



CERNE

ISSN: 0104-7760

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Universidade Federal de Lavras

Brasil

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CERNE, vol. 22, núm. 4, 2016, pp. 415-422

Universidade Federal de Lavras

Lavras, Brasil

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Keywords:

Plant hydraulics
Non-destructive techniques
Electrical moisture measurements

Histórico:

Recebido: 28/04/2016
Aceito 25/11/2016

Palavras chave:

Hidráulica de plantas
Técnicas não destrutivas
Medições elétricas da umidade

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ESTIMATING WATER IN LIVING WOODY STEMS – A REVIEW

ABSTRACT: Predicted climate changes due to greenhouse gas emissions will alter site and ecological conditions, increase instability in many ecosystems and expand the value of forest carbon and wood energy. Woody plants most often are faced with drought stresses, not only because of erratic rainfall, but also the result of climatic changes. Natural variability among wood species in terms of changes in induced water stress in stem moisture content is large. Under severe water deficit, plants have to face the dilemma of dying by drying or being starved of carbon. Changes in the water content of extensible tissues of the stem are readily reversible, causing diurnal variation driven by changing water potential in the xylem. This review intends: 1. to address how stems in woody species play an important role in water storage relevant to plant hydraulics, and 2. to present methodologies to estimate water content in stems of wood species.

ESTIMATIVA DE ÁGUA EM CAULE LENHOSOS VIVOS – UMA REVISÃO

RESUMO: Mudanças climáticas previstas alterarão o local e as condições ecológicas, aumentarão a instabilidade em muitos ecossistemas e expandirão o valor do carbono florestal e da energia da madeira. Plantas lenhosas na maioria das vezes são confrontadas com déficit hídrico, não só causado por chuvas irregulares, mas também resultante das mudanças climáticas. A variabilidade natural entre as espécies lenhosas em termos de mudanças induzidas pelo estresse hídrico no teor de umidade do tronco é grande. Sob déficit hídrico severo, as plantas enfrentam o dilema de morrer por falta de água ou de carbono. Mudanças no conteúdo de água dos tecidos elásticos do caule são facilmente reversíveis, causando variação diurna impulsionadas pela mudança do potencial de água no xilema. Esta revisão pretende abordar como caules de espécies lenhosas desempenham um papel importante no armazenamento de água relevante ao sistema hidráulico das plantas e apresentar metodologias atuais para estimar o teor de água no caule de espécies lenhosas.

DOI:

10.1590/01047760201622032169

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INTRODUCTION

Future trends of global climate indicate a worldwide increase in the risk of acute droughts and heat waves (ALLEN et al., 2010). Under the scenario of drought induced by climate change, an important concern in forestry is if intraspecific genetic resources available to tree species hold enough variability to cope with future climate change (ALBERTO et al., 2013).

Environmental biotic stresses have adverse effects on plant growth and productivity and it can also become more widespread in future decades. Therefore, rapid and sensitive quantification of stress in trees due to irrigation practices, drought, salinity, pollution, lack of nutrients or diseases should be considered as necessary research proposals (NADLER; TYREE, 2008).

Under severe water stress, terrestrial plants tend to close the stomata to avoid water loss. Prevention of hydraulic failure by stomatal closure results in carbon starvation by plants (HARTMANN, 2015). It is therefore commonplace to infer that an important imbalance between uptake and loss of either carbon or water would be responsible for plant death (ALLEN et al., 2010; McDOWELL, 2011; COCHARD; DELZON, 2013).

Therefore, accurate measurements of plant water status are essential for a better understanding of productivity and management practices of wood species under various present and future environmental conditions.

Variations in wood stem water content are generally related to seasonal rainfall. Size fluctuations of stem diameter are associated particularly with variation in the water content of the bark and sapwood swelling and contraction.

DROUGHT EFFECTS ON WOOD SPECIES

Forest mortality associated with climate-related events have been reported with increasing frequency in tropical rainforests (PHILLIPS et al., 2009), temperate mountainous and Mediterranean forests (CARNICER et al., 2011) and boreal forests (PENG et al., 2011). Both hydraulic failure and carbon starvation plant processes contribute to mortality according to current leading hypothesis (SEVANTO et al., 2014). Expected hydraulic failure occurs when water loss from transpiration is sufficiently greater than uptake by roots resulting in progressive cavitation and conductivity loss of the xylem. Carbon starvation is hypothesized to result from avoidance of hydraulic failure through stomatal closure causing negative carbon balance (McDOWELL et al., 2008).

When transpiration starts in the early morning tension is created in the xylem tissue originated from the evaporative surface of the leaves down to every organ of the plant. Part of the water stored in plant tissues during

the night is then lost, allowing the plant to respond rapidly to changes in atmospheric demand without the need to rely on water uptake by the roots. This affects every water-storing organ of the plant (Figure 1) so diurnal diameter changes occur in all parts of the plant, including the stem, branches, roots, leaves, and fruits.

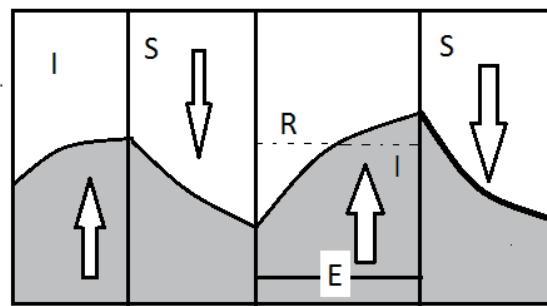


FIGURE 1 Two days of radial stem diameter measurements. (I) increment, (S) shrinkage, (R) recovery, and (E) expansion (after Drew and Downes, 2009).

Changes in the water content of extensible tissues of the stem are readily reversible, causing diurnal variation driven by changing water potential in the xylem. Water can be withdrawn from the inner woody tissues of the xylem but then cavitation rather than shrinkage occurs because this tissue is less elastic. The water stored in elastic tissues of the stem buffers the lag between roots and shoot preventing embolisms and ensuring optimal transpiration rates (PERAMAKI et al., 2005).

Drought-induced mortality would result from a non-mutually exclusive interaction of several mechanisms (NARDINI et al., 2013; SEVANTO et al., 2014). According to several authors (HARTMANN et al., 2013; URLI et al., 2013) events such as hydraulic failure, carbon starvation and biotic agent demographics are the most notorious mechanisms involved in mortality induced by drought.

Xylem tensions that cause 5 to 30 % loss of water transport capacity could generate a runaway embolism and lead to catastrophic xylem dysfunction that result in hydraulic failure. Plant carbon starvation is argued to be a consequence of avoiding hydraulic failure by means of stomatal closure. Drought drives changes in the demographics of biotic mortality agents resulting in tree mortality (PLAUT et al., 2012).

Recent work by Rowland and collaborators (2015) using data from a long-term experimental drought study at the Brazilian Amazon region concluded that tropical rainforests are likely to experience exceptional high mortality resulting from hydraulic processes rather than by gradual carbon starvation.

WATER FROM WOOD STEMS

The natural variability among wood species in terms of their water-stress-induced changes in stem moisture content is large. Plants have evolved different strategies in facing the potential risks of drought-induced hydraulic failure. Some species tend to take a conservative water-use strategy, while others are inclined to exhibit an adventurous strategy for more prodigal water use and high growth rates (HAO et al., 2010, 2013). The physiological responses of plants to water deficit and their relative importance for crop productivity vary with species, soil type, nutrients and climate.

Presence of a woody stem is a key feature that differentiates woody plants from herbaceous plants. Zweifel et al. (2001) reported that in young *Picea abies* L. trees the percentage of available water from the respective total tissue water reserves was up to 25 and 6% for crown and stem, respectively. Stem traits emerge as important plant functional traits because of their role for stability, defense, architecture, hydraulics, carbon gain and growth potential (CHAVE et al., 2009).

In angiosperm tree species, wood or xylem is composed of three types of tissues that fulfill different functions. The extent in which wood plant species can conduct water and resist xylem cavitation in the stem is determined by vessel adaptation. Failure of the conductive tissue to resist high negative pressures can result in collapse of the conduit walls resulting in cavitation.

Species with high wood density have xylem conduits less susceptible to cavitation and embolism during the dry season (MEINZER et al., 2009) as well as tend to accumulate less water than those with low-density wood (OSUNKOYA et al., 2007). Less porous wood shows more space filled with cell walls composed by cellulose, hemicellulose and lignin. As a result, less water is stored within the stem wood (McCULLOH et al., 2011). Dias and Marrenco (2016) reported a negative correlation between wood water content and wood density in 28 tree species from a terra-firme rain forest in central Amazonia.

Water deficit measured in terms of water potential has a direct impact on plant performance. As water potential declines, plant growth and gas exchange followed by yield and finally survival are impacted as water potential progressively decreases. Under severe drought stress, plants may experience severe hydraulic failure or even diebacks (ANDEREGG et al., 2013).

Water is transported from the roots to the leaves through the xylem of woody plants under negative pressure (TYREE, 1997). One important aspect of stems

in woody species is that of water storage (HOLBROOK, 1995). The water content of stems varies as xylem water potential increases and decreases, respectively. Therefore, a non-destructive method to measure stem water content (θ_{stem}) = (volume of water) ÷ (volume of stem) could be useful in monitoring the drought stress status of plants.

DESTRUCTIVE METHODOLOGY

The simplest technique of measuring stem water content (θ_{stem}) sometimes referred as stem relative water content (RWC_{stem}) is to collect stem cores and directly measure the water content by weighing tissue samples before and after drying (CLARK and GIBBS, 1957). Such traditional gravimetric measurement is labor intensive, difficult to automate and harmful for the tree after repeated sampling (LÓPEZ-BERNAL et al., 2012).

Gravimetric determination of θ_{stem} is simple and does not require expensive equipment. It involves obtaining measurements of fresh weight, turgid weight, and dry weight made on the same sample. It is calculated by $[(W-DW) / (TW-DW)] \times 100$, where W is the sample fresh weight, TW is the sample turgid weight and DW is the sample dry weight.

NONDESTRUCTIVE METHODOLOGIES

Stem water content (θ_{stem}) of terrestrial plants has been measured in situ using various sensor techniques.

Stem psychrometers are used to record plant water potential of living plants without damaging them. The stem psychrometer is attached to stem with diameters up to 5.5 cm by clamps using light pressure. Measurement can be either psychrometric (wet bulb thermometer measurement) or hygrometric (measurement of dew point) resulting in precise and reproducible measurement of the plant water potential (VOGT, 2001).

More recent instruments are gamma-ray densitometry (EDWARDS; JARVIS, 1983; BROUGH et al., 1986), magnetic resonance imaging (REINDERS et al., 1988; WINDT et al., 2009; CHOAT et al., 2010; SCHEPPER et al., 2012), x-ray computer tomography (RASCHI et al., 1995), stem diameter transduction (FERNANDEZ; CUEVAS, 2010), time domain reflectometry (CONSTANTZ; MURPHY, 1990; HOLBROOK et al., 1992; IRVINE; GRACE, 1997; WULLSCHLEGER et al., 1998; SPARKS et al., 2001), compensate heat pulse (SWANSON, 1962) and frequency-domain (FD) capacitance (HOLBROOK et al., 1992; KUMAGAI et al., 2009; HAO et al., 2013).

Among the techniques above listed, gamma ray instruments are highly accurate and noninvasive (BROUGH et al., 1986; JONES, 2004) but carry a potential risk of radiation exposure restricting their application (IRVINE; GRACE, 1997).

The magnetic resonance imaging (MRI) method is also noninvasive and safe, but it is costly and impractical for long-term monitoring of plant water status in natural conditions. The imaging branch of nuclear magnetic resonance (NMR), namely MRI can estimate in vivo the amount of water in tree stems and allows differentiation between different stem tissues (WINDT et al., 2009). For example, Schepper et al. (2012) evaluated the relationship between MRI and trunk diameter variations in 2 year-old *Quercus robur* L. with a stem diameter of 1.4 ± 0.1 cm and a height of 112 ± 3 cm. The authors reported a strong correlation between transpiration-induced changes in stem diameter and the amount of stem water, demonstrating the value of stem diameter variations for estimation the in vivo use of internally stored water.

Different types of sensors for measuring stem diameter variation (SDV) have been used to provide information about water storage because the diurnal recharge and discharge of water in stems causes stem tissue to swell and shrink. However, interpretation of SDV values are not straightforward especially when plants grow under different degrees of drought stress, as pointed out by Fernandez and Cuevas (2010). Additionally, SDV is modulated by plant age, measured position on the stem and the irreversible change of stem diameter caused by plant growth.

The compensate heat pulse method (CPH) is based on the measurement of the temperature difference between sensors located above and below a heater inserted in the tree trunk. CHP has been widely used to determine the dynamics of transpiration by measuring sap flow in conductive organs of woody plants (SWANSON; WHITFIELD, 1981) and presents a great potential for irrigation scheduling (FERNÁNDEZ et al., 2008). On the other hand, the method assumes that wood acts as an isotropic medium, which is unrealistic and may slightly affect the accuracy of the technique.

Time domain reflectometry (TDR) and heat field deformation (HFD) sensors are invasive techniques because both depend on inserting two or more waveguide lines into the stem, causing some tissue damage in the stem. The damaged tissue response to the probe insertion could last a few of weeks until the sensor signal becomes 'normal' (WULLSCHLEGER et al., 1998; LU et al., 2002; NADLER et al., 2003). Compared to

other techniques, TDR is safe, quick, non-destructive and simple to use allowing easy replication in the field. An advantage of HFD sensors compared to TDR sensors is that the geometry of HFD probes can be very adaptable, facilitating development of a variety of configurations (SUN et al., 2005).

TDR appears to be a suitable candidate for routine monitoring of water content of tree stems for being relatively free of ground interferences and automatable and to follow diurnal changes in the water status of a tree trunk. However, because the dielectric constant of water ($\epsilon \approx 80$) is larger than that of other soil constituents ($\epsilon_{\text{air}} = 1$, $\epsilon_{\text{solids}} = 2-5$), any change in the bulk dielectric of a composite material containing water, soil and air reflects a change in water content. Therefore, an empirical relationship (i.e. calibration equations) is estimated and used to convert TDR measurements of ϵ into volumetric water content ($\text{L}\cdot\text{L}^{-1}$) values.

Three sources of experimental error have already been identified with TDR use (NADLER et al., 2003). Operator error described as technical error obtained when measuring volumetric water content by the same TDR probe because of poor probe installation or air gaps around the TDR rods. A systematic error in the measurements arising from the temperature influence on the coaxial cable dielectric length and an experimental error due to radial variability of stem morphology.

Trunk dendrometers have been widely assessed in fruit trees to monitor plant water status (ORTUÑO et al., 2010). When transpiration (E_p) begins early in the morning, a tension is created in the xylem from the evaporative surface of the leaves to every organ of the plant. In large plants such as woody species, the water stored within the trunk may contribute substantially to E_p (CERMÁK et al., 2007). Water from the phloem and related tissues such as cambium and green bark as well as from living tissues of the outer xylem (ZWEIFEL et al., 2000) is withdrawn and lost by E_p resulting in a reduction of trunk diameter.

Depending on the dendrometer model and the purpose of the measurement, nails or screws may have to be driven into the trunk either to support the instrument or to serve as a fixed reference. This disturbance frequently results in abnormal growth acceleration at the vicinity of the injury. Therefore, the dendrometer holder is usually attached tightly to the trunk by elastic straps.

Dendrometers are installed on the side of the trunk opposite to the sun's trajectory, to minimize negative effects of heating by direct solar radiation. In addition, dendrometers should be placed distant from the ground to avoid interference from growing weeds, and as far as possible from any trunk scars.

Two indexes of trunk diameter variations (TDV) from dendrometer records are normally calculated namely the maximum diurnal trunk shrinkage (MDS) and the trunk growth rate (TGR). MDS has the potential to serve as plant water stress indicator (FERNÁNDEZ; CUEVAS, 2010) because MDS is normally higher in plants with soil water deficit than in well-irrigated trees. In several woody species such as citrus (ORTUÑO et al., 2004), peach (MARSAL et al., 2002), apple (DOLTRA et al., 2007), plum (INTRIGLIOLO; CASTEL, 2006), almond (GOLDHAMER; FERERES, 2001), pomegranate (INTRIGLIOLO et al., 2011) and persimmon Kaki (BADAL et al., 2010). MDS was described to be a reliable indicator while in others such as olive (MORIANA; FERERES, 2002) and grapes (INTRIGLIOLO; CASTEL, 2007) it was not useful.

In spite of the accuracy of the above described techniques, there are still opportunities for development of a method with a straightforward and less expensive alternative, such as electrical resistance that may be practical, easy to use and economical. Hand-held moisture meters provide a rapid method for obtaining the moisture content of wood and wood products during processing. Hand-held moisture meters measure electrical properties that correlate with the amount of water in the wood (GILLIS et al., 2001). Types of moisture meters available in the market are either resistance-type or dielectric-type moisture meters.

Generally, in porous materials and solutions, electrical conductivity (σ) is linearly related to the product of the volume and ion concentration (NADLER, 2005). However, in stems, bulk stem electrical conductivity (σ stem) is far more sensitive to changes in volumetric water content (θ) than to changes in sap ionic concentration (NADLER et al., 2006).

Variations in electric resistance have been used to measure water content of soils and cut timber (SKAAR, 1988) and to detect decaying wood in trees (SHIGO; SHORTLE, 1985). In wood stems, the resistance to low frequency alternating current (i.e. impedance) depends mainly on the ion content and quantity of cell sap released into the apoplast by living cells wounded during insertion of the electrodes. Resistance varies with the fraction of living cells in the bark and sapwood of a stem and with the water status of these tissues (BLANCHARD et al., 1983).

Borchert (1994) reported stem water content measured as electric resistance between nails driven 20 mm deep into tree trunks of more than 30 species from Costa Rica correlated with wood density and saturation water content measured with a pressure chamber.

FINAL CONSIDERATIONS

Water availability influences the distribution, structure and composition of terrestrial plant communities. At the same time, plants are a major conduit for water to return to the atmosphere, and hence influence climate and exert strong effects on hydrologic fluxes in the land-atmosphere system.

Terrestrial plants have mechanisms of internal water flux regulation, which uncouple plant water status from atmospheric, and soil hydrological control linked to morphological and physiological traits (ZWEIFEL et al., 2002).

Stems and trunk have functional role of internal water storage in wood forest species. Therefore, it is likely that the functional importance of internal water storage in trees will increase to insure fast establishment and survival of tree seedlings through artificial regeneration especially under future scenario of climate change.

Nondestructive monitoring of water content in living trees and seedlings offers opportunities for development of sensors and technologies suitable for irrigation, real-time detection of plant water stress and for studies of water use mechanisms in trees and storage ability of wood stems.

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