

Commentary

Radial stem variations – a source of tree physiological information not fully exploited yet

Time series of stem radius (SR) variations offer information about radial stem growth and tree water relations in unmatched quality and resolution (Steppe *et al.* 2006; Zweifel *et al.* 2006). However, the task of turning raw SR displacement readings into physiologically reasonable measures is more complicated than it appears at first sight. There is thus great potential still waiting to be discovered in terms of interpreting dendrometer readings. Chan *et al.* (2015) have added another important piece of knowledge to this topic with their approach presented in this issue of *Plant, Cell & Environment*.

The main difficulty to mechanistically interpreting radial stem variations (measured over living bark) is due to potentially co-occurring and partially opposing processes. On the one hand, there is the irreversible stem expansion of growing cells, namely, the radial increase because of dividing and enlarging wood and bark cells in the cambium (termed growth, GRO). On the other hand, there is the reversible, tree water deficit-induced shrinking and swelling of the stem (in the former called TWD), caused by imbalances between transpiration and root water uptake (Zweifel *et al.* 2005), and processes altering osmotic water potentials, for example, sugar loading and unloading in the phloem (Mencuccini *et al.* 2013). GRO is a one-directional process that only ever increases SR, whereas changing water potentials is bi-directional and can either lead to increasing or decreasing SR. Consequently, radial shrinking of the stem is always clearly attributable to decreasing water potentials and thus increasing TWD under the assumption that there is no structural degradation of the existing stem tissue structure. Radial increase, however, can either be induced by returning water and therefore swelling tissues or by GRO (Drew & Downes 2009). Consequently, any partitioning approach for SR time-series data needs a concept to define potential growth processes during periods of contracted stems, because this process is not *a priori* deducible from a single dendrometer measurement.

Chan *et al.* (2015) solved this problem with an approach that is based on two SR readings measured in parallel over the bark and on the xylem. They combine these measurements with a model calculating xylem water potentials as the main driver of diurnal stem radius fluctuations. The difference between the modelled and measured fluctuations is interpreted as growth (cambial activity) and osmotic pressure changes. The model needs (only) two parameters to be determined and is therefore ranked in about the middle of approaches ranging from very complex, multi-parameter, tree water relations and carbon transport models (De Schepper & Steppe 2010; Sevanto *et al.* 2011; Mencuccini *et al.* 2013) to very simple approaches separating growth-related and tree water-related

fractions of stem radius readings without the need of a model or additional measurements (Zweifel *et al.* 2005; Deslauriers *et al.* 2007). The entire range of approaches has their specific pros and cons and faces different levels of difficulties and most likely also inaccuracies.

Of all the various types of dendrometer applications, the over bark measurement is by far the most frequently applied worldwide. The abundance of tree physiological information in this SR time series is still poorly exploited, and one reason for that may be the difficulties mentioned in turning displacement readings into physiologically realistic measures. Other reasons may be of a more technical or practical nature, because models to separate SR data into GRO and TWD often require additional physiological data to parameterize the model, particularly data that might not be available or are difficult to measure over longer time periods (Zweifel *et al.* 2014), such as the on-xylem SR measurements needed for the method of Chan *et al.* (2015). Simple approaches for disentangling GRO and TWD without a modelling component, however, may not be accurate enough to allow for a proper separation of the two main fractions determining SR fluctuations. Nevertheless, a simple SR disentangling approach is needed that has high physiological accuracy to allow separating the two main fractions of SR time series from a single dendrometer, from studies measuring SR over bark.

Is such an approach just wishful thinking? Maybe yes, but let me put forward a hypothesis that could help solve the problem:

Stem radii below a precedent maximum indicate a complete inhibition of any cell division and cell elongation in the cambium. Or in other words, as soon as the conditions in a stem induce a shrinkage in radius – measured over (inner) bark – the turgor and water potential conditions in the cambium are assumed to cross a threshold which do not enable GRO.

With this assumption, SR measured over bark could simply and clearly be separated into irreversible GRO and reversible TWD without any further data input needed (Fig. 1). A current SR value above the precedent maximum is attributable to GRO, a current SR value below a precedent maximum is attributable to TWD. Consequently, this assumption implicitly means that an increasing SR below a precedent SR maximum is always induced by changing tree water relations and never by growth.

In fact, this approach would solve the initially posed problem of not being able to separate SR increases into GRO and TWD when stems are in a shrunken status under lowered water potentials. The SR displacement readings would become easily transformable into the biological measures GRO and TWD (Fig. 1). Summed up GRO curves then appear in a stepwise shape, clearly distinguishing between periods of growth and

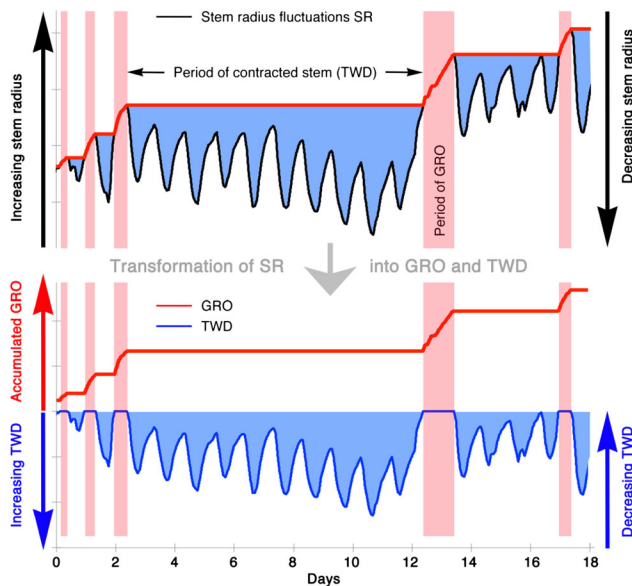


Figure 1. Transformation of stem radius fluctuations (SR, black line) into growth-induced irreversible expansion of the stem radius (GRO, red line) and reversible tree water deficit-induced shrinkage of the stem (TWD, blue line) under the assumption of completely inhibited growth processes (cell division and elongation) for periods of contracted stem radii. Red areas indicate periods of GRO, and blue areas indicate periods of TWD.

periods of increased TWD without growth. Growth in terms of cell division and cell expansion could be analysed not only in a weekly or daily resolution but even in resolutions only limited by sensor and data acquisition systems.

However, does such a hypothesis make sense? There are good arguments that cambial activity is strongly turgor and water potential driven (Lockhart 1965; Steppe *et al.* 2006) and that decreasing turgor pressures and water potentials first lead to an inhibition of cell enlargement and later to an inhibition of cell division. Hydraulic plant models have taken up this physiological functionality and successfully simulated threshold-dependent growth behaviour of trees in relation to measured stem radius changes (Steppe *et al.* 2008). However, this does not necessarily mean that such a threshold for growth would have to be at conditions of fully expanded SR. One can imagine that growth processes also could occur at slightly decreased SR. Interestingly, there are dendrometer analyses which apply concepts very similar to the one suggested here (Deslauriers *et al.* 2007; Drew & Downes 2009) but partially with other intentions. However, nobody has analysed the physiological plausibility of such an assumption in detail so far. It is up to future studies to do so, and to test to what degree the idea of no growth during periods of contracted stems is true and applicable. It would be a temptingly easy solution to a decades-old problem in the field of radial stem variation analyses.

Once we are able to properly separate water potential-induced SR changes from growth-induced ones, the high-

temporal resolution of dendrometer readings will enable us to explore new levels of microclimate-growth relationships. We might finally be able to elucidate precisely when and under what conditions plants in general, and trees in particular, grow. Further, we may be able to utilize TWD as a biological indicator for drought stress, because decreasing tree stems (= increasing TWD) indicate missing water needed to bring the stem radius back to its original size. TWD might also be of value to compare stress levels of individual trees and different species in a stand, or of a certain number of trees in a forest to quantify a biological drought stress indicator for an entire forest ecosystem. In fact, radial stem variations are a great source of tree physiological and ecological information, and our interpretations of them have not tapped the full potential residing in this technique yet.

Roman Zweifel

Forest Dynamics, Swiss Federal Research Institute
WSL, Birmensdorf, Switzerland

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