Tree Physiology review

Stem diameter variations as a versatile research tool in ecophysiology

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High-resolution stem diameter variations (SDV) are widely recognized as a useful drought stress indicator and have therefore been used in many irrigation scheduling studies. More recently, SDV have been used in combination with other plant measurements and biophysical modelling to study fundamental mechanisms underlying whole-plant functioning and growth. The present review aims to scrutinize the important insights emerging from these more recent SDV applications to identify trends in ongoing fundamental research. The main mechanism underlying SDV is variation in water content in stem tissues, originating from reversible shrinkage and swelling of dead and living tissues, and irreversible growth. The contribution of different stem tissues to the overall SDV signal is currently under debate and shows variation with species and plant age, but can be investigated by combining SDV with state-of-the-art technology like magnetic resonance imaging. Various physiological mechanisms, such as water and carbon transport, and mechanical properties influence the SDV pattern, making it an extensive source of information on dynamic plant behaviour. To unravel these dynamics and to extract information on plant physiology or plant biophysics from SDV, mechanistic modelling has proved to be valuable. Biophysical models integrate different mechanisms underlying SDV, and help us to explain the resulting SDV signal. Using an elementary modelling approach, we demonstrate the application of SDV as a tool to examine plant water relations, plant hydraulics, plant carbon relations, plant nutrition, freezing effects, plant phenology and dendroclimatology. In the ever-expanding SDV knowledge base we identified two principal research tracks. First, in detailed short-term experiments, SDV measurements are combined with other plant measurements and modelling to discover patterns in phloem turgor, phloem osmotic concentrations, root pressure and plant endogenous control. Second, long-term SDV time series covering many different species, regions and climates provide an expanding amount of phenotypic data of growth, phenology and survival in relation to microclimate, soil water availability, species or genotype, which can be coupled with genetic information to support ecological and breeding research under on-going global change. This under-exploited source of information has now encouraged research groups to set up coordinated initiatives to explore this data pool via global analysis techniques and data-mining.

Keywords: carbon relations, dendrometer, irrigation scheduling, linear variable displacement transducer (LVDT), nutrients, phloem, plant water relations, sap flow, stem radius changes, xylem.

Introduction

Since their first appearance in the 1970s (Klepper et al. 1971, Kozlowski 1971, Huck and Klepper 1977), point or band dendrometers have been used increasingly to study high-resolution

(1–10 µm) stem diameter variations (SDVs). These first observations have demonstrated the close link between diel variations in plant water status and diel variations in stem diameter, and have induced extensive research efforts on the application of

such measurements for drought stress detection and plant-based irrigation scheduling in the following decades. Reviews by Fernandez and Cuevas (2010) and Ortuño et al. (2010) have highlighted the potential of SDV in irrigation scheduling, but additionally evoked important limitations: besides plant water status, other plant physiological and biophysical processes affect the diel SDV pattern, as such impeding the interpretation of the SDV signal with respect to the plant water status per se. In the last decade, these other mechanisms (and their effect on SDV) have been studied by combining SDV with other plant measurements or modelling. This approach has highlighted the potential of SDV as a method to study fundamental plant physiological mechanisms underlying whole-plant functioning and growth, including among others carbon relations, phenology and hydraulics. This article therefore aims to review the important insights that have arisen from these more recent SDV applications, to identify current trends in fundamental research and to demonstrate the use of modelling as a tool to better exploit SDV data. First, the basic mechanisms underlying SDV are briefly discussed, including the contribution of different stem tissues to the overall SDV signal. Second, the use of SDV in combination with plant modelling as a means to integrate and expand knowledge about plant water and carbon relations and whole-plant functioning is discussed, which demonstrates how SDV are applied as a tool in different eco-physiological research areas. Finally, trends and expectations for future research are outlined.

Basics of SDVs

Diel SDV are the combined result of mainly four simultaneously co-acting mechanisms: (i) reversible contraction and expansion of dead conducting xylem elements due to the increase and relaxation of internal tensions, (ii) reversible shrinkage and swelling of living tissues in response to different levels of tissue hydration, (iii) irreversible radial stem growth and (iv) thermal expansion and contraction (Daudet et al. 2005). In addition, as a fifth component, lunisolar tidal forces have been suggested to influence SDV, but this has not yet been unequivocally evidenced (Zürcher et al. 1998, Vesala et al. 2000, Barlow and Fisahn 2012).

The stem of dicots consists of the following tissues (from inside to outside): (i) non-functional xylem (heartwood), (ii) functional xylem (sapwood), (iii) cambium, (iv) functional phloem, (v) non-functional phloem, (vi) cortex and (vii) epidermis or periderm. Due to the rigidity of the xylem tissue, reversible shrinkage and swelling in the xylem are generally believed to contribute little to total SDV (Cermak and Nadezhdina 1998, Scholz et al. 2008). As such, Irvine and Grace (1997) reported for 41-year-old Scots pine trees that <10% of SDV occurred in xylem tissues. According to Scholz et al. (2008) this low contribution, and thus low elasticity of the xylem for several species of savannah trees could partly be explained by a higher density of the xylem, compared with the storage tissues outside the xylem.

As such, the denser sapwood exhibited smaller changes in cross-sectional area per unit change in water potential compared with the living storage tissues. Because the heartwood is not actively participating in water and sugar transport, its contribution to SDV is often neglected (Hölttä et al. 2006, De Schepper and Steppe 2010).

In contrast to these reports, where xylem diameter variations (XDV) contribute only marginally to total SDV, Sevanto et al. (2002) reported that the amplitude of XDV in Scots pine was ~30–50% of SDV. In *Eucalyptus*, the contribution of XDV varied between 30 and 60%, but showed an opposite pattern with a daytime increase in XDV, whereas the inner bark showed the expected daytime decrease (Zweifel et al. 2014, Pfautsch et al. 2015a, 2015b). While Zweifel et al. (2014) explained this particular behaviour by the high specific tissue elasticity of the non-lignified xylem cells, Pfautsch et al. (2015a) hypothesized a different mechanism that involves reversal of radial transport of carbohydrates. Similarly, differences in relative amplitude of XDV and SDV between different heights in a tree and between tree species were also attributed to differences in wood elasticity (Sevanto et al. 2003).

The phloem tissue mainly consists of sieve tubes, companion cells, phloem fibres and phloem parenchyma. The functional phloem is responsible for the vertical sugar transport and generally corresponds with the latest annual growth ring (Raven et al. 1999, Rosner et al. 2001), whereas the non-functional phloem consists of the older, remaining phloem growth rings in which the sieve tubes have lost their transport ability. Magnetic resonance images (MRI) demonstrated that contribution to SDV of the functional phloem and cambium is much lower compared with the other bark storage tissues (non-functional phloem, cortex and periderm), although the former contain the highest amount of water (De Schepper et al. 2012). This low contribution is probably due to the high concentration of osmotically active substances in the cambium and functional phloem. Hence, it seems that the less physiologically active living tissues (i.e., non-functional phloem, cortex and periderm) contribute most to the stem's water storage capacity and thus to SDV.

Modelling SDV

Although SDV are predominantly the result of dynamics in water transport between tissues, many different physiological mechanisms and mechanical properties can alter the SDV profile. Consequently, SDV are not always easy to interpret, but are a potential untapped source of dynamic information on these mechanisms and properties. To unravel these dynamics and to extract information on plant physiology or plant biophysics from SDV, mechanistic modelling has proved to be a valuable tool. Models can include the different mechanisms underlying SDV, and help us to understand complex and interlinked relationships between the various plant mechanisms.

Models describing SDV generally divide the plant into vertical and/or radial compartments, in which total, hydrostatic and osmotic potential are calculated. Water flows between consecutive compartments (F in g h^{-1}) are driven by a total water potential gradient (if crossing of a semi-permeable membrane is required; Eq. (1): $\sigma > 0$) or a hydrostatic water potential gradient (absence of a semi-permeable membrane; Eq. (1): $\sigma = 0$) (Steudle and Tyerman 1983, Passioura and Munns 1984):

$$F = \frac{\Delta P + \sigma \Delta \Pi}{R} = L \cdot (\Delta P + \sigma \Delta \Pi), \qquad (1)$$

where Δ denotes gradient, P is the hydrostatic pressure (MPa), Π is the osmotic potential (MPa) (and total water potential = $\Psi = P + \Pi$), σ is the reflection coefficient for solutes ranging between 0 and 1 (dimensionless), R is the hydraulic resistance (MPa h g^{-1}) and L is the hydraulic conductance (g MPa^{-1} h^{-1}) (= $1/R$). As such, incoming and outgoing flows determine water accumulation or depletion in each compartment, ultimately resulting in volume and diameter changes.

During the past decades, there has been an evolution towards increased complexity in these models. Initial models divide the tree into different vertical compartments between which water flows (Zweifel et al. 2001, Figure 1a, Perämäki et al. 2001, Figure 1b). This vertical water flow between consecutive compartments ($F_{i \rightarrow i+1}$) is calculated based on the transport-resistance electric analogue concept of van den Honert (1948) (Eq. (2)):

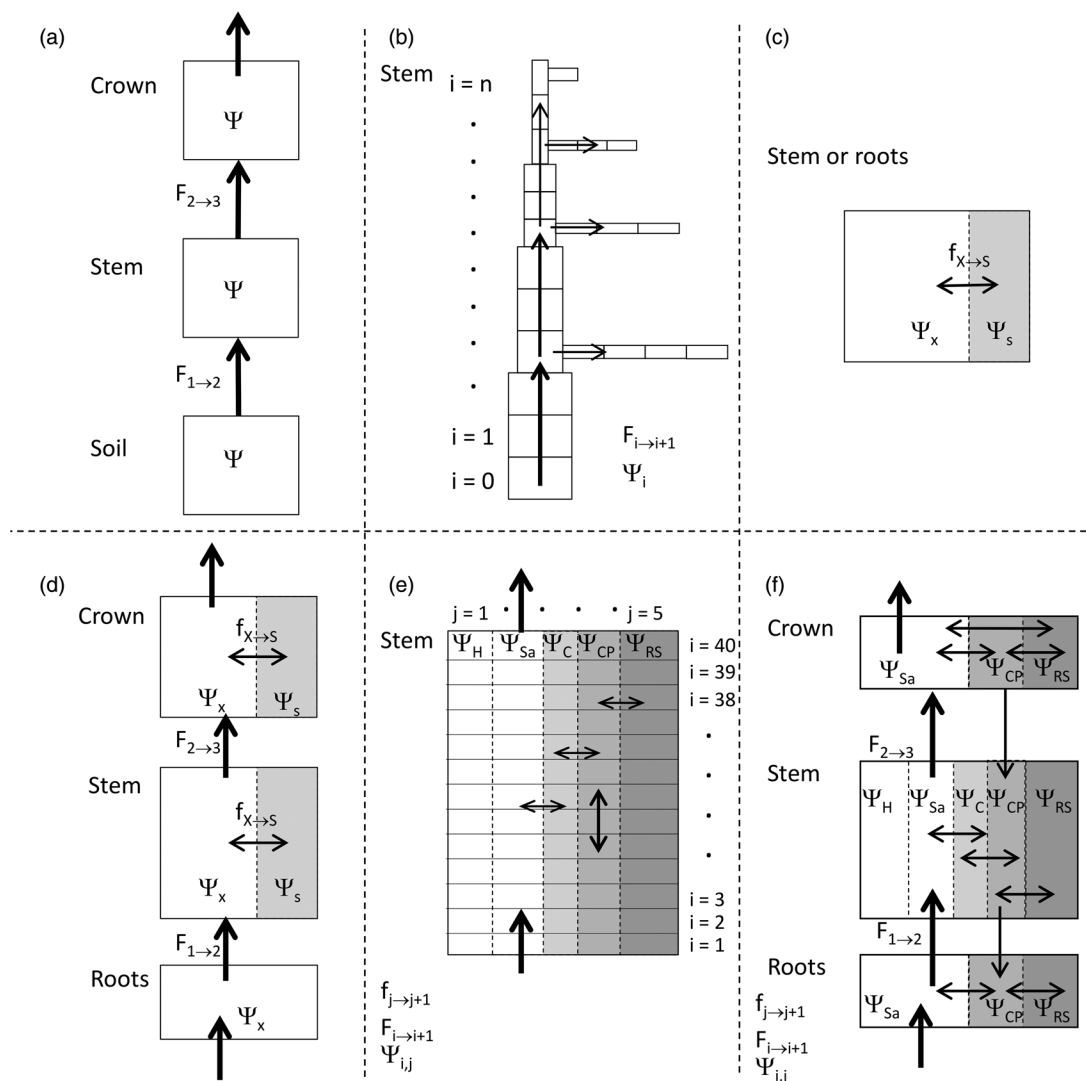$$F_{i \rightarrow i+1} = \frac{\Psi_i - \Psi_{i+1}}{R_x}, \qquad (2)$$

Figure 1. The first models (a and b) simulate stem diameter variations by considering the stem as one tissue which can be vertically divided, together with vertical water flow (F); subsequent models (c and d) radially divide the stem in xylem tissue (X) and storage tissue, which is pooled as one storage tissue (S), as such they consider also radial water flow (f); the most complex models (e and f) subdivide the stem tissue in heartwood (H), sapwood (Sa), cambium (C), conductive phloem (CP) and remaining storage tissues (RS). Schematic presentation of the models by: (a) Zweifel et al. (2001); (b) Perämäki et al. (2001); (c) Génard et al. (2001); (d) Steppe et al. (2006); (e) Hölttä et al. (2006); and (f) De Schepper and Steppe (2010).

where Ψ is the total water potential (MPa). Water storage (W_i) in each of these compartments is calculated as the difference between incoming and outgoing flows:

$$\frac{dW_i}{dt} = F_{i-1 \rightarrow i} - F_{i \rightarrow i+1} - \sum F_{branch} \tag{3}$$

where $F_{i-1 \rightarrow i}$ is the incoming water flow in element i, $F_{i \rightarrow i+1}$ is the outgoing water flow towards element $i + 1$ and F_{branch} is the outgoing water flow towards a side branch at level i (Figure 1b). These models did not discriminate between radial tissues, and thus, radial transport between xylem and bark was not modelled. The relation between water potential and water content (W) in an element was calculated using Hooke's law (Perämäki et al. 2001, Eq. (4)):

$$\frac{dW}{dt} = \frac{W}{\varepsilon} \cdot \frac{d\Psi}{dt}, \tag{4}$$

where ε is the elastic modulus of the considered element (MPa), or using a desorption curve (Zweifel et al. 2001, Eq. (5) and Figure 2):

$$\Psi_i = \frac{\Psi_{i,min}}{\exp((-k_{1,i} + W_i)/k_{2,i}) + 1}, \tag{5}$$

where $\Psi_{i,min}$ is the minimum of Ψ_i (MPa), $k_{1,i}$ is the amount of water stored at the inflection point of the desorption curve (g) and $k_{2,i}$ is the index for the slope of Ψ (W) at the inflection point (Figure 2).

In a next approach, the (woody) stem was represented as a set of two coaxial cylinders corresponding with the mature xylem and the extensible storage tissues (Figure 1c, Génard et al. 2001). The extensible tissues were assumed to behave as a single cell, separated from the mature xylem by a virtual membrane. As such, the water flow between both cylinders was calculated using Eq. (1). Furthermore, this approach includes temperature effects on the mature xylem and the extensible tissues, and describes the reversible shrinkage and swelling of the living tissues based on Hooke's law:

$$\frac{dV_s}{dt} = \frac{V_s}{\varepsilon} \frac{dP_s}{dt}, \tag{6}$$

and the irreversible growth, which is described by the Lockhart (1965) equation:

$$\frac{1}{V_s} \frac{dV_s}{dt} = \phi(P_s - Y) \quad \text{if } P_s \geq Y, \tag{7}$$

where V_s is the volume of the storage tissue, ϕ is the cell wall extensibility (MPa^{-1} h^{-1}), P_s is the turgor pressure (MPa) and Y is the turgor threshold above which wall yielding occurs (MPa).

Subsequently, the basic flow equations, the vertical structure of Zweifel et al. (2001), and the detailed analysis of radial elastic and plastic variations, as introduced by Génard et al. (2001), were combined into a dynamic water flow and storage model (Steppe et al. 2006). As such, three consecutive vertical compartments are linked by axial water transport (Figure 1d). Each of these compartments contains a xylem and a storage pool, separated by a virtual membrane allowing radial water transport as described by Génard et al. (2001). The development of this model demonstrated that a constant hydraulic capacitance of the storage tissue resulted in equal model performance with less parameters compared with the use of a bended desorption curve (Figure 2, Eq. (5)). With a constant capacitance, the desorption curve equals a straight line with a slope equal to the inverse of the hydraulic capacitance (Figure 2).

Recent models take higher radial complexity into account, often in combination with the description of vertical phloem transport. For instance, Hölttä et al. (2006) developed a model that only describes the stem compartment, but it is vertically discretized into 40 elements (Figure 1e). Radially, the stem compartment discriminates between five concentric tissue layers: heartwood, sapwood, cambium, sieve elements and the remaining living bark tissue. Axial water transport inside the xylem and the phloem is described based on pressure gradients, as was stated by the cohesion and Münch (1930) theory. Radial water transport
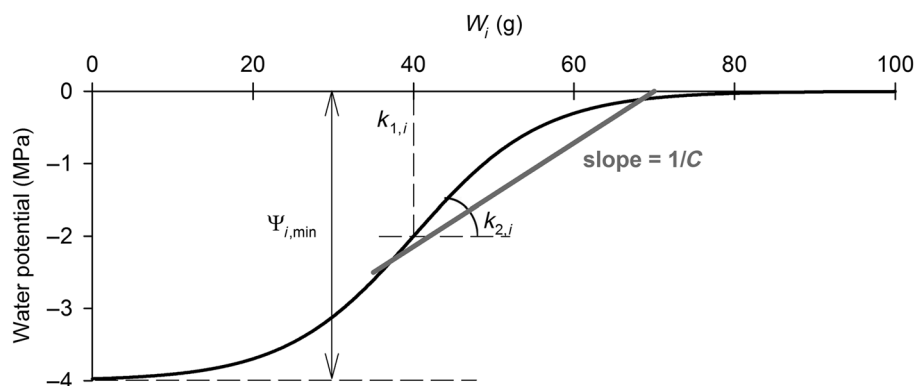
Figure 2. Desorption curves, describing the tissue water content in relation to the tissue water potential, after Zweifel et al. (2001) (black line) and Steppe et al. (2006) (grey line). The depicted parameters $k_{1,i}$, $k_{2,i}$ and $\Psi_{i,min}$ are used to describe the desorption curve in Eq. (5). C is the capacitance and W_i is the water content of the storage tissue.

between adjacent compartments is according to Eq. (1) (considering *F* is radial flow and *R* is radial hydraulic resistance) and resulted only in reversible shrinkage and swelling of the stem, without integration of irreversible stem growth. This model includes variations in xylem diameter as a result of variations in internal tension in the xylem as described by Hooke's law (Eq. (4)). More recently, this model was coupled with a detailed model that predicts cambial softwood growth (Hölttä et al. 2010).

Aiming to better understand whole-tree transport processes, De Schepper and Steppe (2010) combined the vertical structure of Steppe et al. (2006) and Zweifel et al. (2001) with the radial structure of Hölttä et al. (2006). In addition to reversible shrinkage and swelling of all radial tissues, this model includes irreversible stem diameter growth originating from the cambial zone between the xylem and the phloem. Recent models of De Swaef et al. (2013a, 2013b), Mencuccini et al. (2013) and Sevanto et al. (2014) use parts of these concepts applied to specific research questions. A comparative non-exhaustive summary of the basic models of SDV, differing in complexity, is presented in Table 1.

Implementation and application of models has propelled our knowledge on whole-plant functioning and growth, and is essential to integrate functioning with internal and external factors (Steppe et al. 2015b). To visualize effects of variable plant physiological, environmental or biophysical conditions on SDV, we performed a manual sensitivity analysis with the model of Steppe et al. (2006) optimized for tomato (De Swaef and Steppe 2010), which is implemented in the plant modelling software PhytoSim (Phyto-IT BVBA, Mariakerke, Belgium). Simulated SDV using a set of reference parameter values were compared with simulated SDV with one parameter value altered, keeping the other parameter values constant. This analysis aimed to visualize the effect of individual parameters, and should not be interpreted quantitatively, since co-occurring changes in multiple parameters alter the quantitative outcome. The reference parameter values are hypothetical, but within the range found in the literature, and are given in Table 2. The resulting graph of this analysis (Figure 3) is used to illustrate the concepts discussed in the following paragraphs.

Table 1. Comparison of different basic models describing SDV.

	Zweifel et al. (2001)	Perämäki et al. (2001)	Génard et al. (2001)	Steppe et al. (2006)	Hölttä et al. (2006)	De Schepper and Steppe (2010)
Vertical components	Roots (1) Stem (1) Crown (1)	Stem (*n*) Branches	Stem (1) or root (1)	Roots (1) Stem (1) Crown (1)	Stem (40)	Roots (1) Stem (1) Crown (1)
Radial components	One pool	One pool	Xylem Storage	Xylem Storage	Heartwood Sapwood Cambium Functional phloem Non-functional living cells	Heartwood Sapwood Cambium Functional phloem Non-functional living cells
Vertical transport	Water	Water	No	Water	Water Sugar	Water Sugar
Radial transport	No	No	Yes	Yes	Yes	Yes
Reversible SDV	Yes	Yes	Yes	Yes	Yes	Yes
Irreversible growth	No	No	Yes	Yes	No	Yes
Xylem	–	–	Rigid	Rigid	Elastic	Elastic growing

Table 2. Reference parameter values used for the model simulations.

Parameter	Unit	Value	Literature range[1]
Maximum transpiration	g h⁻¹	100	–
Soil water potential	MPa	−0.1	–
Xylem hydraulic resistance	MPa h g⁻¹	0.01	4×10^{-4}–0.05
Elastic modulus of storage tissue	MPa	1	1–50
Wall extensibility	MPa⁻¹ h⁻¹	0.02	8×10^{-4}–0.324
Threshold for wall yielding	MPa	0.6	0.2–0.9
Radial hydraulic conductance	g MPa⁻¹ h⁻¹	2000	12.5–12,500[2]
Carbon concentration	g sucrose eq. g⁻¹ [3]	0.15	0.08–0.24

[1]Values were taken from De Schepper and Steppe (2010) and Fishman and Génard (1998).
[2]Depends on the stem diameter. Values were therefore recalculated for stems of 1 cm, as the simulations were done for a hypothetical tomato.
[3]Expressed as sucrose ($C_{12}H_{22}O_{11}$) equivalents because sucrose is the major transport form of carbon.
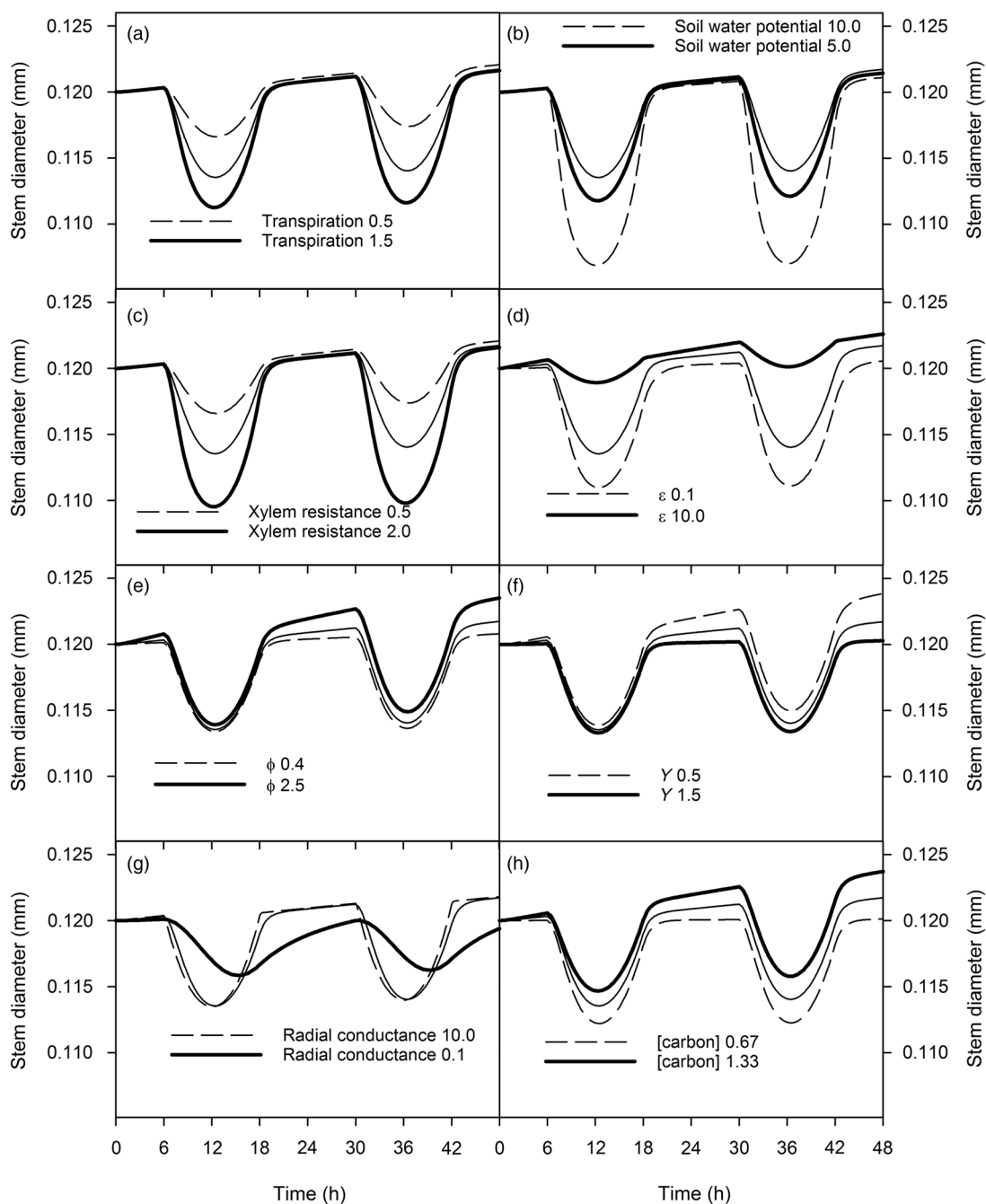
Figure 3. Visualization of the effects of different parameters on the dynamics in SDV using hypothetical data for two consecutive days: (a) transpiration, (b) soil water potential, (c) xylem hydraulic resistance, (d) elastic modulus of the living tissue (ε), (e) cell wall extensibility of the storage tissue (ϕ), (f) the threshold for wall yielding of the storage tissue (Y), (g) radial hydraulic conductance between xylem and storage tissue, and (h) carbon concentration of the storage tissues ([carbon]). The regular line represents the simulation using the reference parameter values given in Table 2. The dashed and thick lines represent the simulation with reference parameter values multiplied by the factor depicted in the graph.

Stem diameter variations as an ecophysiological research tool

Plant water status and elastic SDV

The diel course of SDV represents the sum of all internal and external conditions affecting tree water relations (Zweifel and Hasler 2001, Steppe et al. 2015a). Effects of variations in transpiration, soil water availability and xylem hydraulic resistance

on SDV dynamics are demonstrated in Figure 3a–c, respectively. In accordance with the cohesion tension theory (e.g., Dixon and Joly 1895, Meinzer et al. 2001, Steudle 2001), these processes (Figure 3a–c) have a direct effect on stem xylem water potential (Ψ_x), leaving Ψ_x to be the best direct indicator of plant water status (Jones 2004). Variations in Ψ_x result in XDV according to Hooke's law (Daudet et al. 2005, Sevanto et al. 2008). Using

this equation, Irvine and Grace (1997) used XDV as an indirect, non-intrusive method to measure variations in Ψ_x, with the elastic modulus (ε_x) as allometric parameter, dependent on the elastic properties of the wood.

Because of the hydraulic coupling, varying Ψ_x from an initial state of equilibrium initiates radial water transport between the conductive xylem and the surrounding storage tissue. Cochard et al. (2001) related changes in stem diameter (ΔD m) to the water potential gradient between the storage and the xylem tissues ($\Delta\Psi$) via the hydraulic capacitance of the storage tissue (C in MPa m^{-1}):

$$\Delta D = C \cdot \Delta\Psi. \qquad (8)$$

In many studies, C is defined somewhat differently as the ratio of the change in the amount of water (volume or mass) present in the storage tissue to the change in Ψ_s (e.g., Jarvis et al. 1981, Hunt et al. 1991, Jones 1992, Steppe et al. 2006) (g MPa^{-1}or m^3 MPa^{-1}):

$$C = \frac{dW_s}{d\Psi_s}. \qquad (9)$$

The hydraulic capacity of trees to use internally stored water helps them to maintain the maximum rates of transpiration for a longer fraction of the day, and thus to maintain leaf water status (Goldstein et al. 1998). Reported daily contributions of internally stored water to daily transpiration range from ~5% in young beech trees in the growth chamber (Steppe and Lemeur 2004) to 9–15% in five tropical forest canopy trees (Goldstein et al. 1998), and up to 22% in temperate broad-leaved tree species (Kocher et al. 2013). In Norway spruce, internally stored water contributes ~10% to daily transpiration on sunny days and up to 65% on cloudy days (Zweifel et al. 2001). At the time of maximum transpiration, the contribution of internally stored water to transpiration could even reach 75% (Zweifel et al. 2001).

Whereas C quantifies the change in W_s for a given change in Ψ_s (Eq. (9)), ε_s describes the link between W_s (or V_s) and P_s (Eq. (6)). Consequently, parameters C and ε_s are closely related. For instance, high ε_s defines inelastic tissue in which a small change in W_s produces a large change in P_s (Eq. (6)) and consequently in Ψ_s (Figure 3d). According to Eq. (9), the hydraulic capacity of the tissue to contribute to the transpiration stream is consequently small.

Plant water status and irreversible growth

In addition to the elastic deformation of the different tissues (Eq. (6)), SDV result from plastic, irreversible growth (Eq. (7)). According to Cosgrove (1993), growing tissues maintain a water potential gradient via cell wall loosening when turgor exceeds Y. The capacity of cell wall loosening is represented by ϕ (Eq. (7)), and can vary between species, between tissues and with age. Tissues with higher ϕ can maintain a higher water

potential gradient and consequently grow faster (Figure 3e). Additionally, lower Y values favour tissue growth (Eq. (7), Figure 3f). This concept of plastic and elastic growth has also been used to investigate the development of growing fruit (Léchaudel et al. 2007, Liu et al. 2007), and has potential to explain leaf growth in terms of plant water status. The latter may be of utmost importance when studying functional and structural feedback mechanisms of leaves in conditions of limited water availability. Reduced leaf elongation is as such a direct consequence of the water-limited conditions, but also serves as a protective mechanism against excessive evaporative water loss (Pantin et al. 2012, Tardieu et al. 2015).

Drought stress and hydraulic resistance in the xylem

The effect of drought stress on SDV and possible applications of SDV as a drought stress indicator in irrigation scheduling have already been summarized in very comprehensive reviews (Fernandez and Cuevas 2010, Ortuño et al. 2010) and are not the scope of the present review. However, the use of SDV as an indicator for drought stress is not restricted to irrigation solely, but has important applications in ecology as well. Impacts of climate change-induced drought on radial stem growth in trees are an active area of research. Time series analyses of SDV are increasingly used to investigate responses and resilience of trees to drought in natural conditions (e.g., Turcotte et al. 2011, Biondi and Rossi 2014) and in rain exclusion experiments (e.g., Belien et al. 2014), and forest management actions to reduce stand vulnerability to drought have been proposed based on high-frequency SDV data (Van der Maaten 2013). Moreover, direct plant stress sensing by SDV has been recommended for a quantitative understanding of drought stress effects on biogenic volatile organic compound (BVOC) emissions, as different levels of drought stress might have fundamentally different effects on BVOC emissions (Šimpraga et al. 2011). Although tree stem growth has huge ecological implications, it is poorly understood, and an integrative theory to understand the causes and consequences of stem growth patterns, and to predict impacts of drought on annual tree growth patterns remains lacking (Steppe et al. 2015a).

Mechanistic plant models aiming at integration are likely to become increasingly important in furthering our knowledge of plant hydraulic functioning during drought (Steppe et al. 2015a, 2015b). Xylem hydraulic resistance (Eq. (2)) is one of the key model parameters capturing the effect of drought stress and affecting the amplitude in SDV (Figure 3c). Enhanced hydraulic resistance lowers Ψ_x, which consequently enhances the transport of water from the storage tissue towards the xylem tissue and causes increased shrinkage.

Steppe and Lemeur (2007) used a mechanistic water flow and storage model (Steppe et al. 2006) to evaluate the effect of diffuse (in beech; *Fagus sylvatica* L.) or ring-porous xylem (in oak; *Quercus robur* L.) on the hydraulic resistance to axial water

transport. Parameters in this model were optimized using SDV measurements. These measurements showed a larger shrinkage in beech compared with oak, partly due to a higher elasticity of the storage tissue and partly due to a more negative xylem water potential, although soil water potential and transpiration rate were similar for beech and oak. Xylem hydraulic resistance in beech was found to be about twice that of oak because of their different xylem anatomy (Steppe et al. 2004).

In addition, hydraulic resistance in the xylem can be influenced by embolism, i.e., water conduits becoming filled with gas under high water tensions in transpiring plants. Recently, Schenk et al. (2015) highlighted that most bubbles in the xylem sap are small and harmless, and that these nanobubbles do not pose a threat to plant hydraulic functioning. However, when the gas nanobubbles enlarge with increasing tension or when an excessive number of bubbles coalesce into larger ones, then nanobubbles become unstable and form embolisms, which hinders the axial water transport in the conduit (Schenk et al. 2015, Steppe et al. 2015a, 2015b), and increases hydraulic resistance. This is a very recent finding, and is currently under experimental validation. In a model approach, Hölttä et al. (2002) theoretically demonstrated that XDV can be linked to the frequency and extent of embolism under field conditions. This link was experimentally confirmed by combining measurements of XDV and acoustic emissions (AE) under field conditions (Hölttä et al. 2005). By combining continuous measurements of AE, XDV and gravimetrical water loss, Vergeynst et al. (2013, 2015) developed a new method to assess both the decrease in hydraulic conductivity (i.e., vulnerability curve) and the change in hydraulic capacitance during bench dehydration of twigs and branches, which revealed that loss in hydraulic conductivity was accompanied by a gain in hydraulic capacitance. A certain degree of cavitation may thus be favourable for plants to survive periods of drought stress (Vergeynst et al. 2015).

Baert et al. (2015) implemented a dynamic function to describe xylem axial hydraulic resistance in the model of Steppe et al. (2006), instead of the previously applied constant parameters, which greatly improved model performance for drought-stressed conditions.

Radial hydraulic coupling

Decreasing radial conductance (L_{rad}) to water transport between the xylem and the storage tissue enhances the time lag between transpiration and SDV dynamics (Figure 3g). Moreover, when this conductance is too low, plants might not be able to refill their water storage tissues during the night.

Combined measurements of XDV and SDV are a promising tool for studying the radial hydraulic interactions between different stem tissues under field conditions. Using such combined measurements, Scholz et al. (2008) studied the hydraulic coupling between xylem and storage tissue. They concluded that the relatively small lag time between dimensional changes in

xylem and storage tissues suggested that they were hydraulically well connected and thus that radial hydraulic conductance was high. Similar experiments (Sevanto et al. 2011) in which the hydraulic connections were manipulated, while other effects like osmotic concentration, elastic properties and thickness of the living tissue were (assumed) constant, confirmed this tight hydraulic coupling between xylem and living tissue based on changes in the ratio of amplitude and time lags between diameter variations of both tissues. This high radial conductance has been associated with the abundance and/or activity of aquaporins in the plasma membrane, facilitating radial water transport (Sevanto et al. 2011, Steppe et al. 2012).

The radial hydraulic conductance is generally accepted to be constant over time (e.g., Génard et al. 2001, Steppe et al. 2006, 2008a, De Pauw et al. 2008, De Swaef and Steppe 2010, De Schepper and Steppe 2010, 2011). However, recent findings suggest the opposite: Mencuccini et al. (2013) demonstrated seasonal fluctuations in this radial conductance based on a SDV data driven model. Similarly, recalibration of model parameters throughout the growing season indicated that radial conductance was not constant across the growing season for oak and beech (Steppe et al. 2008b). Baert et al. (2015) demonstrated a substantially better model performance when radial (and axial) hydraulic conductance was described by a dynamic function instead of fixed parameter. Furthermore, Steppe et al. (2012) demonstrated the putative role of aquaporins in modulating radial hydraulic conductance between the xylem and the bark by correlating SDV measurements with changes in water potential, altered by perfusion of twigs with d-mannitol solutions having different osmotic potentials, and performing temperature and cycloheximide (a protein synthesis inhibitor) treatments. More recently, Dawes et al. (2014) found smaller diel stem contraction and expansion and a delay in the timing of daily maximum and minimum stem diameter values in larch trees. Based on these observations they suggested that higher CO_2 concentrations in the air lead to a reduced coupling between xylem and surrounding tissues. In contrast, Leuzinger and Bader (2012) did not find a significant effect of CO_2 enrichment on the contribution of storage tissues in Norway spruce.

Recent SDV model studies (Hölttä et al. 2006, De Schepper et al. 2010) showed that xylem water tension influences sieve element turgor pressure and, thus, sugar flow rates as a consequence of their tight hydraulic coupling. According to the model of Hölttä et al. (2006), a higher radial conductance enables higher sugar flow rates as water acquisition is more easily achieved by the conductive sieve elements. Water released from the storage tissues serves as an important buffering system for smoothing abrupt changes in xylem water potential. It is suggested to prevent xylem dysfunction by cavitation events that might occur when sudden transpiration peaks exceed root water uptake (Zweifel et al. 2001). Therefore, a tight hydraulic coupling enables water stored in the elastic storage tissues to contribute

directly to the transpiration stream (Simonneau et al. 1993, Génard et al. 2001, Zweifel et al. 2001, Steppe and Lemeur 2004, Steppe et al. 2006, 2012, Sevanto et al. 2011).

Tight hydraulic coupling of xylem and inner bark has also been attributed to explain the inverse diel patterns of xylem and inner bark thickness in *Eucalyptus* (Zweifel et al. 2014, Pfautsch et al. 2015a, 2015b). Zweifel et al. (2014) explained this opposite pattern observed in *Eucalyptus* by radial transfer of water from inner bark into non-lignified, elastic immature xylem cells, whereas Pfautsch et al. (2015b) proposed an alternative mechanism in which radial transport of carbohydrates can be reversed because of specific ray anatomy. However, both explanations have yet to be confirmed with sufficient experimental evidence.

The radial hydraulic coupling is thus important for long-distance sugar transport in plants, but it may also have importance for local processes such as embolism refilling (Salleo et al. 2004, 2006, 2009, Zwieniecki and Holbrook 2009, Schmitz et al. 2012, Vandegehuchte et al. 2015), circulation of nutrients (Biddulph and Cory 1957, Zwieniecki et al. 2001) and growth (Steppe et al. 2006, 2015a, De Schepper and Steppe 2010, Hölttä et al. 2010, De Swaef et al. 2013a).

Plant carbon relations

SDV are influenced by several carbon-related processes, such as leaf photosynthesis, sink activity, woody tissue photosynthesis and respiration (Steppe et al. 2015a). These processes influence the carbon content in the storage tissues by intervening in loading or unloading mechanisms (Figure 3h).

Manipulation experiments (Daudet et al. 2005, De Schepper et al. 2010, 2011) altering the sink activity (i.e., carbohydrate consumption) of roots and stem demonstrated an effect on irreversible radial stem growth, which was coupled to an altered stem carbohydrate content. Similarly, the response of stem diameter growth in peach trees to increased crop load (i.e., sink strength) was attributed to a decrease in stem carbohydrate content (De Swaef et al. 2014). In addition, the modified carbohydrate content due to altered sink activity caused detectable changes in the timing of stem diameter shrinkage (De Schepper et al. 2010). Sevanto et al. (2002, 2003) illustrated the effect of both leaf photosynthesis and sink activity on the time lag between XDV and SDV during the growing season. If the radial hydraulic conductance is known, osmotic changes in the living tissue might be deduced from the difference between XDV and SDV (Sevanto et al. 2011). Hence, Mencuccini et al. (2013) compared this SDV–XDV difference with model predictions, which were purely driven by water relations. The discrepancy between simulations and measurements yielded non-destructive estimates of osmotic changes in living stem tissue, and were related to canopy photosynthesis on both diel and seasonal scales. Sevanto et al. (2014) used this technique to estimate turgor pressure gradients in the phloem of piñon pine, and were

able to discriminate between hydraulic failure and carbon starvation as causes for tree death. Model studies support the idea that diel changes in osmotic concentration in the storage tissues could cause detectable changes in the dynamics of XDV and SDV (Génard et al. 2001, Hölttä et al. 2006, De Schepper and Steppe 2010, De Swaef et al. 2013a). Chan et al. (2015) elaborated on the approach of Mencuccini et al. (2013) to make a distinction between cambial growth (including osmotic concentration changes) and water potential induced changes on the SDV pattern. Using this approach, they could correlate growth rates with osmotic concentrations in the phloem and to environmental variables such as temperature and water availability.

In addition, radial stem growth can be used to estimate the contribution of woody tissue photosynthesis to overall plant carbon gain (Saveyn et al. 2010, Steppe et al. 2015a). Its contribution seems significant and also important for the development of new leaves. Woody tissue photosynthesis might also be a key factor in the resilience of trees to drought stress by maintaining both the plant carbon economy and hydraulic function (Bloemen et al. 2014, Vandegehuchte et al. 2015). Furthermore, several studies (Daudet et al. 2005, Saveyn et al. 2007a, 2007b) combined SDV with CO_2 efflux measurements to investigate growth and maintenance respiration of stem storage tissues. Saveyn et al. (2007a, 2007b) and Steppe et al. (2007) found a close correlation between diel fluctuations in CO_2 efflux and the SDV swelling and shrinkage pattern, which they attributed to changes in metabolic activity in response to stem water status changes. Gruber et al. (2009) found that the seasonal CO_2 efflux was more closely correlated to the number of living (and thus respiring) cells then to radial stem growth, probably because the latter also reflects the enlargement of cells, which is less related to respiration. On the other hand, Etzold et al. (2013) demonstrated some cases of positive correlation between radial stem growth and internal CO_2 concentrations in the xylem sap during the wood growth phase of *Pinus*.

Plant nutrition

Based on stem (and fruit) diameter variations, the effect of nutrient deficiencies in the nutrient solution on plant water relations and carbon partitioning has been investigated for tomato (Fujita et al. 2003, Kanai et al. 2007, 2008). Phosphorus (P) deficiency has been identified to reduce root hydraulic conductance, stomatal conductance and fruit carbon partitioning in tomato (Fujita et al. 2003). Thus, in our modelling approach P deficiency could be mimicked by reduced hydraulic resistance (Figure 3c), transpiration (Figure 3a) and carbon concentration (Figure 3h) simultaneously, resulting in a combined effect on SDV. Deficiency in potassium (K) immediately resulted in an increased diel shrinkage without affecting the recovery during the night in the early stages of the treatment (Kanai et al. 2007). This corresponds to the situation displayed in Figure 3c, indicating that K deficiency might increase the hydraulic xylem resistance (van Ieperen

2007). Furthermore, the reduced irreversible stem growth, which appeared after several days, indicated reduced assimilate partitioning, which corresponds to the simulated SDV where carbon concentration was reduced (Figure 3h). Deficiency in nitrogen (N) resulted in a decreased leaf photosynthesis and carbon allocation from leaves towards sinks, and additionally affected stomatal conductance and transpiration (Kanai et al. 2008). The effect of N deficiency on SDV is therefore a combination of reduced transpiration (simulated in Figure 3a) and reduced assimilate loading, which in turn has a consequence on the storage tissue concentration (simulated in Figure 3h).

Freezing

Zweifel and Häsler (2000) studied SDV in response to freezing and reported reversible freeze-shrinkage and thaw-expansion of the storage tissue. Their hypothesis is based on the initial freezing of water in the xylem resulting in a water potential gradient between bark (solution) and wood (ice). As such, they indicated the frost-induced water transport from the storage tissue towards the xylem in *Picea abies* (L.) Karst. Améglio et al. (2001) reported similar SDV in response to freeze–thaw cycles in walnut (*Juglans regia* L.) but found that these dynamics were not entirely due to water transport from the storage tissue towards the xylem. They hypothesized that extracellular ice crystals fill the air pores in the storage tissue. Extracellular ice formation resulted in reduced water content in the protoplast, causing an increase in the concentration of osmotic components, and thus protection against frost. As such, the authors depicted the possible application of SDV for cold tolerance screening. Moreover, the application of SDV proved useful as a non-invasive tool to test cold acclimation in field conditions (Cocozza et al. 2009). King et al. (2013) reported frost-induced stem shrinkage in *Larix decidua* Mill. and *P. abies* whenever temperature decreased below −5 °C, suggesting the ability of trees to avoid freezing of the xylem sap above this air temperature.

Tree phenology and dendroclimatology

Time series analyses of SDV data enable identification of more or less distinct phenological stages throughout the growing season. Firstly, studies over multiple years in different conifer tree species have identified three phenological stages: a progressive increase in stem radius beginning in spring, a plateau in late summer, and a decrease during the winter months when freezing occurs (Deslauriers et al. 2007b, Turcotte et al. 2009, King et al. 2013). Within the first stage, Rossi et al. (2006) found an interactive effect of day length and temperature on the diameter growth rate in conifer species (genera *Picea*, *Abies*, *Pinus* and *Larix*). Secondly, graphical inspection of diel shrinkage and expansion patterns of Qilian juniper in north-western China revealed roughly two phenological phases, separated from each other by the occurrence of days with average daily temperature of 0 °C (Wang et al. 2012). Third, Cocozza et al. (2012) used

time series analysis of SDV to identify four phenological stages in the growing season of olive (dormancy, spring induction, rapid growth and slow expansion), each of which characterized by a different pattern in SDV.

Seasonal SDV data on *P. abies*, *Pinus sylvestris* L. and *Q. pubescens* Willd. were used to identify seasonal drought (Zweifel et al. 2005) and to discriminate between water and carbon status in different phenological stages (Zweifel et al. 2006). Steppe et al. (2008b) demonstrated that information on the overall seasonal hydraulic and growth behaviour could be derived from recalibrating a SDV-driven model during different phenological stages. Via the close relationship between SDV and dynamics in overall plant productivity, phenological stages could be related to dynamics in net ecosystem productivity throughout the season (Zweifel et al. 2010). The link between climatic conditions, plant water status and radial growth has been studied via causal models, linear mixed-effect models and derivative functions based on SDV datasets covering multiple years and species (e.g., Deslauriers et al. 2003, 2007a, 2011, King et al. 2013, Cocozza et al. 2015). Such approaches help researchers to more accurately quantify and attribute changes in forest productivity in response to future warming (King et al. 2013), and advance dendroclimatological research as the formation of tree rings is better understood. As such, Van der Maaten et al. (2012) emphasized the importance of such studies to increase the understanding on growth determinisms, because comparable annual growth can be achieved through very different seasonal growth patterns. Furthermore, the use of SDV allows better understanding of how wood properties are linked to the formation of tree rings, as is reviewed by Downes et al. (2009) and Drew and Downes (2009). An increasing number of studies use time series of SDV to address dendroclimatology for different species: genera *Fraxinus*, *Acer*, *Carpinus*, *Tilia* and *Fagus* (Kocher et al. 2012, Van der Maaten et al. 2012), *Larix* and *Picea* (King et al. 2013), *P. hartwegii* Lindl. (Biondi et al. 2005, Biondi and Hartsough 2010), *P. nigra* J.F. Arnold and *Q. faginea* Lam. (Forner et al. 2014), *Q. ilex* L. (Gutiérrez et al. 2011), *Eucalyptus* and *Callitris intratropica* F. Muell. (Drew et al. 2009, 2011a, 2011b), *Tamarix ramosissima* Ledeb. and *Populus euphratica* Oliv. (Xiao et al. 2014a, 2014b), and different tropical tree species (Krepkowski et al. 2011, Volland-Voigt et al. 2011).

Trends and future prospects

In general, SDV measurements have enormous potential whenever the instantaneous response of plants to their dynamic environment needs to be assessed. Dependent on the type of study the representativeness of a point measurement has to be critically evaluated, because SDV signals may vary due to *intra-* and *inter-*plant variability. However, the availability of wireless networks and the reducing costs of dendrometers facilitate the installation of a larger set of sensors for individual experiments.

In recent publications we can distinguish a dual experimental approach: (i) longer-term time series analysis using statistical methods to correlate SDV with (micro-)meteorological conditions, which are predominantly found in the field of phenology and dendroclimatology (section *Tree phenology and dendroclimatology*) and (ii) very detailed experiments, where measurement of SDV is combined with other physiological measurements and mechanistic models.

For the first approach, coordinated initiatives (COST action STReESS) allow gathering of an enormous amount of SDV data. Via global analysis techniques and data-mining, this information pool could be explored to enhance understanding of growth, phenology and survival in relation to the microclimate, soil water availability, species or genotype. Coupling these phenotypic data with genetic information would be very valuable for ecological and breeding research under on-going global change.

Within the second approach, we can identify a specific approach where unknown physiological patterns are extracted, by studying systematic discrepancies between SDV measurements and SDV simulations based on known processes. In this approach it is unnecessary to formulate hypotheses on unknown patterns (Mencuccini et al. 2013). As such, patterns of phloem turgor (Sevanto et al. 2014), phloem osmotic concentration (Mencuccini et al. 2013), cambial growth (Chan et al. 2015) and root pressure (De Swaef et al. 2013b) have been extracted, and hypotheses on the influence of ray anatomy (Pfautsch et al. 2015a, 2015b) or elasticity of non-lignified xylem cells (Zweifel et al. 2014) on the unfamiliar behaviour of xylem thickness in *Eucalyptus* species could be experimentally validated. Furthermore, Vandegehuchte et al. (2014a) measured in *Rhizophora stylosa* Griff., a C_3 mangrove species, daily SDV patterns, which exhibited a non-regular behaviour where stem diameter increased in the morning and decreased in the evening. Using the aforementioned approach, the unique SDV pattern of *Rhizophora* was attributed to strong endogenous control mechanisms such as ion and carbohydrate compartmentalization (Popp 1984a, 1984b, Krauss and Ball 2013) counteracting the temporal hydraulic imbalances (Vandegehuchte et al. 2014b). This detailed approach of coupling measurements and mechanistic models can further be applied, with new sophisticated measurement tools like isotopes or magnetic resonance imaging to further discriminate between different external and internal drivers of plant physiology and growth. As such, De Schepper et al. (2013) recently reviewed the current understanding of phloem transport and functioning, and highlighted that much is yet to be discovered in this research area. The application of SDV and biophysical modelling can undoubtedly contribute to further enhance our understanding of phloem functioning, which is a prerequisite to better understand whole-plant functioning, source–sink relationships, and crop and fruit production.

As we are facing climate change with the expected increase in frequency and intensity of drought, interest in plant water relations and plant responses to drought will only increase further in the coming years. In this field of research, SDV measurements in combination with biophysical modelling can contribute to automatically and continuously monitor plant water status (see Steppe et al. 2008a) or to assess global tree physiological responses to drought (Steppe et al. 2015b). Such detailed definition of plant water status and physiological responses may help in identifying plant traits, which is of utmost importance in breeding programmes focusing on drought tolerance (Giovannelli et al. 2007). However, the identified plant traits are also ecologically important, as these will determine how natural ecosystems will cope with drought. Furthermore, factors other than water status that were identified to influence the SDV signal and limited its application in irrigation scheduling (Ortuño et al. 2010) can be taken into account via the biophysical modelling approach.

Finally, insights into water and carbon dynamics arising from the large amount of SDV data can be transferred to understand dynamics in other organs like leaves (Tardieu et al. 2015) or fruits (De Swaef et al. 2012).

Conclusions

Stem diameter variations are relatively easy to record automatically using point or band dendrometers connected to data acquisition systems, and have been used extensively in research on irrigation scheduling. However, SDV are an extensive source of information on different interacting plant processes, instigating research efforts in the broader scope of plant ecophysiology in the last decades. As such, SDV have been used as a tool in different ecophysiological research fields by combining different measurements and/or mechanistic functional modelling: plant water relations, carbon status and transport, radial and axial hydraulic connections, plant phenology and endogenous control. Continuing the use of SDV in combination with other state-of-the-art technology and methods such as isotopes or imaging, and with biophysical models, will undoubtedly speed up the acquisition of much-needed insights in plant functioning.

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Conflict of interest

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