



## Commentary

# The potential of the tree water potential

Kathy Steppe<sup>1,2</sup>

<sup>1</sup>Laboratory of Plant Ecology, Department of Plants and Crops, Faculty of Bioscience Engineering, Ghent University, Belgium; <sup>2</sup>Corresponding author (kathy.steppe@UGent.be)

Received April 5, 2018; accepted May 22, 2018; published online June 12, 2018; handling Editor Danielle Way

Non-invasive quantification of tree water potential is one of the grand challenges for assessing the fate of trees and forests in the coming decades. Tree water potential is a robust and direct indicator of tree water status and is preferably used to track how trees, forests and vegetation in general respond to changes in climate and drought. In this issue of *Tree Physiology*, Dietrich et al. (2018) predict the daily canopy water potential of mature temperate trees from tree water deficit derived from stem diameter variation measurements.

**Keywords:** desorption curve, drought, hydraulic capacitance, mechanistic tree modelling, stem diameter variation, tree water status, water relations, water storage.

## Why tree water potential matters

Water potential is a key variable in plant functioning at different scales for several reasons. The water potential dictates the movement of water through any system from areas of high (less negative) to areas of low (more negative) water potential (Nobel 2009). In a tree, this movement of water can be directed axially, from deep to shallow roots via hydraulic redistribution (Neumann and Cardon 2012), from roots to leaves as defined in the soil–plant–atmosphere continuum (Nobel 2009) or from leaves to roots, when foliar water uptake occurs (Goldsmith 2013, Steppe et al. 2018). But water can also move radially within the sapwood or between the sapwood and the bark. This radial water transport is not only important to explain diel patterns of stem shrinkage and swelling, as explained in this current issue by Dietrich et al. (2018) (but also see De Swaef et al. (2015) and Steppe et al. (2015)), it also governs the tight coupling between xylem and phloem, and hence ultimately interrelates water and carbon transport and dynamics in trees (Sevanto 2014, Hubeau and Steppe 2015). This implies that a realistic quantification of tree water potential is also crucial when assessing hydraulic failure and carbon starvation mechanisms to understand and predict drought-induced tree mortality (McDowell et al. 2008). Furthermore, water potential, and not just stomatal conductance, is key to distinguish isohydric from

anisohydric behavior during drought and to quantitatively compare between tree species (McDowell et al. 2008, Klein 2014). Finally, in many conceptual frameworks, water potential acts as the independent physiologically meaningful variable to identify critical levels or thresholds related to the functioning or performance of trees, forests or even biomes, which has been exemplified by the use of xylem vulnerability curves to compare and typify vulnerability of forest biomes to drought-induced cavitation (Choat et al. 2012). In this issue, Dietrich et al. (2018) add to this concept with their proposed logistic relationship between normalized tree water deficit (TWD), derived from continuous stem diameter variation measurements, and canopy water potential (Figure 1).

## Beyond a tight link between tree water deficit and canopy water potential

In essence, the relationship between the loss of mass or volume of water from a sample with decreasing (more negative) water potential represents a desorption curve (Zweifel et al. 2000, Cochard et al. 2001). Desorption curves are increasingly gaining importance in plant research, as they quantitatively distinguish different water storage locations: (i) capillary water stored in the lumina of inactive xylem elements and in intercellular spaces, (ii) elastic water stored within living cells and (iii) water

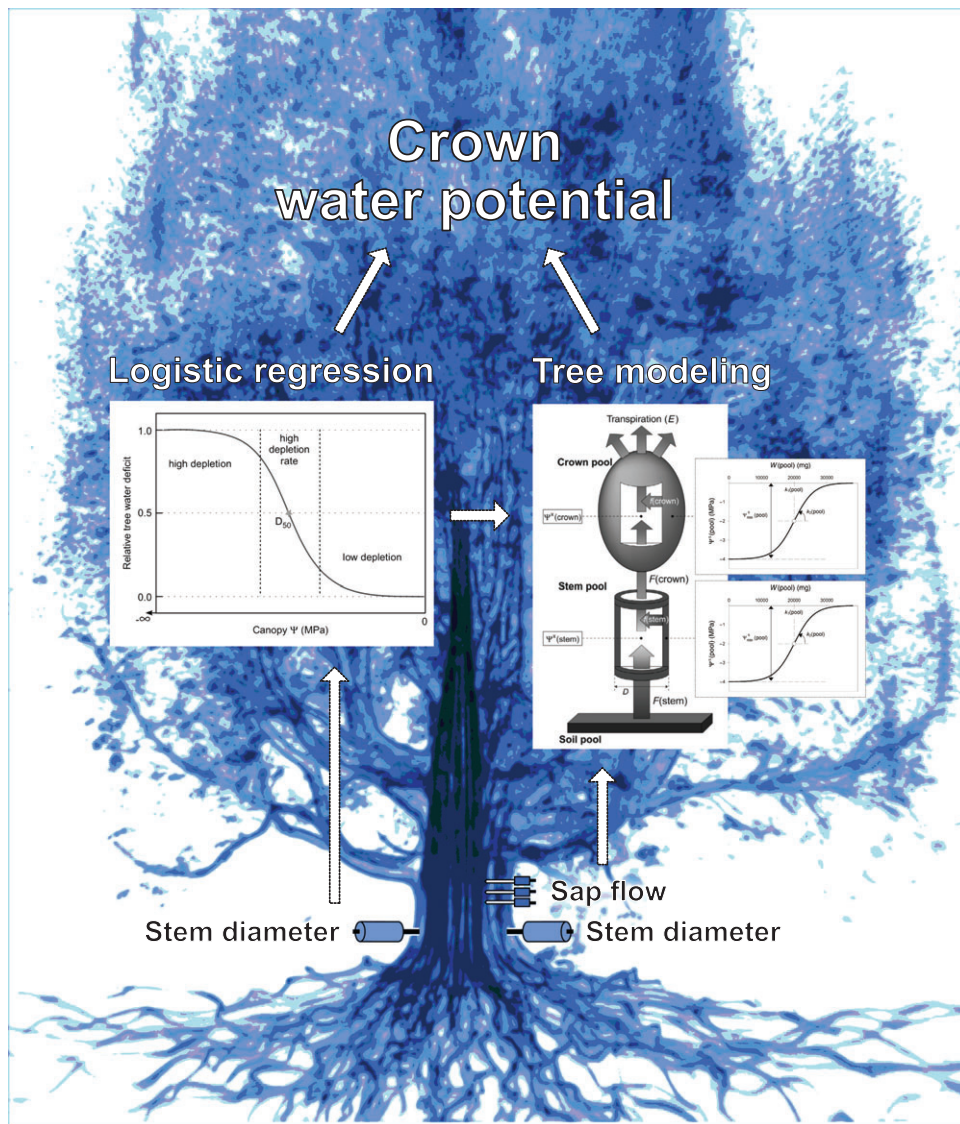


Figure 1. Conceptual representation of two approaches to quantify crown water potential as substitute for the labor-intensive manual measurements, which are a particular challenge in large trees. The logistic relationship proposed by Dietrich et al. (2018) (left) relates relative tree water deficit, derived from stem diameter variation measurements, to daily canopy water potential (canopy  $\Psi$ ). Canopy water potential can also be simulated using measurements of sap flow and stem diameter, and mechanistic tree modeling. The so-called flow and storage models that can be used for this purpose include for each storage pool a desorption curve (right), linking changes in water content ( $W$ ) in a specific water storage pool (stem, crown) to changes in associated water potential from which hydraulic capacitance values can be derived. To be successful, these models need at a certain point in time absolute and accurate canopy or stem water potential estimates for model calibration or validation. This highlights that any non-invasive approach that is able to supply tree water potential holds immense potential in both monitoring and modeling studies (basic figures adapted from Dietrich et al. (2018), Steppe et al. (2006) and <https://www.zdf.de/nachrichten/heute-in-europa/baeume-twittern-100.html>).

released during cavitation when air replaces the water-filled lumina (Zweifel et al. 2000, Cochard et al. 2001). Hydraulic capacitance of the different water storage pools can be calculated from the distinct slopes displayed in a desorption curve. These slopes define the change in amount of water present in the storage tissue for a given change in water potential of the tissue (Jarvis et al. 1981, Jones 1992), and the critical water potential value associated with the transition from the elastic storage pool to cavitation release (i.e., storage water released

by embolism) is then interchangeable with the P12-value (i.e., onset of embolism) derived from xylem vulnerability curves.

In this issue, Dietrich et al. (2018) establish desorption curves in mature individuals of six different European forest tree species, with the difference that TWD, as a proxy for tree water loss, is related to crown (or leaf) water potential instead of stem water potential if quantification of stem hydraulic capacitance had been targeted. Their proposed logistic relationship between TWD and canopy water potential also shows three distinct

phases (Figure 1), with TWD only slightly increasing at high and low crown water potentials, partly reflecting the contributions of capillary and cavitation-released water, respectively, and strongly increasing close to the point of 50% depletion of internal storage tissues (D50). The authors attribute the strong linear phase of the dependency of TWD on crown water potential to strong radial water flows from storage pools to the sapwood. Stem dehydration indeed provokes variation in stem diameter predominantly caused by shrinkage of the elastic tissues located in the bark (Zweifel et al. 2000, Cochard et al. 2001) but also by tension developed within the xylem according to the apparent elastic modulus (Irvine and Grace 1997). Mass loss per volume change (calculated from variations in stem diameter) of dehydrating stems is typically close to unity, when water is lost from living tissues (i.e., elastic hydraulic capacitance), but beyond a critical water potential threshold the ratio becomes higher than unity, when water is also lost from the less-elastic xylem tissue due to cavitation (i.e., inelastic hydraulic capacitance) (Zweifel et al. 2000, Cochard et al. 2001). This explains the logistic pattern of the relationship between TWD and canopy water potential observed by Dietrich et al. (2018), showing an asymptotically maximum TWD that cannot be further exceeded by water withdrawal from the living cells and indicating where the contribution of cavitation release begins. The D50 values that can be derived from the logistic relationship of Dietrich et al. (2018), and associated crown water potential, should be used with care when compared with P12 and P50 (i.e., the water potential at which 50% loss of conductivity occurs) values derived from xylem vulnerability curves, because capacitively stored water released from the leaves in the canopy may buffer changes in water potential. Interestingly, D50 values of the six study tree species was reached at about 50% of the normalized midday leaf water potential (see Figure 7B in Dietrich et al. (2018)), and the question arises whether this presents a general pattern or is rather related to how the reference minimum water potential value for each species has been defined.

### Challenges related to the application of the logistic relationship

The approach presented by Dietrich et al. (2018) demonstrates that stem and canopy water relations are tightly coupled on a daily basis. The beauty of the approach is that when normalized values for TWD and canopy water potential were used, a universal logistic relationship was found for the six temperate tree species (see Figure 7B in Dietrich et al. (2018)), and most likely will be found in more, if not all, tree species. The shape of the relationship (steepness of the function), however, varied depending on the study species when crown water potential was not normalized (see Figure 7A in Dietrich et al. (2018)), which can be attributed to differences in hydraulic resistances to water flow and in hydraulic capacitances linked to the elastic properties (elastic

moduli) of the tissues involved in shrinkage. Therefore, a species- and site-specific calibration curve is currently recommended by the authors, at least until future research shows that for a certain tree species a universal relationship can be established across diameter at breast height and age classes.

When applying the approach of Dietrich et al. (2018) with relative TWD and to enable comparison across studies, it is important that the highest TWD value or reference value used for normalization is reported. The shape of the logistic relationship will be determined by this reference value. In their study, Dietrich et al. (2018) used the highest species-specific TWD value measured over a wet and a dry growing season. Because of the measurements in the dry season, the logistic relationship could be fitted, which had been impossible if only the wet season data had been used. The D50 values identified are also dependent on this reference value, shaping the logical relationship. From a theoretical point of view, a far-reaching tree dehydration, at least until the living cells in the bark have lost most of their turgor, is preferable to determine the reference value and will enable construction of the logistic relationship of a species. Water released into the transpiration stream during cavitation will not be captured by this approach, because embolised inelastic xylem elements unlikely contribute to changes in stem diameter (Irvine and Grace 1997), but the stored water released during embolism will affect crown water potential.

Dietrich et al. (2018) further recommend working with absolute instead of normalized TWD values when continuously measuring stem diameter variations in a forest. While the use of TWD without further calibration is indeed meaningful in large-scale monitoring studies and can be used for a qualitative assessment of tree water status, the ultimate goal remains to non-invasively quantify canopy or stem water potential as substitute for the labor-intensive manual measurements of daily canopy water potential, which are challenging in large trees.

### The search for potential continues

The work of Dietrich et al. (2018) provides an important impetus to carry on our search for automated, non-invasive methods capable of continuous operation to quantify water potential. Whereas in their work, Dietrich et al. (2018) were seeking for daily point values of crown water potential, continuous quantification of diel water potential dynamics could be another quest. Steppe et al. (2008) predicted stem water potential dynamics using a combination of mechanistic tree modeling and continuous measurements of stem diameter variations and sap flow (Figure 1). The so-called water flow and storage models used in these applications include logistic relationships similar to the one presented by Dietrich et al. (2018) and link changes in water content in a specific tree part (trunk, crown) to associated changes in water potential (e.g., Zweifel et al. 2001, Steppe et al. 2006) (Figure 1). An advantage of tree models

being supplied with continuous measurements of sap flow is that absolute values of water potentials can be calculated. Instant visualization of real-time calculated water potential dynamics is also pursued within the TreeWatch.net initiative (Steppe et al. 2016). Tools such as these are much-needed in the forest monitoring networks of the future and are suitable for incorporating into larger-scale models to improve forecasting of tree responses and drought-induced tree and forest mortality (Hartmann et al. 2018). However, it is important to highlight that at a certain point in time any plant hydraulics model will need absolute and accurate canopy or stem water potential estimates, be it for calibration or validation purposes or to increase the set of identifiable model parameters and break correlations between model parameters.

In conclusion, any non-invasive approach that is able to supply water potential data as a substitute for the labor-intensive manual measurements holds immense potential in both monitoring and modeling studies to better represent the mechanisms that drive the responses of trees and forests to drought and projected climate changes. In this sense, it is certainly worthwhile to further explore the predictive power of stem diameter variation measurements for water potentials, as was pursued by Dietrich et al. (2018) in this issue.

### Conflict of interest

None declared.

### References

- Choat B, Jansen S, Brodribb TJ et al. (2012) Global convergence in the vulnerability of forests to drought. *Nature* 491:752–756.
- Cochard H, Forestier S, Ameglio T (2001) A new validation of the Scholander pressure chamber technique based on stem diameter variations. *J Exp Bot* 52:1361–1365.
- De Swaef T, De Schepper V, Vandegehuchte MW, Steppe K (2015) Stem diameter variations as a versatile research tool in ecophysiology. *Tree Physiol* 35:1047–1061.
- Dietrich L, Zweifel R, Kahmen A (2018) Daily stem diameter variations can predict the canopy water status of mature temperate trees. *Tree Physiol* 7:941–952.
- Goldsmith GR (2013) Changing directions: the atmosphere–plant–soil continuum. *New Phytol* 199:4–6.
- Hartmann H, Moura CF, Anderegg WRL et al. (2018) Research frontiers for improving our understanding of drought-induced tree and forest mortality. *New Phytol* 218:15–28.
- Hubeau M, Steppe K (2015) Plant-PET scans: in vivo mapping of xylem and phloem functioning. *Trends Plant Sci* 20:676–685.
- Irvine J, Grace J (1997) Continuous measurements of water tensions in the xylem of trees based on the elastic properties of wood. *Planta* 202:455–461.
- Jarvis PG, Edwards WRN, Talbot H (1981) Models of plant and crop water use. In: Rose DA, Charles-Edwards DA (eds) *Mathematics and plant physiology*. Academic Press, London, pp 151–194.
- Jones HG (ed) (1992) *Plants and microclimate. A quantitative approach to environmental plant physiology*. University Press, Cambridge, UK.
- Klein T (2014) The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. *Funct Ecol* 28:1313–1320.
- McDowell NG, Pockman WT, Allen CD et al. (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytol* 178:719–739.
- Neumann RB, Cardon ZG (2012) The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. *New Phytol* 194:337–352.
- Nobel PS (ed) (2009) *Physicochemical and environmental plant physiology*. Academic Press, Oxford, UK.
- Sevanto S (2014) Phloem transport and drought. *J Exp Bot* 65:1751–1759.
- Steppe K, De Pauw DJW, Lemeur R, Vanrolleghem PA (2006) A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth. *Tree Physiol* 26:257–273.
- Steppe K, De Pauw DJW, Lemeur R (2008) A step towards new irrigation scheduling strategies using plant-based measurements and mathematical modelling. *Irrig Sci* 26:505–517.
- Steppe K, Sterck F, Deslauriers A (2015) Diel growth dynamics in tree stems: linking anatomy and ecophysiology. *Trends Plant Sci* 20:335–343.
- Steppe K, von der Crone J, De Pauw DJW (2016) TreeWatch.net: a tree water and carbon monitoring network to assess instant tree hydraulic functioning and stem growth. *Front Plant Sci* 7:Article 993.
- Steppe K, Vandegehuchte MW, Van de Wal BAE, Hoste P, Guyot A, Lovelock CE, Lockington DA (2018) Direct uptake of canopy rainwater causes turgor-driven growth spurts in the mangrove *Avicennia marina*. *Tree Physiol* doi:10.1093/treephys/tpy024.
- Zweifel R, Item H, Hasler R (2000) Stem radius changes and their relation to stored water in stems of young Norway spruce trees. *Trees* 15:50–57.
- Zweifel R, Häsler R, Item H (2001) Link between diurnal stem radius changes and tree water relations. *Tree Physiol* 21:869–877.