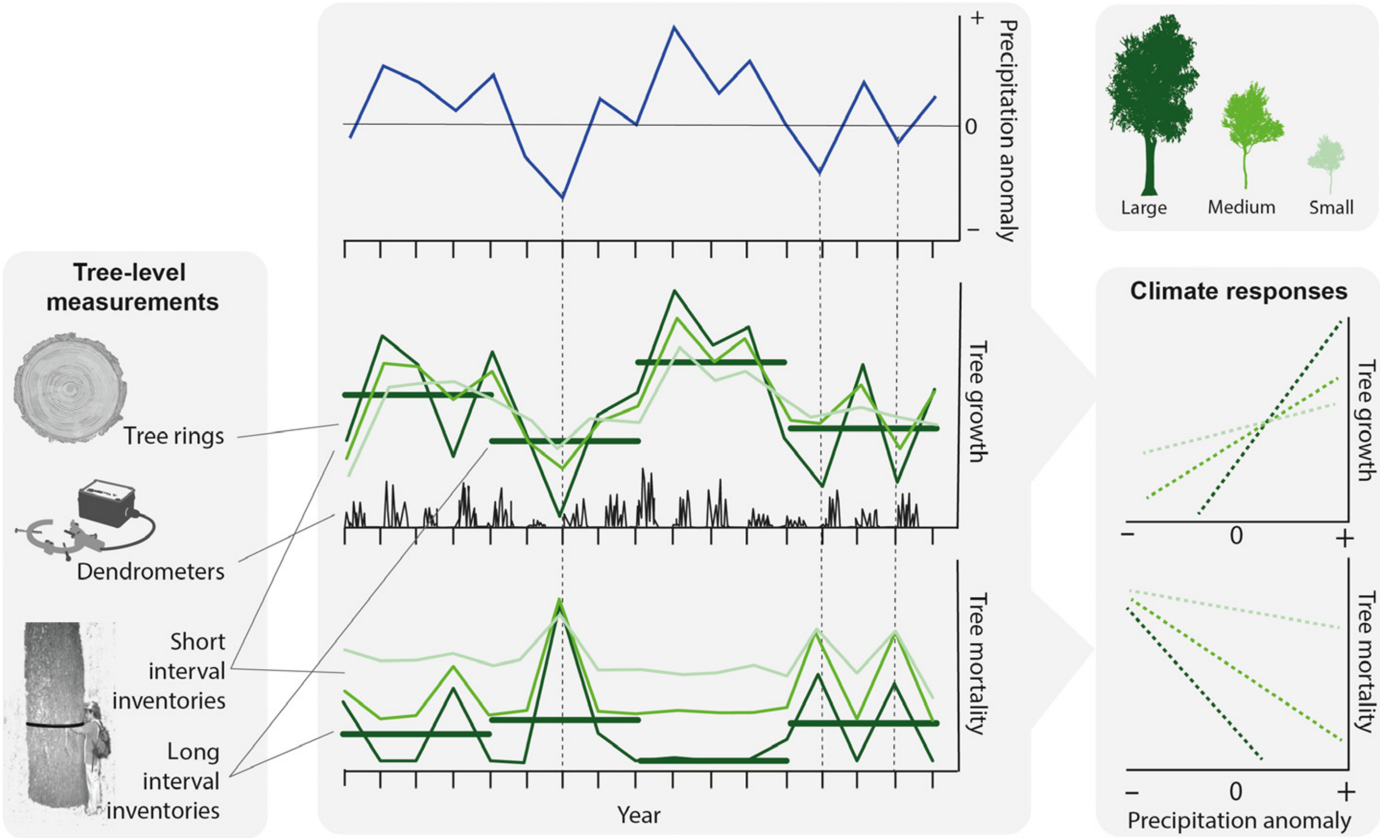

Fig. 1 Examples of tree-level measurements that could quantify sensitivity of tree growth and mortality to climatic variation and extremes. Hypothetical growth and mortality data (middle panels; black and green lines) obtained from different methods are shown in conjunction with precipitation anomalies (upper panel; blue line, extremes indicated by dashed vertical lines), for differently sized trees (green shades). Horizontal dark green lines in the middle panels indicate 4-year average values as derived from forest inventories with long census intervals (large trees only). Plots of precipitation anomalies vs growth or mortality (right panels, dashed lines) show climate responses per tree size class.

recent methodological progress has been made to overcome the limitations of long census intervals by merging tree-ring and plot-based data (Evans *et al.*, 2017). These methods have now been used to quantify the effects of past climate variation and predict responses to future climate change on tree growth (Heilman *et al.*, 2022).

In stark contrast with the increasing body of knowledge on tree growth is the rudimentary knowledge on tree mortality responses to disturbances and climate extremes (Hartmann *et al.*, 2022). Poor empirical insights into the drivers of tree mortality importantly limit model inferences of possible shifts in forest mortality under future climate change (McDowell *et al.*, 2020; Hartmann *et al.*, 2022). Studying tree mortality is hard: individual-tree death is often a stochastic event resulting from unpredictable factors such as wind throw, lightning or insect outbreaks; but it can also be a very slow process (Cailleret *et al.*, 2017). Understanding the drivers of tree mortality requires establishing climate response functions for mortality, in an analogous approach to that for tree growth (Fig. 1). The difficulty is that current methods used to study forest dynamics are generally not suitable for establishing such relations: census intervals of permanent forest plots and forest inventories are usually too long (5–10 years), tree-ring studies cannot be used to reconstruct tree mortality rates, and most satellite imagery cannot record individual-tree mortality (Hartmann *et al.*, 2022).

To close the tree mortality knowledge gap, data at the appropriate temporal and spatial resolution need to be obtained. We highlight three methodological developments that could provide such data. First, developments in remotely sensed recognition of individual-tree crowns from drone-based or airborne imagery offer the potential to monitor individual-level tree mortality (Koontz *et al.*, 2021). These methods can cover areas larger than plots, but are labour, cost and technology intensive, and can therefore not be applied on a large scale. Second, the temporal resolution of data acquisition on tree mortality in current plot studies could be increased by implementing additional, (sub) annual tree mortality assessments between regular censuses (Fontes *et al.*, 2018) or after climate extremes (Phillips *et al.*, 2009). Such assessments could be limited to larger trees (or include smaller trees in subplots) and focus on a representative subset of plots within a network. A less labour-intensive alternative could be to 'pin' a large share of trees during regular censuses, by driving a nail in the stem (or making use of existing tree-tagging nails). Pinning has been used to validate annual growth-ring formation, by counting the number of growth rings formed after the wound left by pinning (Tolera *et al.*, 2013). In plot studies, this count can identify the year of death retrospectively for ring-forming species. A third methodology is the establishment of climate responses in an indirect fashion, for example through quantifying the relationships between mortality and growth (Russo *et al.*, 2021). This method yields estimates of mortality risk as a function of growth anomalies, can be applied on a larger scale, but is likely to produce less accurate estimates of the climate sensitivity of tree mortality.

The Piponiot *et al.* study convincingly shows how massive amounts of tree-level data available from permanent plots can produce valuable insights into the drivers of forest dynamics. We argue that an important next step in forest dynamics studies is to increase the temporal resolution of tree-level growth and mortality measurements. This will generate insights into climate sensitivity of forest dynamics and therefore improve the ability to understand and predict forest responses to global change.

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