

Substituting Stem's Water Content by Electrical Conductivity for Monitoring Water Status Changes

Arie Nadler*

Dep. of Environmental Physics and Irrigation
Institute of Soil, Water and Environmental Sci.
ARO
Volcani Center
Ministry of Agriculture
POB 6
Bet Dagan
Israel, 50250

During 2007at:
Dep. of Renewable Resources
444 Earth Sciences Building
Univ. of Alberta
Edmonton, AB
Canada, T6G 2E3

Melvin T. Tyree

Dep. of Renewable Resources
444 Earth Sciences Building
Univ. of Alberta
Edmonton, AB
Canada, T6G 2E3

Rapid and sensitive detection of stress in trees due to irrigation practices, draught, salinity, pollution, lack of nutrients, or diseases may be useful for research and practical purposes. Tree stress could be monitored by following changes in wood water content via time domain reflectometry (TDR). We have searched for a user-friendly and less expensive tool because, although TDR is perhaps the most suitable method, it is too expensive and complicated for everyday use. The objective of this study was to understand the relations between the electrical conductivity (σ_{stem}) and water content (θ_{stem}) in tree stem segments of seven species with TDR probes installed. By leaching stem segments with salt solutions or air we were able to change the salinity and water content independently. We have shown that (i) σ_{stem} is more sensitive to changes in θ_{stem} than to changes in salinity of the sap, and (ii) 30-mm-long rods on the TDR probe can sensitively and accurately measure θ_{stem} . We propose that σ_{stem} changes might be used as a proxy for changes in stem water content or stem water potential. Hence, electrical resistivity measurements may substitute for water content measurements with the following advantages: improved accuracy, higher flexibility in probe construction, application to stem diameters <30 mm, and significantly lower costs.

Abbreviations: TDR, time domain reflectometry; σ , electrical conductivity; θ , volumetric water content; ϵ , dielectric constant.

Daily water status in trees in commercial orchards can be monitored for irrigation scheduling by measuring leaf water potential or soil water content (θ_{soil}). Throughout the growth season, however, soil locations where the roots take up water vary horizontally and vertically according to water availability, which depends on irrigation method (furrows, sprinklers, and drippers), irrigation intervals, salt accumulation, soil type, and tree species. Leaf water potential measurements have the advantage of providing an integrated measurement of available water in the soil, but such measurements are labor intensive and cannot be automated. Measurements of θ_{soil} by TDR can be automated but have to allow for spatial heterogeneity. Accordingly, a close monitoring will require installing and measuring dozens of sensors to follow the ever-changing water source locations in large soil volumes (2–10 m³). We

have excluded several noninvasive techniques like nuclear magnetic resonance, neutron moderation, network analysis, and imaging due to their high costs and complexity. Noninvasive capacitance methods (Holbrook and Sinclair, 1992) were not adopted due to the capacitance-in-series nature of the measurement, which attributes an exaggerated effect of the bark and outer tissues on θ_{stem} , resulting in θ_{stem} overestimation. To overcome these obstacles, one could monitor θ_{stem} by an automated TDR method and rely on the fact that roots “integrate” soil water content. The first to measure water content in stems using the TDR technique were Constantz and Murphy (1990). They have reported, for native trees, both a wide annual range of water content (0.20–0.70 m³ m⁻³), and also small changes of -0.02 m³ m⁻³ in 2 wk due to lack of rain and a 0.03 m³ m⁻³ increase in θ_{stem} within 4 d due to flooding, while emphasizing that measured values were strongly dependent on stem structure and compass orientation.

The TDR method is expensive and complicated, however. Replacing it with a straightforward, less expensive alternative, e.g., an electrical conductivity method, may be practically and economically desired. Generally in porous materials and solutions, the electrical conductivity (σ) is linearly related to the product of the volume and ion concentration (Moore, 1965; Nadler, 2005), but in stems, bulk stem electrical conductivity (σ_{stem}) is far more sensitive to changes in θ than to changes in sap ionic concentration (Nadler et al., 2006, Table 2).

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*Corresponding author (vwnad@volcani.agri.gov.il).

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Time domain reflectometry has an advantage over most θ -sensing instruments by being the most accurate, least sensitive to media properties, and easily automatable. In a previous study on whole living trees (Nadler et al., 2006), θ_{stem} and σ_{stem} were studied under several stress situations and θ_{stem} was found to respond within 4 h to water application with a high sensitivity ($\theta_{\text{stem}} = 0.001 \text{ m}^3 \text{ m}^{-3}$ out of a typical $0.04 \text{ m}^3 \text{ m}^{-3}$ daily cycle). Evaluating stem water changes from σ_{stem} measurements are expected to be similar or even more accurate than its estimation from capacitance measurements. While $\theta_{\text{stem}} - l_a$ (virtual rod length) relationships are exponential, σ_{stem} -resistivity relationships are linear. Namely, when the length of probe rods is reduced threefold, the measurement error will increase by 3 or 9 when measuring resistivity or dielectrics, respectively. The present study reports short-term θ and σ values of stem segments.

We studied the σ_{stem} dependence on sap ion concentration and θ_{stem} while maintaining one parameter constant and changing the other. To verify that the experimental treatments applied on the stem segments have resulted in σ_{stem} and θ_{stem} changes comparable to those taking place in a living tree, we have included results of σ_{stem} and θ_{stem} obtained by the same measurement technique in living trees. The purpose of our study was to verify and understand the mechanism of the $\sigma_{\text{stem}} - \theta_{\text{stem}}$ relationships found in living trees by studying the behavior of $\sigma_{\text{stem}} - \theta_{\text{stem}}$ in stem segments or branches of seven species leached with a range of salt concentrations.

THEORETICAL AND EXPERIMENTAL CONSIDERATIONS

Dry wood is an excellent electrical insulator ($\sigma = 10^{-15} \text{ mS m}^{-1}$), yet σ increases dramatically to $10^{-9} \text{ mS m}^{-1}$ as θ increases to $0.07 \text{ m}^3 \text{ m}^{-3}$. The value of σ_{stem} further increases, though less dramatically, until θ is at fiber saturation ($\sim 0.12 \text{ m}^3 \text{ m}^{-3}$), with a linear relation between $\log(\sigma_{\text{stem}})$ and $\log(\theta_{\text{stem}})$. Generally, θ_{stem} and temperature (T) are the two most important factors affecting σ_{stem} , with a significant scatter attributed to variability in stem principal constituents (cellulose, hemicellulose, and lignin). Yet, at high moisture contents, the increase in σ_{stem} with θ_{stem} is more sensitive to electrolyte content because it is essentially a function of the numbers and kinds of ions in the cell lumen water. In addition, θ distribution is generally more erratic above fiber saturation so that σ paths tend to be discontinuous and circuitous (Skaar, 1988).

Therefore, $\sigma_{\text{stem}} - \theta_{\text{stem}}$ relations should differ from such relations in aqueous solutions mainly due to stem anisotropy and pronounced cell wall electrical properties. Stems are mostly vascular structured, consisting of living cells with pronounced elongation along the axis (producing a strong electrical anisotropy) containing continuous liquid columns with porous connections between the tube-like cells. As a result, a high σ_{stem} is expected in the axial direction due to the structurally limited ionic conductivity (Arnold and Andrews, 2004). There are few or no conduits oriented in other directions (tangential or radial), however, hence σ_{stem} should be lower in these directions. Also, the inner part of the stems is drier and σ_{stem} should be lower there. And indeed, using an Agilent 4194A impedance analyzer, Arnold and Andrews (2004) have found σ_{stem} of freshly cut monterey pine (*Pinus radiata* D. Don) and shining gum [*Eucalyptus nitens* (H. Deane & Maiden) Maiden] sections to be highly correlated with θ_{stem} . The range of their σ_{stem} values for the two trees ($1\text{--}40 \text{ mS m}^{-1}$) overlaps the results of this study and previous studies (Nadler et al., 2003, 2006).

Hearle (1953) proposed a simple theory to explain the strong moisture dependency of σ_{stem} (for $\theta < 0.08 \text{ m}^3 \text{ m}^{-3}$), stating that σ_{stem} increases are primarily due to an increase in the dielectric constant (ϵ), explaining that conduction is by ions in the cell wall. Ionic conduction is dependent on the total number of potential charge carriers per area of cell wall and their degree of dissociation. The electrolyte concentration remains essentially constant with moisture changes in the stem; therefore, increases in the degree of dissociation and ion mobility cause the great increase in σ_{stem} with θ .

Lin (1965) further extended this explanation by proposing that the conducting ions may be located at two different sites, each with a different energy level: the sites of lowest potential energy (= ion-generating sites), where ions are held by strong forces of electrostatic attraction to ions or to groups in the basic wood structure of opposite polarity, and the second kind of sites (= dissociated sites) of considerably higher energy levels. The dissociated ions on these sites are relatively mobile compared with those bound to the low-energy ion-generating sites. Lin (1965) measured σ_{stem} of several heartwoods and softwoods as a function of θ_{stem} from dry conditions to $0.39 \text{ m}^3 \text{ m}^{-3}$ across the T range from -50 to 150°C . The relations obtained resulted in a family of curves of $\log(\sigma_{\text{stem}}) - \log(1/T)$ (K), each for a constant θ_{stem} , with essentially linear relations at low θ_{stem} becoming less so as θ_{stem} increased. Thus, both the mobility and degree of association increase with increasing θ_{stem} , although the latter increases more dramatically, in agreement with Hearle's theory. Accordingly, a wide range of resistivities within a single stem was found in oak (*Quercus suber* L.) and olive (*Olea europaea* L.), using a ring array of multielectrodes (Hagrey et al., 2003). They measured concentric resistivities in an oak tree, with 1600Ω in the stem center decreasing outwardly to 50Ω ; an even higher resistivity range was measured in a 50-yr-old olive tree, with $42,000 \Omega$ in the center decreasing symmetrically toward the rim to 40Ω (Hagrey, 2006). A wide natural variability was also reported for θ_{stem} in oak (*Quercus agrifolia* Née) and redwood [*Sequoia sempervirens* (D. Don) Endl.] ($\Delta\theta = 0.08\text{--}0.26 \text{ m}^3 \text{ m}^{-3}$, Constantz and Murphy 1990), in red maple (*Acer rubrum* L.) and white oak (*Quercus alba* L.) (Wullschleger et al., 1996), and in pine (*Pinus sylvestris* L.) (Irvine and Grace, 1997). Within a single birch (*Betula pendula* Roth) stem cross-section, from the center to the rim, the dielectric constant decreased from 20 to 8 and for a fir from 31 to 7 (Franchois et al., 1998). More specifically, pronounced differences (up to one order of magnitude, $1\text{--}11 \text{ mS m}^{-1}$) were noted between measurements of the structurally limited σ_{stem} along the axial, radial, and tangential directions (Arnold and Andrews, 2004).

Our conclusions from the above facts and explanations are: (i) in the stem, the effect of θ on σ will be nonlinear and may vary with both the dynamic range of θ_{stem} and the tree species; and (ii) measured changes in σ_{sap} , under either natural or experimental conditions, are relatively small compared with the high background value of cell wall σ .

MATERIALS AND METHODS

During the winter of 2006–2007, stems of seven local species (Manitoba maple [*Acer negundo* L.], European mountain ash [*Sorbus scopulina* Greene], Bebb's willow [*Salix bebbiana* Sarg.], white spruce [*Picea glauca* (Moench) Voss], pin cherry [*Prunus pensylvanica* L. f.], paper birch [*Betula papyrifera* Marshall], and trembling aspen [*Populus tremuloides* Michx.]) were collected (Edmonton, AB, Canada) and stored at -20°C . While still frozen, stem segments 0.32 to 0.70 m long, having a diameter $<35 \text{ mm}$ and volumes ranging from 0.37 to 0.70 L , were each installed with a thermocouple and two TDR probes

(30-mm-long rods, 20-mm interrod spacing) through predrilled holes. The probes were connected to a cable tester (1502 Tektronix, Beaverton, OR) with a 4-m-long 50 Ω (RG58) coaxial cable through a 16-channel multiplexer (Dynamax, Houston, TX).

Leaching Stem Segments with Saline Solution

A compression fitting (Dynamax, Houston, TX) was tightly mounted on one end of the stem and 3-mm o.d. tubing was connected to it, enabling delivery of KCl or NaCl (input $\sigma = 9\text{--}280 \text{ mS m}^{-1}$) solutions under pressures of 1 to 400 kPa (flow rate $> \sim 20 \text{ mL h}^{-1}$). Using suitable software, each probe was automatically measured at 3-min intervals for θ_{stem} and σ_{stem} . Long-term leaching of stem segments is prone to a reduction in hydraulic conductance because of microbial growth in the stem. To stretch the leaching time (up to 25 d) while minimizing the risk of stem cells decaying, KCl solutions were prepared from distilled water, and were further purified by passing, under pressure, through three additional columns that exchanged the soluble ions and removed organic matter and particles $>0.42 \mu\text{m}$, and finally were thoroughly degassed. Between runs, all tubing and containers in contact with the leaching KCl solutions were flushed with a bleach solution and rinsed with distilled water. Each of the KCl solutions ($0.001\text{--}0.34 \text{ mol l}^{-1}$, equivalent to $\sigma = 10\text{--}3600 \text{ mS m}^{-1}$) leached the stem until stable θ_{stem} and σ_{stem} levels were attained—3 to 12 d, depending on the stem's dimensions and hydraulic conductivity. On termination of each run, the stems were split open to extract the probes and were visually examined, revealing no signs of cell degradation. An oven-dried stem of a pin cherry, assigned as a control stem and left untreated, was installed with a similar TDR probe and measured along with all the leached stems. Throughout a period of 3 mo (excluding the first 12 d it took the stem to adjust to room temperature and humidity), its θ values fluctuated $0.15 \pm 0.015 \text{ m}^3 \text{ m}^{-3}$.

Changing Water Content in Stem Segments

We found that θ_{stem} could be changed by leaching the stem segments with compressed air via the compression fitting. An air pressure of 200 to 400 kPa gradually applied for 2 h on the stem through the compression fitting was sufficient to cause air bubbles to appear in the drainage side of the tested stem and to cause a significant drop in θ_{stem} .

Changing Electrical Conductivity in Stem Segments

Changes in σ_{stem} were achieved by leaching stem segments with various concentrations of KCl or NaCl for 6 to 12 d until the conductivity of the drainage solution equaled that of the input solution. Leaching pressure ranged from 1 to 300 kPa depending on species. Typically, θ_{stem} also changed when stems were leached with salts, and to evaluate only the impact of salinity of the leaching solution on changes in σ_{stem} , we have selected data sets where θ_{stem} remained constant within $\pm 0.01 \text{ m}^3 \text{ m}^{-3}$.

Measurements on Living Trees

Any soil traces from the root system of the purchased trees were washed away and the trees were planted inside 70-L containers filled with perlite. Holes of 2.9-mm diameter were drilled in each stem, through a metal leader, and a TDR probe made from three 30-mm-long rods of 3-mm-diameter stainless steel at 50-mm spacing was installed, with rods plane parallel to the stem's long axis as follows. According to previous experience regarding the effect of stem tissues curing on the TDR measurement (Wullschlegler et al., 1996; Nadler, 2004), we waited 200 d to reduce any installation curing effect for

stable θ_{stem} values before reporting measurements. Data acquisition and analysis were similar to that of the stem segments. Trees were irrigated twice a week in excess of their needs. The purpose for collecting the live tree data was to compare them to the stem segment findings and ensure that the experimentally applied treatments induced θ_{stem} and σ_{stem} changes within similar ranges.

Cell activity was proven negligible by getting insignificantly different values and scatter of θ_{stem} and σ_{stem} before and after vacuum infiltrating the stems for 4 h while immersed in water inside a desiccator, followed by heating at 60°C in 0.32 dS m^{-1} KCl solution for 30 min.

Time Domain Reflectometry Methodology

The TDR method, using a Tektronix cable tester (1502C, Beaverton, OR), involves transmitting an electromagnetic (EM) pulse composed of a wide range of frequencies (10 kHz–1.4 GHz). The propagation velocity of the EM pulse is $V_p = l/t$, where l is the distance (m) and t is the time (s); V_p is also related to the dielectric constant (ϵ) through $V_p = c/\epsilon^{0.5}$, where c is the speed of light. Using $\epsilon = (ct/2l)^2$ and rearranging results in $\epsilon = (l_a/l)^2$, where l_a is the measured (apparent) distance from the beginning to the end of the waveguide and l is the real (physical) length.

Wullschlegler et al. (1996) produced an empirical relationship converting TDR measurements of ϵ into θ values for four different tree species (red maple, white oak, chestnut oak [*Quercus montana* Willd.], and black gum [*Nyssa sylvatica* Marshall]) that were in good agreement with the Constantz and Murphy (1990) calibration. The combined data were fitted to the second-order quadratic equation:

$$\theta = -0.251 + (4.66 \times 10^{-2})\epsilon - (4.93 \times 10^{-4})\epsilon^2 \quad [1]$$

We emphasize that the precision, i.e., the uncertainty of the true value, is not as important as the accuracy, i.e., the repeatability of the values. The θ values derived from the measured ϵ have not been corrected for any temperature (T) effect on ϵ because the mutually compensating interaction among $\theta\text{--}\sigma\text{--}T$ is negligible (Pepin et al., 1995; Irvine and Grace 1997). All findings and conclusions relate to the tree stems under our experimental conditions. The dielectric constant of water ($\epsilon_w \sim 80$) is larger than that of stem tissues and any changes in measured capacitance may be attributed to stem moisture changes. When the EM pulse travels through a waveguide embedded in any medium, the amplitude of the waves are attenuated due to dielectric losses and the σ of the medium (Cassel et al., 1994). Due to pulse energy attenuation along the probe rods, measurement sensitivity decreases exponentially for short rods, depending on probe geometry, impedance match, and the uniformity of θ_{stem} and σ_{stem} . The load resistance (R_L) can be measured after all multiple reflections have faded away and the pulse alternating-current voltage becomes direct current. At very low frequencies, Z_L is the load resistance (R_L of the TDR probe embedded in the stem), hence:

$$R_L = Z_0[(1 + \rho_\infty)/(1 - \rho_\infty)] \quad [2]$$

where Z_0 is the load impedance. Identical R_L values would have been obtained even if stem resistivity was measured by a separate device like a high-impedance resistivity meter, as hopefully will be the routine field procedure once the suggested approach for irrigation scheduling is adopted. In the present study, however, because we had to use the cable tester anyway, we preferred to measure σ_{stem} by the cable tester also, assuring in this way that θ_{stem} and σ_{stem} are measured simulta-

neously, at exactly the same volume, with the same software and a single logging system. The reciprocal of R_L equals the direct current conductance and can be converted to bulk electrical conductivity (σ_a) by applying the geometric cell constant K_c of the TDR probe:

$$\sigma = K_c f_T / R_L \quad [3]$$

where f_T is the temperature factor and K_c is determined from the measurement of R_L in solutions of known σ . All reported σ values were obtained at a room temperature of $20 \pm 1.5^\circ\text{C}$. Measurements of θ_{stem} and σ_{stem} are independent, although obtained by the same metering device and the same probe and in the same sampled volume.

Obtaining σ data with a resistivity meter was the stated aim of this study. Because in the present study, under our specific experimental conditions and objectives, we ought to have used the cable tester, however, we took advantage and used it also for electrical conductivity measurements.

Stem-Segment Hydraulic Conductivity

The hydraulic conductivity of the stem segment was measured during the leaching process. It was found to drop by an order of magnitude from an initially high value during the first 5 to 7 d and remained constant thereafter. The drop was attributed to unavoidable blockage of xylem vessels by microbial growth and will not be further discussed. Microbial growth is also likely to occur whenever TDR probes are installed in living trees and is likely to result in the gradual formation of heartwood in the region where TDR probes are inserted.

Accuracy and Scatter

The maximal theoretical accuracy of $\pm 1\%$ for θ measurements by TDR probes with 30-mm-long rods can be predicted from the cable tester's specifications. It is assumed that the maximal resolution is ± 1 pixel out of 122 (half those available; the TDR trace does not fill up the screen most efficiently).

In previous studies (Nadler et al., 2002, 2006), a typical scatter (SD of $\pm 0.05\%$ [$0.00025 \text{ m}^3 \text{ m}^{-3} / 0.50 \text{ m}^3 \text{ m}^{-3}$]) was found for 200-mm-long rods. From a practical aspect, and keeping in mind the exponential relations between l_a and θ , shortening the rods from 200 to 30 mm should increase the scatter SD approximately 40-fold to 2%. We have found a SD ($n = 60$, two probes for each rod length) of 0.0005, 0.0095, and $0.044 \text{ m}^3 \text{ m}^{-3}$ for θ measured in tap water with 200-, 70-, and 30-mm-long rods, respectively, which agrees with the l_a - θ exponential dependency. We further tested the 30-mm-rod probes in sand saturated with solutions having salinities of 80 and 280 mS m^{-1} (two probes for each salinity); SD averaged values ($n = 780$) for the four probes were 0.052 for θ_{stem} and 0.061 for σ_{stem} .

During our study, after stem thawing and sufficient leaching, a typical $\theta = 0.6 \text{ m}^3 \text{ m}^{-3}$ ($l_a = 121 \text{ mm}$) was reached. During experimentation we were able to decrease θ by up to $0.16 \text{ m}^3 \text{ m}^{-3}$ ($l_a = 101 \text{ mm}$), which means that within our dynamic range ($l_a = 100$ – 120), the maximal expected accuracy is $0.008/0.16$ or $\pm 5\%$. Experimentally, data quality could benefit from the use of longer rod probes. Conflicting experimental needs forced us to compromise, however: longer rods would have implied (i) sampling a larger proportion of heartwood and a smaller representation of the conducting vessels, (ii) larger compression fittings, and (iii) a longer leaching period, increasing the risk of internal structure changes due to rotting. Of course, rod lengths $>70 \text{ mm}$ are recommended where possible.

The primary objective of this study was to test the hypothesis that changes in σ_{stem} depend much more on θ_{stem} than on changes

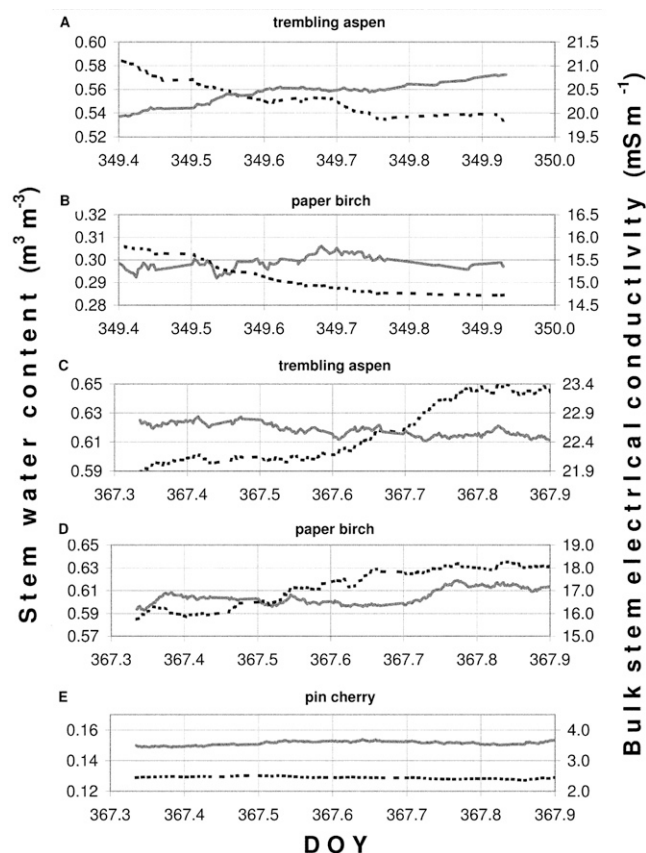


Fig. 1. Stem water content (solid line) and stem electrical conductivity (dashed line) after the electrical conductivity of incoming solution (σ_{input}) was decreased from 70 to 32 mS m^{-1} in (A) trembling aspen and (B) paper birch or increased from 16 to 39 mS m^{-1} in (C) trembling aspen and (D) paper birch, and in (E) an untreated, oven-dried, pin cherry stem equilibrated with room humidity; DOY = day of the year.

in the salinity of xylem sap within physiological concentration ranges. Stem segments were leached with different concentrations of KCl or NaCl until the σ of the input solution equaled that of the output solution (drainage), i.e., leachate σ values of 9 to 280 mS m^{-1} corresponding to approximately 1.3 to 220 mmol L^{-1} . After obtaining a stable θ_{stem} at any given sap salinity, we were able to increase θ_{stem} by increasing the leaching pressure of the salt solution. Increasing the leaching pressure should compress any air bubbles present in the wood. We were able to decrease θ_{stem} by leaching the stem segments with air at 400 kPa pressure.

RESULTS AND DISCUSSION

Figure 1 shows the effect of decreasing or increasing the salinity of the leaching solution on σ_{stem} , while θ_{stem} was maintained constant (to within $\pm 0.015 \text{ m}^3 \text{ m}^{-3}$). In Fig. 1A and 1B, the conductivity of the leaching solution (σ_{input}) was decreased from 70 to 32 mS m^{-1} . In Fig. 1C and 1D, σ_{input} was increased from 16 to 39 mS m^{-1} . Figure 1E is a control, an oven-dried stem segment, and demonstrates the experimental reproducibility of measured σ_{stem} and θ_{stem} for stable conditions. It can be seen that when the θ_{stem} effect on σ_{stem} was isolated, the σ of the leached stems followed the change in sap flow and changed 1.3 to 2.8 mS m^{-1} while σ_{stem} of the control fluctuated $\pm 0.007 \text{ mS m}^{-1}$ (Fig. 1).

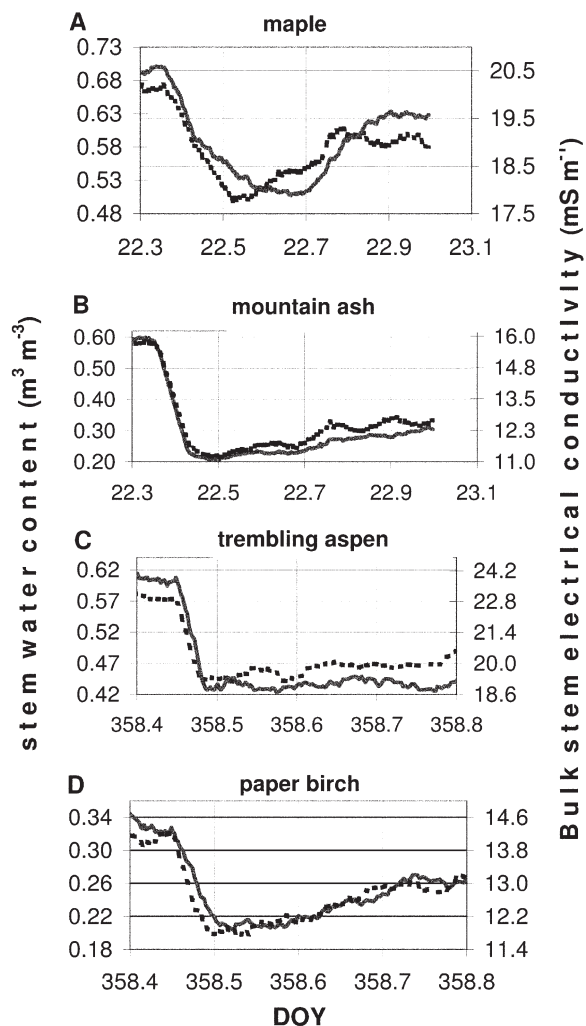


Fig. 2. Stem water content (solid line) and stem electrical conductivity (dashed line) reaction to stem solution displacement with pressured (0.4 MPa) air for 2 h followed by restoring the preceding solution in (A) maple, (B) mountain ash, (C) trembling aspen, and (D) paper birch stems; DOY = day of the year.

Figure 2 shows the much larger impact of changing θ_{stem} on the observed values of σ_{stem} . The large changes in θ_{stem} were achieved by displacing the vessel contents by air. Since the displacement was rapid (about 1 h), the salinity of the leachate did not change. Figure 2 demonstrates four out of 20 similar experiments, showing a drop in θ_{stem} and σ_{stem} following the application of the 400 kPa air pressure for about 2 h, after which the conditions preceding air application were restored. The immediate and steep response of σ_{stem} to the drop in θ_{stem} is clear (Fig. 2).

In Fig. 3, we plotted σ_{stem} vs. θ_{stem} for the six stems shown in Fig. 2. Individual values of σ_{stem} vs. θ_{stem} were plotted for consecutive measurements taken at 3-min intervals. Correlations are variable and average R_{adj}^2 are 0.87 (trembling aspen), 0.80 (paper birch), 0.96 (caragana), 0.51 (maple), 0.95 (ash), and 0.78 (willow). We assume that higher R_{adj}^2 values could be obtained by using TDR probes with longer rods.

To experimentally study our hypothesis, an extremely wide spectrum of water contents and salinity levels was chosen. In real trees growing in typically irrigated commercial orchards, the range of change in these parameters is expected to be, both

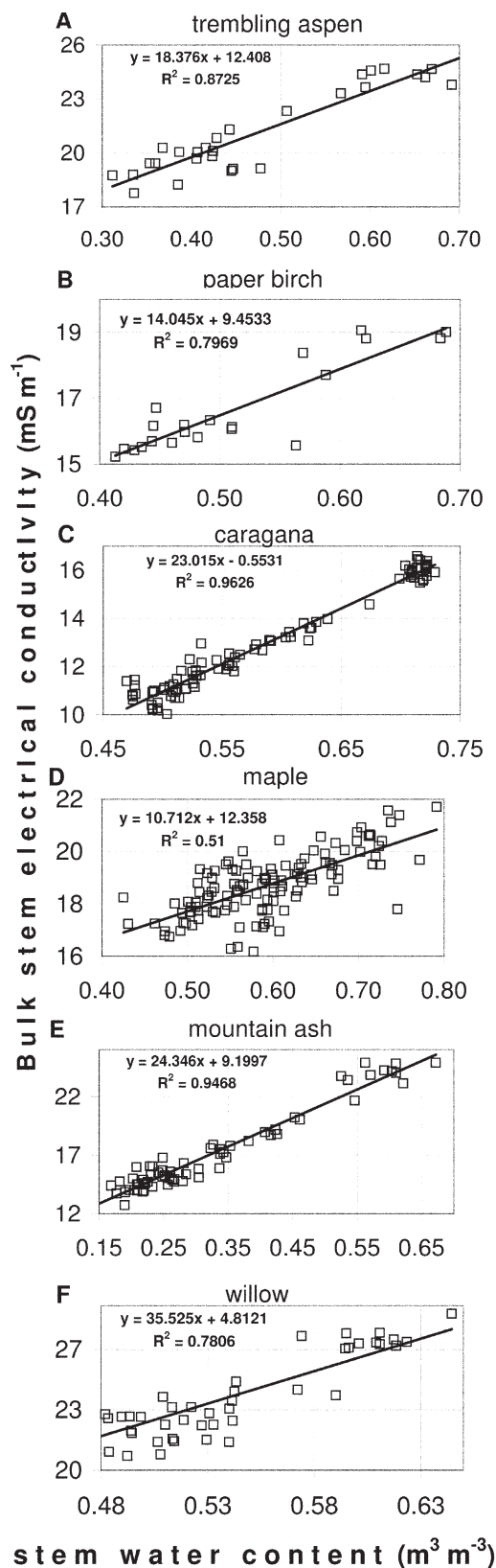


Fig. 3. Stem electrical conductivity–water content ($\sigma_{\text{stem}}-\theta_{\text{stem}}$) relations during displacement of the stem solution by high-pressure air in (A) aspen, (B) paper birch, (C) caragana, (D) maple, (E) mountain ash, and (F) willow. Linear regression and adjusted, squared correlation coefficients are also given.

daily and seasonally, much narrower because: (i) farmers won't allow their trees to be stressed; (ii) under semiarid conditions

Table 1. Seasonal and daily ranges of measured stem water content (θ_{stem}) and stem electrical conductivity (σ_{stem}) in trees irrigated with waters of different salinities in a ascending order of drainage water electrical conductivity ($\sigma_{\text{Irrigation}}$).

Tree species	Experiment location	Seasonal θ_{stem} range	Daily θ_{stem} change	Seasonal σ_{stem} range	Daily σ_{stem} change	$\sigma_{\text{Irrigation}}$	Seasonal σ_{stem} change/ $\sigma_{\text{Irrigation}}$
		$\text{m}^3 \text{m}^{-3}$		mS m^{-1}			
Butternut (<i>Juglans cinerea</i> L.)	lysimeter in a greenhouse	0.26–0.48	0.02	0.26–0.66	4	39	1.69
Apple (<i>Malus domestica</i> Borkh.)	lysimeter in a greenhouse	0.35–0.65	0.04	0.25–0.65	4	39	1.67
Caragana pigmy [<i>Caragana pygmaea</i> (L.) DC.]	lysimeter in a greenhouse	0.27–0.32	0.015	0.22–0.59	6	39	1.51
Caragana globe [<i>Caragana frutex</i> (L.) K. Koch]	lysimeter in a greenhouse	0.30–0.038	0.02	0.22–0.57	7	39	1.46
Grapefruit† (<i>Citrus paradisi</i> Macfad.)	loamy soil	0.28–0.45	0.05	0.06–0.14	13	290	0.05
Banana (<i>Musa acuminata</i> Collo)	lysimeter outdoors	0.50–0.75	0.07	0.50–0.95	7	800	0.12
Date (<i>Phoenix dactylifera</i> L.)	lysimeter outdoors	0.52–0.64	0.03	0.75–1.10	9	1600	0.07
Mango (<i>Mangifera indica</i> L.)	lysimeter outdoors	0.44–0.58	0.04	0.42–0.96	15	1600	0.06
Olive (<i>Olea europaea</i> L.)	lysimeter outdoors	0.39–0.45	0.01	0.13–0.27	03	1600	0.02
Average			0.04		8		

† Nadler et al. (2006).

or anywhere high salinity levels may be encountered, salt resistance grafted trees are selected; (iii) excessive salt accumulation in the soil is prevented by increasing the irrigation dose by 5 to 15% above tree needs, aiming at leaching salt from the root zone; and (iv) due to root membrane selectivity, accumulating salt levels on a daily basis will be minute, which will lead to lower σ_{stem} values. These arguments will narrow the sap salinity range on any time scale. See, for example, the ratio of seasonal maximum σ_{stem} to irrigation water σ (Table 1): while the ratio is 1.46 to 1.69 for freshwater irrigated trees, it ranges from 0.02 to 0.12 for trees irrigated with saline water. A 2-mo σ_{stem} dynamic range in living trees (caragana globe [0.35], caragana pigmy [0.37], butternut [0.40], and apple [0.40], Table 1) was approximately double that found in the experimental stem segments (maple [0.085], aspen [0.13], birch [0.20], willow [0.18], and caragana [0.15]). The wider θ_{stem} range, coupled with the narrower σ_{stem} range found in live trees, may indicate that more favorable conditions for detecting θ_{stem} changes may be encountered in live trees than in stem segments.

Obviously, the experimental procedures used to simulate the effect of the naturally occurring sap salinity in living trees may not necessarily trigger the same dynamics or extent of $\sigma_{\text{stem}}-\theta_{\text{stem}}$ relationships. We should not expect that in living trees θ_{stem} changes occur within 2 to 4 h and the sap solution may include ions other than KCl. Yet the trends, principle, and ranges found in stem segments and live stems were similar.

Wood porosity is very anisotropic. The pores of conduits (vessels or tracheids) are oriented mostly along the long axis of the stem and the conduit length can be 1 to >1000 mm. The electrical and hydraulic conductivity of wood is more than 10 times higher in the axial than in the radial and tangential directions. To verify a lack of tree anisotropy effect on θ_{stem} measurements, we mounted two stems on balances and compared the weighted water loss during high-pressure air application to the calculated water amount lost (by multiplying stem volume by θ_{stem} difference before and after air application). Using θ_{stem} values measured 1 h after restoring solution flow (enabling time for refilling microgaps close to the probe rods), a recovery of 83% for aspen (0.047 out of 0.056 L) and 91% for willow (0.047 out of 0.052 L) was obtained. This quantitative agreement between gravimetric and TDR measurements

indicates that the stem isotropy was correctly taken into consideration in the Wullschleger et al. (1996) equation used for converting dielectric length into θ_{stem} . The missing water has probably evaporated while bubbling as foam out of the TDR probe installation holes or was soaked up by the bark.

In Fig. 4, we examine the relative impact of changes in salinity of the xylem fluid (Fig. 4A) and changes in xylem water content on changes in whole-stem electrical conductance (Fig. 4B–4D). Figure 4A shows that for a fourfold change in salinity ($\sigma_{1,i}/\sigma_{1,f}$ the ratio of the initial to the final electrical conductivity of the solution that is leaching the stem during the xylem salinization phase, plotted on the x axis), the change in whole-stem conductance is significantly smaller, $\sim \pm 10\%$ (initial $\sigma_{\text{stem}}/\text{final } \sigma_{\text{stem}}$ plotted on the y axis). In contrast, in Fig. 4B, 4C, and 4D, we see that a relative change in water content (initial $\theta_{\text{stem}}/\text{final } \theta_{\text{stem}}$ plotted on the x axis) has a much larger effect on stem conductance (initial $\sigma_{\text{stem}}/\text{final } \sigma_{\text{stem}}$ plotted on the y axis).

From Fig. 4A, it can be seen that the impact of sap salinity on initial $\sigma_{\text{stem}}/\text{final } \sigma_{\text{stem}}$ is only $\pm 10\%$ with a slope of 0.082 (aspen) or 0.117 (birch). In comparison, θ_{stem} changes caused quite drastic changes in σ_{stem} , resulting in steeper slopes: 0.65 (aspen), 0.36 (birch), 0.8 (maple), 0.22 (ash), 1.44 (willow), and 1.10 (caragana) (Fig. 4B–4D). These data confirm that changes in σ_{stem} are much more sensitive to changes in θ_{stem} than to salinity changes.

The σ contributed by the cell walls, that together with the sap σ (σ_{sap}) add up to the total σ_{stem} , could be estimated from $\sigma_{\text{stem}}-\sigma_{\text{sap}}$ relations (Fig. 5). The measured $\sigma_{\text{stem}}-\sigma_{\text{sap}}$ data was fitted to a $\log(\sigma_{\text{stem}})-\sigma_{\text{sap}}$ equation. The cell wall σ can be found by extrapolating the $\log(\sigma_{\text{stem}})$ value to $\sigma_{\text{sap}} = 5.5 \text{ mS m}^{-1}$. This σ_{sap} value was chosen because it was the averaged lowest measured σ_{sap} value reached in the solution draining from the stems during leaching with distilled water to steady state. The extrapolated values, attributed to the cell wall contribution, were 0.04 (caragana), 0.08 (birch), 0.12 (ash), 0.14 (aspen), 0.15 (maple), and 22 (willow) mS m^{-1} . When comparing these cell wall σ values to the ones shown in Fig. 3, we can deduce that the σ of cell walls can vary widely among tree species, forming 27 to 95% of the lowest σ_{stem} measured for each stem throughout this study. Practically, it may imply

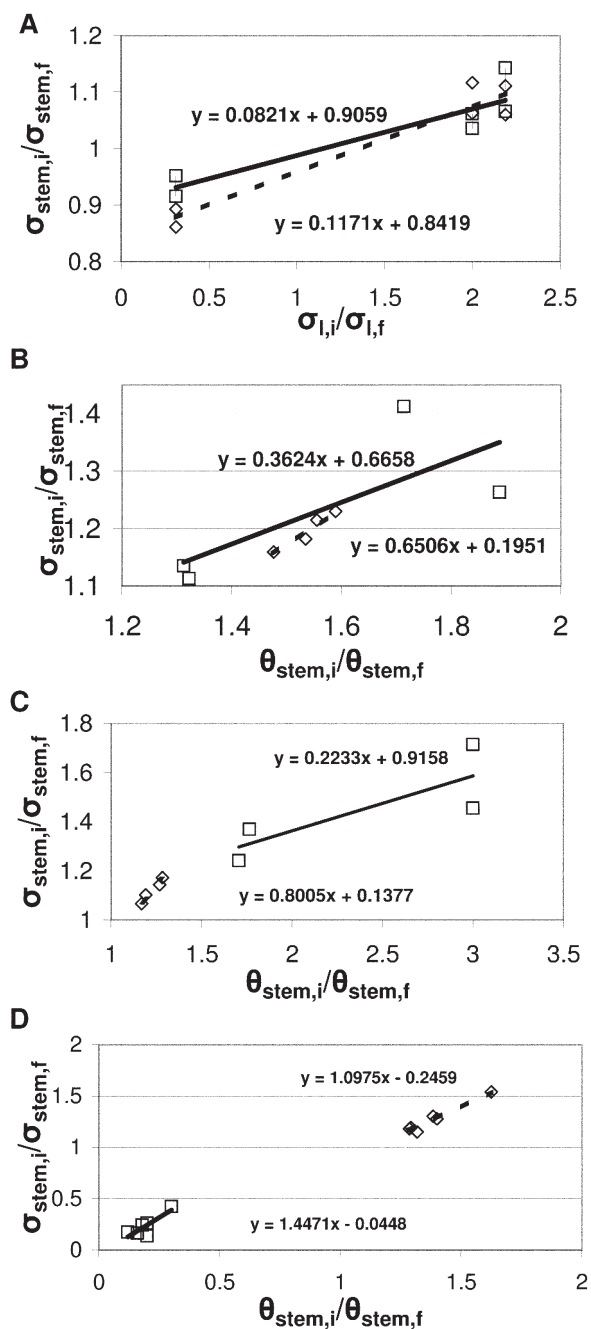


Fig. 4. The extent to which stem electrical conductivity is affected by changing the salinity of the leaching solution in (A) aspen (solid line) and birch (dashed line) or changing the stem water content in (B) aspen (solid line) and birch (dashed line), (C) ash (solid line) and maple (dashed line), and (D) caragana (solid line) and willow (dashed line). In (A), the x axis is the ratio of initial to final leachate conductivity, $\sigma_{l,i}/\sigma_{l,f}$ and the y axis is the resulting ratio of initial to final whole-stem conductivity, $\sigma_{\text{stem},i}/\sigma_{\text{stem},f}$ (aspen, solid line; birch, dashed line). In (B–D), the x axis is the ratio of initial to final stem water content, $\theta_{\text{stem},i}/\theta_{\text{stem},f}$ and the y axis is the resulting $\sigma_{\text{stem},i}/\sigma_{\text{stem},f}$ ratio. The linear regression equation is given next to each line.

that for certain species, such as willow, the changes in σ_{stem} due to sap ionic concentration may be only a small fraction of the total σ_{stem} , making it an even more favorable candidate for water status monitoring by resistivity.

As a rule, the TDR probe provides an integrated measure of water content between the three metal rods, both along the

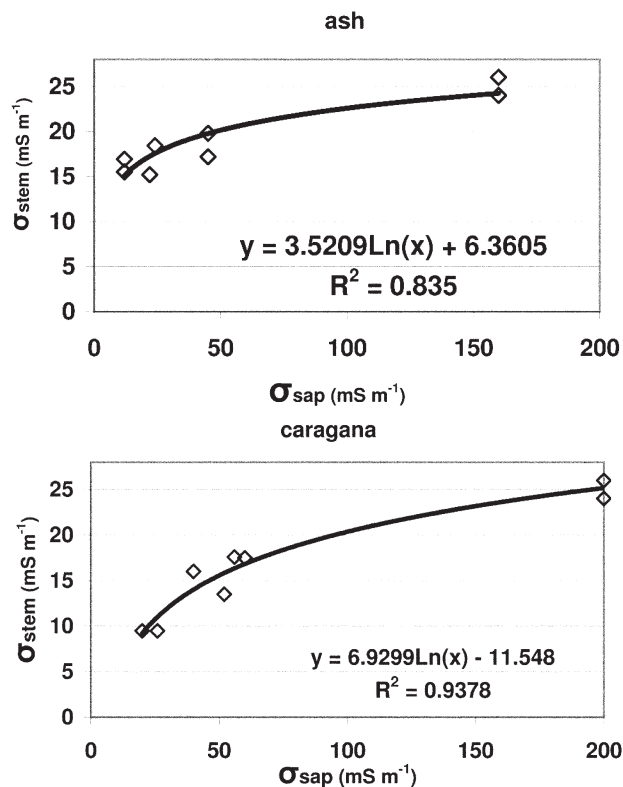


Fig. 5. Stem electrical conductivity–sap solution electrical conductivity ($\sigma_{\text{stem}}-\sigma_{\text{sap}}$) relations for ash and caragana, from which the contribution of the “net” electrical conductivity of the stem cell walls ($\sigma_{\text{cell walls}}$) to the bulk stem electrical conductivity was evaluated by extrapolation to $\sigma_{\text{sap}} \rightarrow 5.5 \text{ mS m}^{-1}$. The linear regression equation and adjusted squared correlation coefficient are also given.

rods and for approximately 20 mm above and below them. Immediately after drilling installation holes for the TDR probe, the conduits are cut open along the diameter of the rods, causing immediate embolism of the vessels. Hence, little of the wood volume between the rods will be functional; however, a TDR probe inserted into a live tree stem and left long enough for full curing will represent the water content of the heartwood (formed during curing of the installation holes), which is in rapid equilibrium with the sapwood (i.e., the outer growth rings actively involved in water movement from roots to shoots). Any change in sapwood water potential is reflected within minutes in the heartwood in terms of changes in volumetric water content.

CONCLUSIONS

Our experiments have shown that σ_{stem} is more sensitive to changes in θ_{stem} than to changes in the salinity (σ) or cation (K^+ vs. Na^+) of the sap leached through stem segments. The range of salinities we used was wider than the physiological range expected in living commercial trees, given that marginal waters are applied with excess to safely leach salts from the root zone and trees tend to exclude salts from saline soil water. Anisotropic stem properties induce high variability in measured σ_{stem} and θ_{stem} values (Arnold and Andrews, 2004). We have shown, however, that the TDR can sensitively and accurately measure θ_{stem} with 30-mm-long rods. The increased scatter of measurements caused by such short rods can be overcome by averaging more frequent measurements.

We propose that measured changes of σ_{stem} in trees might be used as a proxy for changes in stem water content or stem water potential, hence electrical resistivity measurements might substitute for θ_{stem} measurements. The advantages of such a substitution are an improved accuracy and lower costs because resistivity equipment prices are one hundredth that of dielectric meters. Contrary to the θ_{stem} , the σ_{stem} does not depend exponentially on rod length and therefore when shorter rods are used (in smaller plants), the drop in accuracy will be less drastic. Also, unlike TDR probes, no specific configuration is required when measuring σ_{stem} (because no impedance match is required), enabling flexibility in measuring small plant parts, even below the 30-mm rods. Since θ_{stem} is affected by stress from many sources, the suggested approach may provide a useful tool for monitoring water stress caused by drought, disease, or high salinity.

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