Detecting Water Stress in Trees Using Stem Electrical Conductivity Measurements

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Using time domain reflectometry (TDR), we studied stem water content (θ_{stem}), stem electrical conductivity (σ_{stem}), and their ratio for 220 d in stressed, installation-cured, living trees of four species. Lysimeter-grown mango (*Mangifera indica* L.), banana (*Musa acuminata* Colla), date (*Phoenix dactylifera* L.), and olive (*Olea europaea* L.) were subjected to several types of mild (intensity and duration) water stresses simulating horticultural orchard irrigation practices. This study of living trees was triggered by our previous study accomplished in uncured, thawed, native, cut stem segments. We have confirmed in living trees our earlier findings that θ_{stem} reacts sensitively and within minutes to water stress. This response is the main driver of σ_{stem} changes, by far exceeding the salinity effect on σ_{stem}. Known irrigation rates, half-hourly tree weights from load cells, and frequent sampling of drainage solution for volume and salinity independently confirmed our findings. Relative to θ_{stem}, resistivity measurements have lower scatter because θ_{stem}–dielectric constant (ε) relationships are exponential and θ_{stem}–resistivity relationships are linear. With resistivity, there is no need to match impedances among meter, cable, and probe, implying a larger flexibility in probe geometry, longer cables, and higher accuracy with shorter rods. There is a clear economic advantage in resistivity over ε measurements. The linkage between stem resistivity and water status (designated as the *linkage factor*) for lysimeter plants, orchard trees, and cut stem segments demonstrates the potential in scheduling irrigation according to plant water needs with an inexpensive, direct, and simple resistivity measurement.

Abbreviations: DOY, day of the year; LF, linkage factor; TDR, time domain reflectometry; θ, volumetric water content; σ, electrical conductivity; ε, dielectric constant.

Future water shortages have been predicted even for countries and regions (Canada, Australia, California in the United States, and China) that are currently seemingly rich in this resource (Thayalakumaran et al., 2007). A major factor leading to this catastrophe is wasteful water use that accelerates salinization and contamination of soils, rivers, and groundwater, thus triggering deterioration of the soil structure and a rise in groundwater levels. A significant slowing of these negative processes can be obtained by using an irrigation scheduling strategy that refers to plant water needs by using an accurate, sensitive, simple (farmer-friendly), automatable, close monitoring of crops' water status so as to minimize the intensity and duration of stress while maintaining a high-quality yield with the optimal water amount.

The electrical conductivity (σ) of any medium is proportional to the number and mobility of its electrical charges (ions, dissociated molecules, and surface absorbed ions). During the conduction of an electric current, the ionic charges do not really move and the passage of the electric current (including in plant tissues) is achieved by transferring the induced electromagnetic field between neighboring ions, whether they are free or attached to the membranes or cell wall surfaces. The path of current in healthy tissues is through channels of the cell walls, resulting in a current that is related to impedance due to separation of charges (ions) at tissue boundaries. In such healthy tissues, the membrane-screened ions are limited in their contribution to σ (Tattar and Blanchard, 1976) and the number of

Soil Sci. Soc. Am. J. 72:1014-1024
doi:10.2136/sssaj2007.0308
Received 20 Aug. 2007.
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ions in the interstitial fluids of plants is also a function of the relative metabolic activity of tissues; as long as a cell is metabolizing normally, its electrical properties will primarily reflect changes in metabolic rate like ion transfers.

In injured tissues (e.g., immediately after resistance meter electrodes have been inserted into the wood when short-term resistance measurements are made [Blanchard et al., 1983]), however, the membrane depolarizes and electrolytes are released into the intercellular spaces, causing a large local increase of the solution ionic concentration affecting σ_{stem}. Protoplasm cells, containing high concentrations of K^+ ions, release them and in the absence of the insulation membranes effect, injured tissues have a much higher σ_{stem} than intact stems. Consequently, the σ values of ruptured tissues of living trees have nothing to do with the tree's water status although they have been used to identify tree vigor, dormancy, cold-temperature injuries, and infectious diseases (Tattar and Blanchard, 1976). It is therefore clear that no relations are expected between σ_{stem} obtained in intact and injured tissues.

Measuring σ_{stem} may have three advantages over measuring dielectrics for irrigation scheduling. First, there is no need to match impedances among meter, cable, and probe, implying a larger flexibility in the probe's geometry, including shorter rods. Second, interference from long cables is minimal or easily taken into consideration, implying almost unlimited cable length compared with the current limit of 5 to 15 m (depending on cable quality). Third, higher accuracy is expected: while θ_{stem}–l_a (virtual rod length) relationships are exponential, σ_{stem}–resistivity relationships are linear. This means that when a probe's rod length is reduced threefold, the measurement error will increase by 3 or 9 when measuring resistivity or dielectrics, respectively.

In two recent complimentary studies, we have looked into θ_{stem}–σ_{stem} relations. In Nadler et al. (2006), we noted in a lysimeter-grown mango tree, that measured σ_{stem} was significantly more dependent on θ_{stem} than on the salinity level. This somewhat unexpected finding triggered the later study (Nadler and Tyree, 2008), which recreated θ_{stem}–σ_{stem} relations and suggested an explanatory mechanism in stem segments of six different species leached to different salinities while their water content was manipulated. The obvious next step was to study the same θ_{stem}–σ_{stem} relations in living plants having characteristic stem structures and drought resistance: a tropical plant (mango, cv. Kent), a weed (Cavendish banana), a monocotyledon (date), and a drought-resistant plant with a massive stem (olive, cv. Barnea).

The following four fundamental differences between results obtained from the experimental stem segments and living trees are holding us back from applying the conclusions from the former to predict θ_{stem}–σ_{stem} relations in the latter:

1. The θ_{stem}–σ_{stem} relations are obtained in different cell types when measured in segments vs. living trees. While TDR probe rods are in close contact with directional (mainly longitudinal) water-conducting cells in stem segments, in living trees measurements take place in nonconductive heartwood cells formed during the 150 to 200 d of stem curing following probe installation. This may imply a different degree of stem isotropy and also different cell wall background electrical conductance.
2. Dozens of natural physiological processes in the living tree stem are practically nonexistent in stem segments, leaving water movement and salinity redistribution to be solely diffusion dependent. This may affect the rate and extent of water and ion redistribution and therefore measured σ.
3. While voids between probe rods and stem that form during installation are left as are in stem segments, those in the living trees will grow new cells and the voids will disappear. The dielectric measurement is exponentially dependent on the distance perpendicular to the rod direction, making the 1 to 2 mm closest to the rods the most effective. Moreover, these locations were exposed to the atmosphere in the laboratory experimental stem segments, which isn't the case in the cured living trees.
4. To test a wide spectrum of optional sap salinity and water status, we have imposed on the stem segments a quite wide range of θ_{stem} and σ_{stem}. Therefore, we had to make sure that our stem segment measurements are still applicable in live trees and will pick up milder θ_{stem} and σ_{stem} changes naturally occurring in them.

Stem structure can be quite variable. Lu et al. (2000) reported high variability in spatial variations in sap flux density in the trunk of orchard-grown, mature mango trees under changing soil water conditions. They have found that, under nonlimiting soil water conditions, circumferential variation was substantial (CV = 27%), but there was no relation between sap flow density (SFD) and aspect. Hourly SFD during 24 h at different aspects were highly correlated pairwise. The relationships between different aspects were constant (CV = 50%) during well-watered periods but highly variable (CV = 150%) under changing water conditions. The SFD showed marked radial variation within the trunk and a substantial value was observed at the center of the trunk. For each selected aspect, on each tree, changes in SFD with time at different depths were closely correlated but SFD depth profiles differed between trees and even between aspects within a tree, and also varied in an unpredictable manner as water availability changed. Still, during a period of nonlimiting soil water conditions, depth profiles remained relatively constant. The finding of Lu et al. (2000) support earlier ones by Edwards and Jarvis (1983), who measured radial differences in θ_{stem} of an intact pine (*Pinus contorta* Douglas ex Loudon) using attenuation of gamma radiation (calibrated against gravimetric estimates), reporting for a 70-mm depth a θ_{stem} range of 0.185 to 0.847 L L^{-1} with a SD of 1.8 to 26% for the different 10-mm layers. Franchois et al. (1998) found within a single birch (*Betula papyrifera* Marshall) stem cross-section, from the center to the rim, the ε decreased from 20 to 8 and for a fir [*Abies nordmanniana* (Steven) Spach] from 31 to 7. Kenneth et al. (1997), while finding stem water potential of prune (*Prunus domestica* L.), almond [*Prunus dulcis* (Mill.) D. A. Webb], cherry [*Prunus avium* (L.) L.], and pear (*Pyrus communis* L.) to reliably quantify water stress for guiding irrigation, also observed that in many cases of these field studies, systematic tree-to-tree differences in water status were large enough to obscure irrigation treatment effects, and recommended making irrigation decisions on a site-specific basis.

Moreover, for live horticultural orchard tree stems, variability will additionally depend on orchard management techniques

such as branch pruning, planting in rows, localized trickle irrigation, the presence of nearby large branches, or branch removal scars. Even the slow transfer from earlywood to latewood (e.g., in conifers) may affect measured θ_{stem} scatter due to the significant difference between relative water contents of 21.8 to 4.1 in latewood and earlywood, respectively (Jean-Christophe and Gartner, 2002). 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 (1–40 mS m^{-1}) overlaps the results of this study and previous studies (Nadler, 2004; Nadler et al., 2006).

Traditionally, 50- to 70-mm-long rods are considered the minimal length still assuring reasonably accurate results. Such a limitation may be a disadvantage when small stems or young branches are monitored. To test the potential use of shorter rods, we installed and monitored in a mango stem two probes having 48- and 29-mm-long rods.

The objectives of this study were to: (i) verify and quantify, in several species of stressed living trees, the σ_{stem}–θ_{stem} relationships previously found in stem segments; and (ii) test the chances for substituting water status measurements by σ, measured by optimal and short rods, for irrigation scheduling. From our results, we have selected to present those demonstrating the method's reaction time and sensitivity to detect linkage factor (LF) values ($\Delta\sigma_{stem}/\Delta\theta_{stem}$) under moderate water stress conditions during routine daily cycles, different periods of irrigation withholding, increasing salinity, and several irrigation intervals, and the performance of different lengths of probe rods.

MATERIALS AND METHODS

Time Domain Reflectometry Methodology

The TDR methodology, using the Tektronix 1502 cable tester (Beaverton, OR), was used to measure ε and σ of the stems and perlite (Cassel et al., 1994; Nadler et al., 2006). The widely used equation of Topp et al. (1980) relates ε to θ_{soil} by

$$\theta_{soil} = (5.3\times10^{-2})+(2.92\times10^{-2})\varepsilon-(5.5\times10^{-4})\varepsilon^2+(4.3\times10^{-6})\varepsilon^3 \quad [1]$$

The dielectric constant of water (~80) is larger than that of stem tissues or perlite (2–6 and 3–3.5, respectively) or air (ε = 1). Assuming a negligible contribution to capacitance by mass addition due to stem growth, any changes in measured capacitance may be attributed to stem moisture changes. At very low frequencies, the load impedance (Z_L) equals the load resistance (R_L of the TDR probe embedded in the medium), hence

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

where ρ_∞ is the reflection coefficient of the TDR signal. The reciprocal of R_L equals the direct current conductance and can be converted to electrical conductivity (σ) 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 measurement of R_L in solutions of known σ. All reported σ values were adjusted to 25°C according to Eq. [3], where $f_{T25} = 1 - (T_i - 25)0.02$ and T_i is the ith temperature measurement (U.S. Salinity Laboratory Staff, 1954).

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

$$\theta = -0.251+(4.66\times10^{-2})\varepsilon-(4.93\times10^{-4})\varepsilon^2 \quad [4]$$

Under the experiment salinity levels, and according to a recent review by Robinson et al. (2003), the maximal effect of salinity on θ_{stem} is <0.01 m^3 m^{-3}. The θ values derived from the measured ε have not been corrected for the temperature effect on ε because the mutually compensating interaction among θ, σ, and T is negligible (Pepin et al., 1995; Irvine and Grace, 1997).

Experimental Design

From spring to autumn of 2006, the stems and the root zones of eight trees, two trees each of the four different species, were monitored by the TDR method while being subjected to different water stresses. According to previous experience regarding the effect on the TDR-measured θ_{stem} of stem tissues curing after installation (Wullschleger et al., 1996; Nadler, 2004), we waited 200 d before starting continuous measurements.

Between August and October 2005, two each of banana, date, and olive were purchased, any soil traces washed away from the root system, and the trees replanted in perlite-filled 70-L containers. During replanting, a 200-mm-long TDR probe, made from three rods of 3-mm-diameter stainless steel at 50-mm spacing, was horizontally installed inside each container. Holes of 2.9-mm diameter were drilled in the stems through a metal leader, and each tree was installed with a TDR probe made from three 70-mm-long rods of 3-mm-diameter stainless steel at 50-mm spacing, with rods plane parallel to the stem's long axis. Stem diameters ranged between 0.1 m (banana and olive) and up to 0.2 m (date and mango). Stem ages were about 1 yr (banana), 4 yr (date), 10 yr (olive), and 15 yr (mango). A detailed discussion of the significance of the fact that the TDR rods were sampling both sapwood and heartwood is presented in a separate study (Nadler and Tyree, 2008). Before installation of the probes, their geometric factors, relating R to σ, were determined in tap water of known conductivity and temperature. For a given probe configuration and temperature, σ is the reciprocal of resistivity and the two terms will be used interchangeably.

A 4.0-m coaxial cable (RG58U) connected each of the probes to a multiplexer (TR-200, coaxial multiplexer with 16 inputs, one output, Dynamics Inc., Houston, TX) and a 0.9-m cable to the cable tester. Also included in the study were the two previously used Kent mango trees (Nadler et al., 2006), which had, in addition to the 70-mm stem probes, also two shorter probes (48 and 29 mm long) that were installed in one of the mango trees, 0.4 and 0.6 m above the 70-mm probes. The shorter rods were installed above the longer ones and in narrower branches for two reasons: (i) to maintain a safe distance between neighboring probes and thus minimize potential mutual influence (Castiglione et al., 2006), and (ii) to ensure that whatever the rod length was, they would penetrate and sample most of the branch diameter, as is the case with the longer rods. All 11

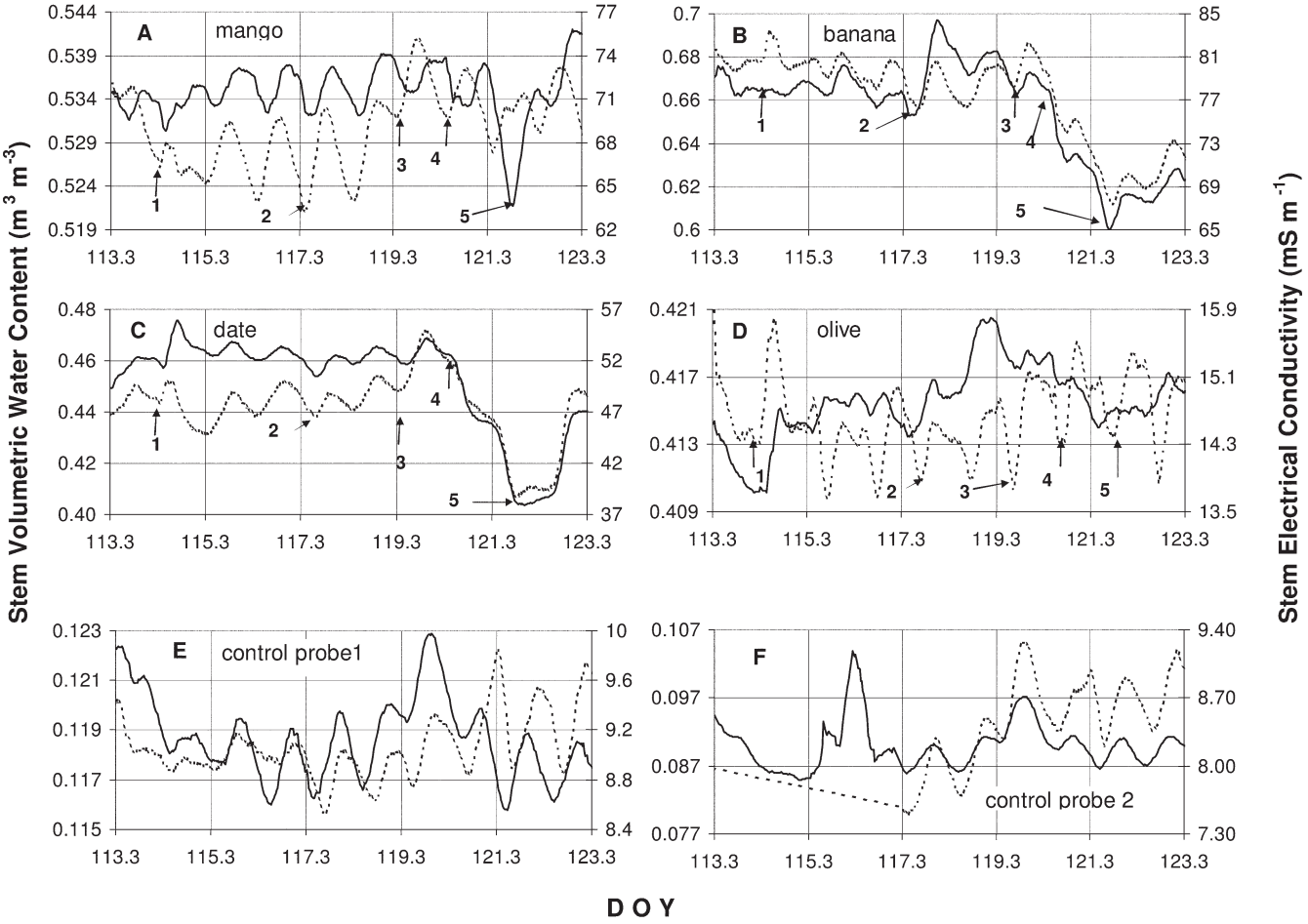

Fig. 1. Stem water content (θ_{stem}, solid line, left scale) and stem electrical conductivity (σ_{stem}, dashed line, right scale) vs. time for (A) mango, (B) banana, (C) date, and (D) olive trees while several water status related events occurred: (1) an 8-mm rain (Day of the Year [DOY] 114), (2) a manual irrigation with distilled water (DOY 117) followed by a manual irrigation with 12 to 15 L of tap water per tree, (3) an exceptionally hot day (DOY 119), (4) a 32-h period of irrigation withholding, followed by (5) an excessive manual irrigation (DOY 120.3). Also shown are (E and F) σ and θ of the control stems (oven-dry stem segments) vs. time. The *y* axis scales of the separate figures were selected to show each curve in its most detailed range.

TDR probes of the mango installed in 2004 (Nadler et al., 2006) were monitored through a second multiplexer. The cables of the TDR probes (50 Ω RG58) were wrapped in aluminum foil to reduce temperature changes. The TDR trace was recorded every 30 min and the apparent length (l_a) of the probe rods was automatically calculated by identifying the beginning and endpoint reflections (S. Green, personal communication, 2000).

Unlike the θ_{stem} values from the 70-mm-rod measurements that were automatically collected and analyzed by the software, for the shorter ones only the dielectric length was automatically measured (due to some software limitation) and was converted to ε using the specific calibration of each of the short-rod probes, from which θ_{stem} was calculated using the equation of Wullschleger et al. (1996) and σ from the resistance and the specifically calibrated geometric coefficient.

Control Probes

A study like ours, consisting of relatively short probe rods (<70 mm), long coaxial cables (>4 m), and a narrow range of studied dielectric changes, may be influenced by experimental factors, environmental conditions, and *T*. In the absence of a simple and direct way of separately evaluating each of these external effects on the TDR measurements, we used an integrated approach. Throughout the study, two control probes, identical to the others, each installed in an oven-dried stem segment and protected by aluminum foil, were monitored for evaluation of data scatter. Hourly ε and *R* changes, converted into θ_{stem} and σ_{stem}, revealed a scatter of ±0.0014 $m^3\ m^{-3}$ and 0.25 mS m^{-1}, compared for example with 0.06 $m^3\ m^{-3}$ and 6 to 14 mS m^{-1} due to a mild water stress (Fig. 1E and 1F).

The automatic irrigation system consisted of a controller, pump, two 200-L containers, and four drippers (2 L h^{-1}) per tree. Unless otherwise mentioned, throughout Days of the Year (DOY) 60 to 300, the trees were excessively irrigated for 12 to 25 min, five times a day (800, 1000, 1200, 1400, and 1600 h) totaling 10 to 20 L d^{-1}. Other irrigation intervals (with the irrigation pulse starting at 0000 h and lasting 7 h) were: DOY 238 to 256, every other day; DOY 264 to 292, every third day; and DOY 258 to 262, every fourth day. Irrigation was withheld from DOY 117.29 to 117.77, 120.29 to 121.75, 135.29 to 136.61, and 149.29 to 151.60, followed by a manual irrigation of 10 to 20 L per container until drainage began. Rain events occurred on DOY 95 (6 mm), 114 (6mm), 265 (9 mm), and 288 (12 mm).

Extremely hot and dry weather (maximum $T > 28$°C) occurred on DOY 103 to 105, 119, 155 to 156, 229 to 236, 250 to 251, 261, and 285 and 286.

Tree water use was calculated from the difference between daily irrigation and drainage volumes and ranged from 2 to 17.5 L d^{-1} for the mango, from 2.4 to 17.5 L d^{-1} for the banana, from 2 to 17 L d^{-1}

for the date, and from 2.2 to 24 L d^{-1} for the olive. Tap water ($\sigma \sim$ 100 mS m^{-1}) was spiked with 55 mL of a liquid fertilizer per 200 L of tap water. The liquid fertilizer was Shefer 1 (Fertilizers and Chemical Materials Ltd., Haifa, Israel), which contained 7:3:7 of N/P_2O_5/K_2O and Fe, Mn, Zn, Cu, and Mo, raising the input solution σ to 150 mS m^{-1} (total N = 50 mg L^{-1}).

Unless otherwise indicated, water and nutrient elements were in excess of tree needs and the trees' mass increased by at least 10 kg. The reason behind the excessive irrigation was to form a stable reference water status to which we will relate the stresses effected by the treatments. This selected high water status is (i) relevant to the routine practice of horticulture farmers (aimed at minimal stress), and (ii) easy to obtain and maintain experimentally. The volume and salinity of drainage waters were determined every 1 to 3 d. Tree containers were placed on scales and weights were collected every 0.5 h with a CR21 logger (CSI, Logan, UT). The θ and σ of the root zone, and the results from load cells, fully supported θ_{stem} measurements and are therefore not shown.

Designed Treatments

Root-Zone Salinity

A combination of arid conditions, low-quality water, and intensive irrigation increase the risk of reaching harmful salinity levels. This being a longer lasting stress (due to ion accumulation in the trees' organs, especially in leaves) and difficult to counteract, special attention should be given to early warning of hazardous saline situations. To test the relative sensitivity of θ_{stem} and σ_{stem} in detecting salinity buildup within the tree, we spiked our routine irrigation water with NaCl. The root zone was gradually salinized (DOY 161–205) and leached (DOY 206–227) by spiking the tap water with increasing amounts of NaCl. Input salinity was increased from 150 to 370 (DOY 162), 550 (DOY 174), 620 (DOY 179), and 810 mS m^{-1} (DOY 186), resulting in a maximum salinity of the drainage water of 1800 (mango), 1080 (banana), 1950 (date), and 2850 mS m^{-1} (olive). The banana salinization was stopped on DOY 185, when irrigation was switched to tap water.

Temperature Corrections

Fifteen temperature sensors (Hobo thermometers and data loggers, Onset Computers, Bourbe, MA) were installed, one in each stem, four in the perlite containers, one in the control stem, and two measured air *T*. The θ_{stem} and σ_{stem} measurements were not corrected for *T* changes. Daily stem temperatures cycled 5 to 8°C throughout the study period. During the salinization phase (DOY 160–210), average temperature (±SD) in the stems were 26.1 ± 1.7°C for mango, 29.6 ± 1.8°C for banana, 28.5 ± 1.8°C for date, and 25 ± 3°C for olive. For the studied period (220 d), the slopes of the θ_{stem}–*T* relation were –0.0026 for mango, –0.0122 for banana, 0.004 for date, 0.0009 for olive, and –0.00004 for the control probe. Expected *T* effect on θ_{stem} values within this *T* range can be assumed negligible relative to the other error sources, especially with the counteracting effect of *T* on σ, which is unavoidably contributing to ε (Pepin et al., 1995). As for σ_{stem}, the slopes for the 220 d for the θ_{stem} and σ_{stem}–*T* relations were –0.039 for mango, –1.387 for banana, 1.275 for date, –0.0023 for olive, and 0.0436 for the control probe. The correction factor is known ($\sim$2% $°C^{-1}$); however, if, as we claim, a significant part of the measured change in σ_{stem} comes from θ_{stem} changes, a full *T* correction may overcorrect and therefore mislead. We decided to present the σ_{stem} values as measured, noting that in the worst case scenario, σ_{stem} values may be ±6 to 8% off.

The ratio LF = $\Delta\sigma_{stem}/\Delta\theta_{stem}$ will be used to represent the linkage between changes in these two parameters during a specific event.

RESULTS

Figures 1 and 2 present the versatility and sensitivity of the TDR technique in measuring θ_{stem} and σ_{stem}. We should emphasize that the θ_{stem} and σ_{stem} reactions to water application were found to be in the order of minutes, and not 4 h as reported earlier (Nadler et al., 2006).

Figure 1 presents θ_{stem} and σ_{stem} values measured during a 10-d period starting at DOY 113.3 that included the following events: (i) an 8-mm rain event (DOY 114); (ii) substitution of the regular, automatic, fertilizer-spiked tap water for drip irrigation by manual replenishment with distilled water, according to the hourly weight loss (from load cells measurements) due to tree water use (DOY 117); (iii) an excessive manual irrigation (12–15 L per tree) applied by the end of this day (1835 h); (iv) an exceptionally hot day (maximum air and stem temperatures were 6°C above the previous day (DOY 119); and (v) a 32-h period of irrigation withholding (again followed by an excessive manual irrigation, DOY 120.3).

The experimental findings were:

1. After the morning rain, σ_{stem} increased following the θ_{stem} increase in all trees, excluding the banana (Fig. 1A–1D).
2. Substituting the150 mS m^{-1} tap water with distilled water throughout the day (DOY 117) did not affect the four trees' σ_{stem} to a measurable extent. The 12- to 15-L manual irrigation in the late afternoon was less noticed by the mango and date (probably due to being close to their momentary maximum water storage capabilities) but is clearly seen in the banana and olive (Fig. 1B and 1D).
3. The extremely warm weather and more intense radiation on DOY 119, presumably inducing higher water demand, still was not reflected in θ_{stem} or σ_{stem} because they were excessively irrigated.
4. Most informative seems the θ_{stem} and σ_{stem} reaction to irrigation withholding (DOY 120) followed by an excessive irrigation. Mango (Fig. 1A): both θ_{stem} and σ_{stem} remained stable on the first day (DOY 120), then dropped (by 0.016 L L^{-1} and 6 mS m^{-1}) and later quickly responded to the recovery irrigation and gained back about 80% of their initial values. Banana and date (Fig. 1B and 1C): θ_{stem} and σ_{stem} dropped to a similar extent (0.03 L L^{-1} and 7 mS m^{-1}) during each day and both slowly recovered in reaction to water application (θ_{stem} with an 1.8-h delay relative to σ_{stem}), gaining back on the following day only 60% of the initial levels. Olive (Fig. 1D): throughout the study, the olive stem hardly reacted to either inducing or relieving water stresses; the excessive irrigation of DOY 117 caused a mere 0.003 L L^{-1} increase in θ_{stem} and 0.8 mS m^{-1} in σ_{stem}, while withholding irrigation for 32 h caused a limited θ_{stem} and σ_{stem} drop (0.004 and 0.7 mS m^{-1}) and recovery was full. So far, among the different trees, LF varied 170 to 300 while going into or coming out of a water stress (Table 1).

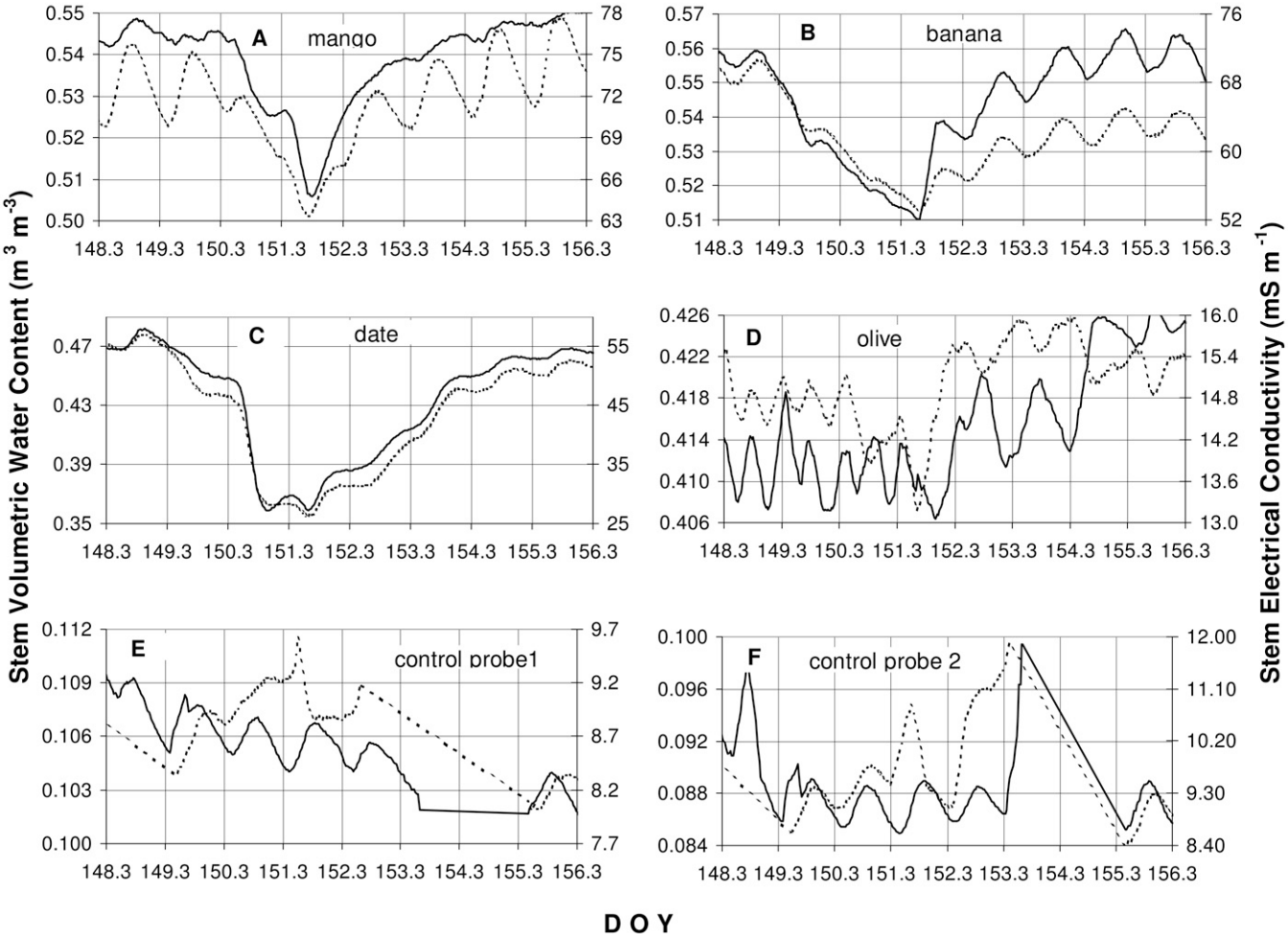

Fig. 2. Stem water content (θ_{stem}, solid line, left scale) and stem electrical conductivity (σ_{stem}, dashed line, right scale) vs. Day of the Year (DOY) for (A) mango, (B) banana, (C) date, and (D) olive trees during irrigation withholding between Days of the Year 149.3 and 151.6. Also shown are (E and F) θ and σ for the two control stem segments. The *y* axis scales of the separate figures were selected to show each curve in its most detailed range.

All of the above θ_{stem} changes were accompanied by the complementary θ changes in the root zone, measured in the perlite with the 200-mm-long TDR probes and the load cells (not shown). Experimental scatter of the two control probes, caused by anything other than imposed θ_{stem} changes, during the same 10 d are shown in Fig. 1E and 1F. Changes in θ_{stem} during the 10 d ranged from 0.006 ± 0.0022 (Fig. 1E) to 0.019 ± 0.0044 (Fig. 1F) and for σ_{stem} 0.8 ± 0.16 mS m^{-1} (Fig. 1E–1F). None of the changes reported for the live trees occurred in the control.

Figure 2 shows θ_{stem} and σ_{stem} vs. time before, during the irrigation stop (DOY 149.3–151.8), and after its renewal.

Mango (Fig. 2A): After a day-long delay, θ_{stem} and σ_{stem} dropped by 0.02 m^3 m^{-3} and 6 mS m^{-1} in each of the two consecutive days (consistent with results reported in Fig. 1) while θ_{stem} was slightly (2 h) delayed relative to σ_{stem} (Fig. 2A). Recovery rate following irrigation renewal was the fastest among the four species and was completed within 48 h.

Banana (Fig. 2B): Soon after irrigation was stopped, σ_{stem} and θ_{stem} started dropping quite linearly with time for 2 d, with a clearly visible slightly reduced rate during the night (Fig. 2B). Total θ_{stem} and σ_{stem} drops were 0.04 m^3 m^{-3} and 15 mS m^{-1}, followed by a 4-d recovery to initial levels induced by the excessive irrigation.

Date (Fig. 2C): In contrast to the mango, σ_{stem} and θ_{stem} started dropping soon after irrigation was stopped, yet more than half of the drop took place in the second day. Total θ_{stem} and σ_{stem} reductions were 0.11 m^3 m^{-3} and 29 mS m^{-1}, followed by a 4-d recovery to initial levels induced by the excessive irrigation.

Olive (Fig. 2D): Measured θ_{stem} and σ_{stem} decreases were 0.001 m^3 m^{-3} and 1.5 mS m^{-1}, close to the experimental error (±0.0014 m^3 m^{-3} and ±0.25 mS m^{-1}) followed by full recovery in less than a day.

In all the above observations, σ_{stem} closely followed θ_{stem} changes, and varied considerably even where no salinity change should be expected.

Note the θ_{stem} and σ_{stem} changes during the night (DOY 149.9–150.3) caused by the lower night evapotranspiration rate and seen as changes in slope of both θ_{stem} and σ_{stem}, leaving only drainage to drive the decrease in water content. It is best seen in the banana and date (Fig. 2B and 2C), which further demonstrate the method's sensitivity.

Table 1. Linkage factor (LF) values, the ratio between the change in stem electrical conductivity ($\Delta\sigma_{stem}$) and the change in stem water content ($\Delta\theta_{stem}$), following several events throughout the growing season.

Tree species	$\Delta\sigma/\Delta\theta$								
	8-mm rain	Recovery after irrigation withholding		No irrigation for				Average	SD
				32 h	55 h	72 h	96 h		
	mS m^{-1} (m^3 m^{-3})$^{-1}$								
Mango	250	220	300	375	300	280	350	296	54
Date	175	NA†	270	230	264	375	280	266	66
Banana	NA	184	200	170	233	180	240	201	29
Olive	220	210	200	175	NA	137	192	195	19

† NA = not available.

We tested the θ_{stem} and σ_{stem} changes and the LF values (Table 1) during the growth season by stopping irrigation for four different periods: 32 h (DOY 120.3), 55 h (DOY 149.3), 72 h (DOY 252.0), and 95 h (DOY 259.0). In all of the species, in response to the induced water stress, σ_{stem} closely followed θ_{stem} changes, significantly decreasing and returning to initial levels even though there was no obvious salinity change involved. The LF values differed widely within and among species, however, ranging from 170 to 375 mS m^{-1} per m^3 m^{-3} (Table 1).

Two additional terms, $\Delta\theta_{rel}$ and $\Delta\sigma_{rel}$, representing the change in θ_{stem} and σ_{stem}, respectively, during a water stress event relative to the initial level (prestress), represent the absolute sensitivity of the σ_{stem} or θ_{stem} measurements. Figure 3 shows the individual $\Delta\sigma_{rel}$ and $\Delta\theta_{rel}$ for stems of the four species as a function of irrigation withholding period. For almost all species, the relative σ_{stem} is more than double the relative θ_{stem} (Fig. 3A–3D).

Figure 4 shows the averaged $\Delta\theta_{rel}$ (Fig. 4A) and $\Delta\sigma_{rel}$ (Fig. 4B) for the four stems (solid line) and the control stems (dashed line) as a function of irrigation withholding period. It can be clearly seen that the control stem slopes are more than 20-fold less steep and practically negligible compared with the same parameters of the living trees.

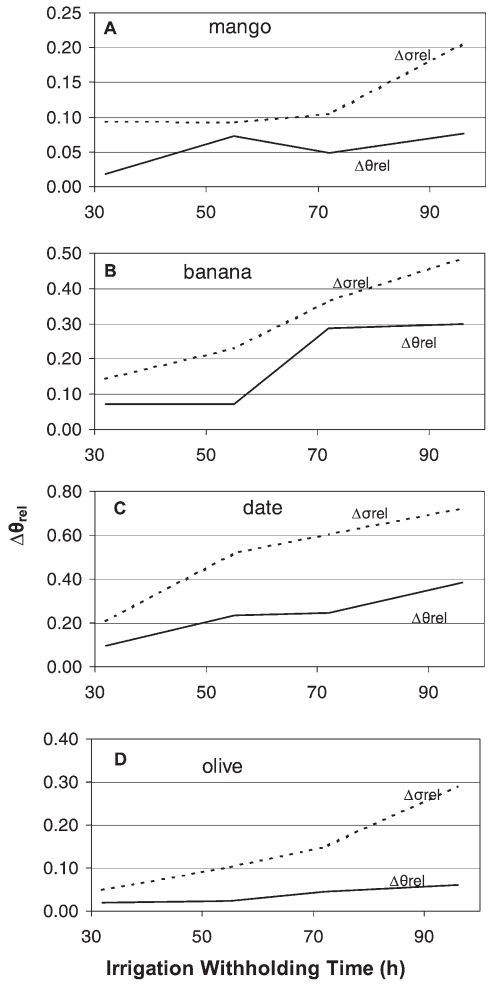

Fig. 3. Changes in stem water content ($\Delta\theta_{rel}$, solid line) and stem electrical conductivity ($\Delta\sigma_{rel}$, dashed line) relative to initial values for (A) mango, (B) banana, (C) date, and (D) olive stems as a function of irrigation withholding period.

Salinity Stress

Between DOY 160 and 206, the salinity of the irrigation water was increased from 150 to 370, 550, 620, and 810 mS m^{-1} (Fig. 5), resulting in maximum drainage σ of 1800 (mango), 1100 (banana), 1900 (date), and 2800 (olive) mS m^{-1} (Fig. 6). Plant θ_{stem} and σ_{stem} response to lowering the available water amount with increasing salinity input was unique for each species (Fig. 5):

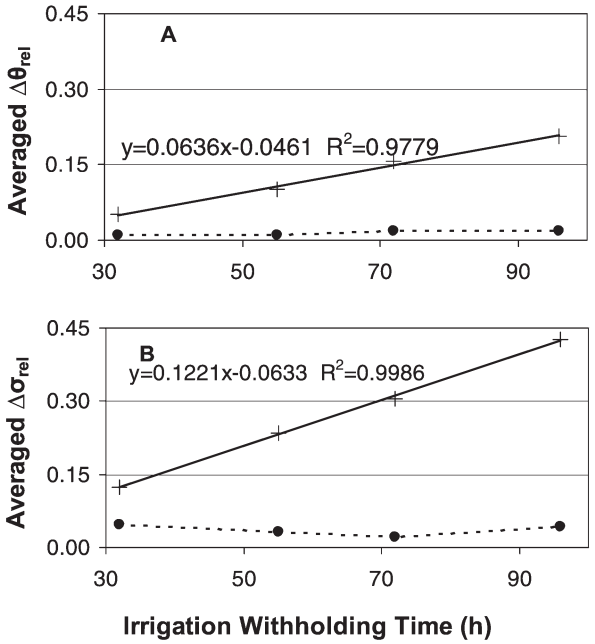

Fig. 4. Averaged (A) stem water content relative to initial values ($\Delta\theta_{rel}$) for the four tree stems (solid line) and the control stem segments (dashed line), and (B) relative stem electrical conductivity ($\Delta\sigma_{rel}$) for the four tree stems (solid line) and control stem segments (dashed line) as a function of irrigation withholding period. The regression equation and adjusted correlation coefficients are also shown.

Mango (Fig. 5A): The values of θ_{stem} and σ_{stem} dropped monotonously from the very start of the salinization process, losing up to 0.07 $m^3\ m^{-3}$ and 16 mS m^{-1}, and recovery was noticed only with desalinization (after DOY 206).

Banana (Fig. 5B): The banana did not reach the fully intended salinization and we had to (at input salinity = 1000 mS m^{-1}) switch back to tap water to avoid the risk of losing the plant altogether. Throughout this 25-d period, both σ_{stem} and θ_{stem} increased at similar rates (19.5 mS m^{-1} and 0.04 $m^3\ m^{-3}$, respectively); however, switching back to tap water had a different effect on σ_{stem} and θ_{stem}. The value of σ_{stem} dropped sharply and almost immediately (3 d) after switching the input solution to its initial value. The value of θ_{stem}, on the other hand, kept increasing for the next 15 d and only then dropped sharply.

Date (Fig. 5C): The values of θ_{stem} and σ_{stem} never dropped below initial values, increased for 25 d after the start of salinization, leveled off when the drainage solution reached 1500 mS m^{-1}, and then further increased in reaction to lowering the input salinity.

Olive (Fig. 5D): Measured σ_{stem} and θ_{stem} changes throughout the salinization process were smaller than the experimental error (±0.25 mS m^{-1} and ±0.0014 $m^3\ m^{-3}$, respectively) obtained from the control stems during the same period.

These salinity-induced results were independently confirmed by plotting daily water consumption and salinity σ vs.

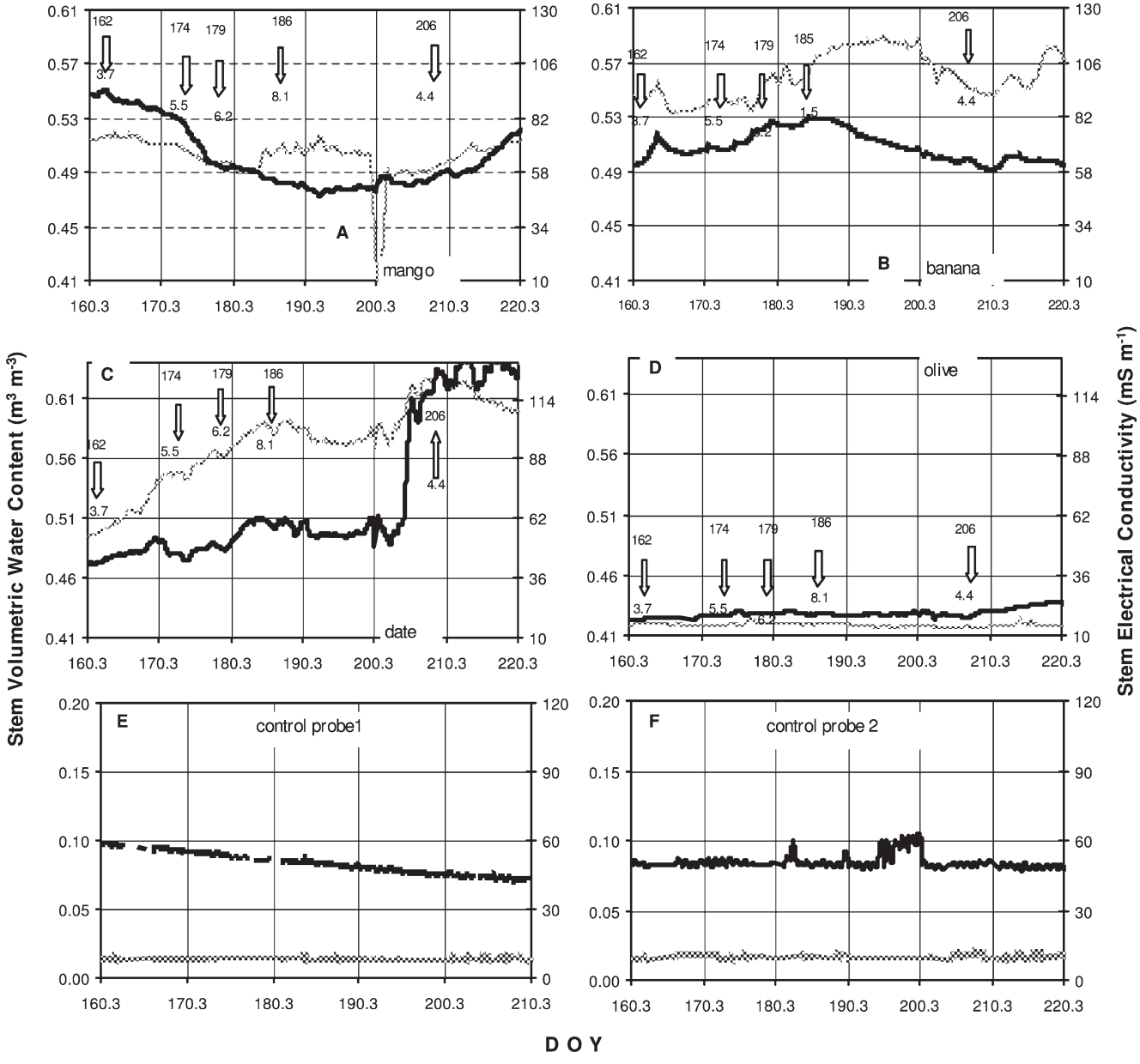

Fig. 5. Stem water content (θ_{stem}, solid line, left scale) and stem electrical conductivity (σ_{stem}, dashed line, right scale) vs. Day of the Year (DOY) for (A) mango, (B) banana, (C) date, and (D) olive trees during a gradual salinization and the beginning of the leaching process. Arrows indicate the Day of the Year (above arrow) and input salinity (below arrow, mS m^{-1}). (The banana was salinized for a shorter period.) Also shown are (E and F) θ and σ for the two control stem segments.

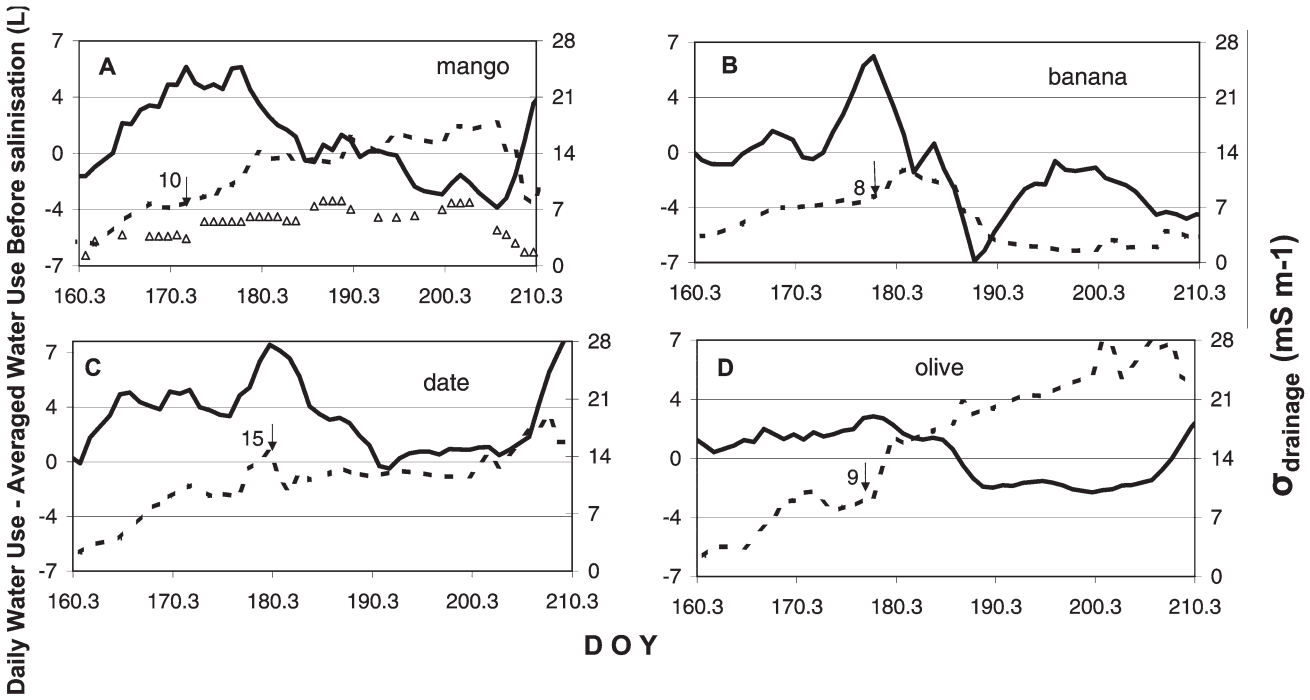

Fig. 6. Daily tree water use during a period of gradual salinization and the beginning of leaching minus the average water use during 6 d preceding salinization (solid line) and drainage water electrical conductivity ($\sigma_{drainage}$, dashed line) vs. Day of the Year (DOY) for (A) mango, (B) banana, (C) date, and (D) olive trees. Arrows indicate the time of a drop in water use and the salinity (mS m^{-1}) at that time. Also shown in (A) is the salinity of the irrigation water (Δ).

time (Fig. 6). The salt-sensitive mango dropped water use by 9.5 L d^{-1} once drainage salinity reached 1000 mS m^{-1} (on DOY 172). The most sensitive species, banana, dropped 13 L d^{-1} when salinity in the root zone reached 800 mS m^{-1} (DOY 178). The less sensitive date dropped its daily use by 8 L when salinity reached 1500 mS m^{-1} but did not go below the daily consumption with tap water. Within ±2 L d^{-1}, salinity had a limited effect on the olive stem, showing a slight decrease in water consumption when drainage σ was >900 mS m^{-1} (Fig. 6).

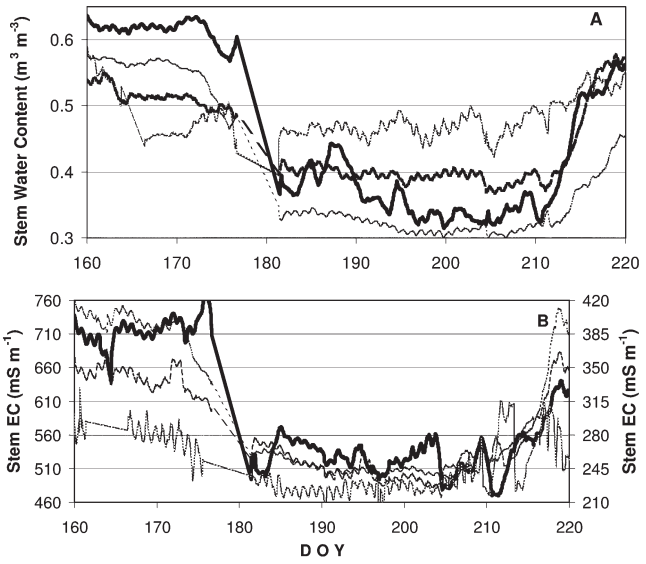

Fig. 7. (A) Stem water content and (B) stem electrical conductivity (EC) in a mango tree vs. Day of the Year (DOY) during a gradual salinization and the beginning of the leaching process as obtained by four probes: two with 70-mm-long rods (thick lines, solid and dashed, left *y* axis), one with 48-mm-long rods (dotted line, right *y* axis), and one with 29-mm-long rods (diffuse line, right *y* axis).

Probe Rod Length

The resulting θ_{stem} and σ_{stem} from the 29- and 48-mm-rod probes, along with the 70-mm ones, during the salinization process and the beginning of recovery (DOY 160–220) are shown in Fig. 7. The two 70-mm-long rods and the two shorter rods show similar trends of θ_{stem} induced by the salinization and leaching phases; however, data scatter is quite wide and the values differ quite significantly. From a first glance, it might seem that the differences in σ_{stem} and θ_{stem} between the short and the longer rods are due to length. A closer look, however, shows rather stable σ_{stem} (SD = ±0.25 mS m^{-1}) and θ_{stem} (SD = ±0.015 m^3 m^{-3}) values obtained by each of the short rods during DOY 182 to 202.

The soundness of using electrical conductivity measurements to represent θ_{stem} changes, by means of 70-mm-long rods, to detect stress conditions in trees was tested by plotting σ_{stem}–θ_{stem} relations in the four studied stems (Fig. 8). All four have linear relations, with R^2_{adj} > 0.5, except the olive tree, which had the narrowest seasonal θ_{stem} range (<0.04 m^3 m^{-3}). The probes with the shorter rods (48 [Fig. 8E] and 29 mm [Fig. 8F]) had different slopes (due to being located in narrower branches) and the expected lower R^2_{adj} values, but may still be acceptable for irrigation scheduling purposes.

DISCUSSION

We have shown that θ_{stem} and σ_{stem} obtained with the TDR clearly emphasize: (i) the detailed reactions of the stems to applied water stress and recovery for the four species regardless of stress source, (ii) the ability to trace even minute and

rapid changes in stem water status, including some small delays between θ_{stem} and σ_{stem}, and (iii) the variable response among the different species. The linear relations obtained for σ_{stem}–θ_{stem} indicate that σ_{stem} measurements can detect stress conditions with at least the same sensitivity. From measurements performed simultaneously in inactive (oven-dried) control stem segments, we have shown that factors that may interfere with setup performance such as temperature, humidity, and weathering of the cable tester, connectors, multiplexers, and cable length are small and negligible compared with changes in live tree θ_{stem} and σ_{stem} values. Our θ_{stem} results were independently supported by weighing (load-cell) measurements and the volume and salinity of drainage solutions.

The feasibility of using short rods (<30 mm) was confirmed. By definition, rod length affects the scatter but not the value itself. The large scatter in both θ_{stem} and σ_{stem} (Fig. 7) may be related to the location of the short rod installation: the shorter rods were installed above the longer ones and in narrower branches (see above).

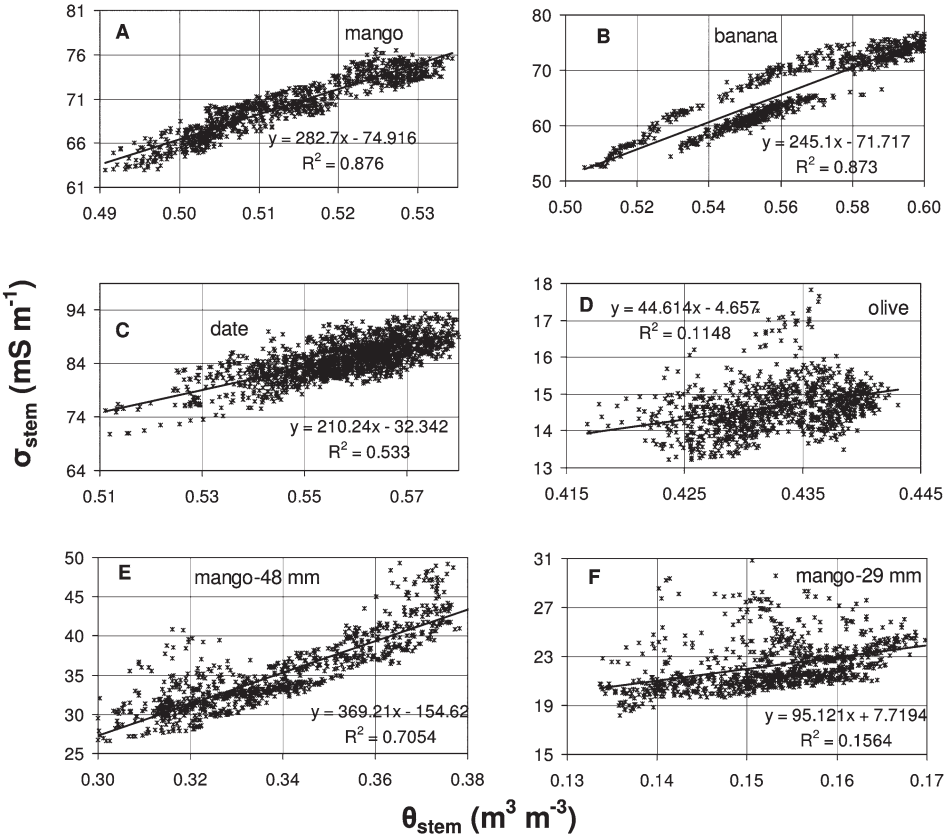

Fig. 8. Stem electrical conductivity (σ_{stem})–stem water content (θ_{stem}) relationships (n > 1000) obtained by probes with 70-mm-long rods in stems of (A) mango, (B) banana, (C) date, and (D) olive trees, and by probes with (E) 48- and (F) 29-mm-long rods in the same mango tree. The linear best-fit regression equation and adjusted correlation coefficients are also shown.

Stem structure variability is wide to an unknown extent, unavoidable, and differs among species. It can be speculated that this variability is caused by natural (height above soil surface, compass directions around the stem circumference, time and dynamics, tree size, transpiration, fluctuations in size of salinity residing in the stem center) and technical parameters (variable T effect, installation angle, cable quality, measurement random error, and scatter of automatic TDR trace analysis). We can exemplify the randomness of stem variability by comparing θ_{stem} and σ_{stem} results obtained by a pair of probes (70-mm-long rods) installed in the same tree with another (similar) pair installed in two different trees of the same species. We looked at the average and SD of the half-hourly differences between these two pairs throughout the study, amounting to >8000 data points. In the same tree, seasonally averaged θ_{stem} difference was 0.00251 ± 0.0238 m^3 m^{-3}, while in the different trees it was 0.0068 ± 0.010 m^3 m^{-3}; i.e., the absolute difference doubled, but the scatter was reduced by 50%. The findings for the differences in σ_{stem} were different: in the same tree, the seasonally averaged σ_{stem} difference was –3.93 ± 6.1 mS m^{-1}, while in the different trees it was 36.8 ± 12.1 mS m^{-1}; i.e., although the absolute σ_{stem} ranges were the same (40 mS m^{-1}) but shifted, the difference increased 10-fold and the σ_{stem} SD doubled.

Such wide scatter ranges agree with similar variability reported in stems of oak (*Quercus agrifolia* Née) and redwood [*Sequoia sempervirens* (D. Don) Endl.] (Constantz and Murphy, 1990), red maple (*Acer rubrum* L.) and white oak (*Quercus alba* L.) (Wullschleger et al., 1996), pine (*Pinus sylvestris* L.) (Irvine and Grace, 1997), yellow birch (*Betula alleghaniensis* Britton) trees (Clark and Gibbs, 1957), rough lemon (*Citrus jambhiri* Lush.), grapefruit (*C. paradisi* Macfad.), and sour lemon (*Citrus aurantium* L.) trees (De Villiers, 1939), Monterey pine and shining gum (Arnold and Andrews, 2004), and birch (Franchois et al., 1998). We can therefore conclude that length-induced differences in measured θ_{stem} and σ_{stem} are unavoidable and small relative to those caused by stem variability, and measured differences are real and not an experimental error.

Scatter of Linkage Factor Values

Calculated LF values, indicating the extent by which resistivity can be substituted for θ_{stem} for detecting stress, were extremely variable for each tree and among the tested species (Table 1). The wide scatter in LF values (Table 1) and lack of closer relations to applied water stress may be explained by stem variability, different weather conditions, different tree growth periods, and the specific water status prevailing before applying the stress. Somewhat lower LF values but with a similar scatter were found in a white grapefruit grafted on three different root stocks ('Troyer,' 'Cleopatra,' and 'Volka'), grown on a sandy loam soil, under saline conditions. Irrigation water salinity ranged from 150 to 340 mS m^{-1}, increasing soil salt content 10-fold (0.1 to 1 kg m^{-2}), and soil solution salinity up to 2300 mS m^{-1} in September, later to be leached to 100

to 200 by rain and tap water in the following January (Nadler, 2004). As a result, throughout this period, θ_{stem} and σ_{stem} were quite variable, ranging from 0.21 to 0.56 $m^3\ m^{-3}$ and 0.9 to 6.7 mS m^{-1}, respectively, but the average LF values for all the experimental trees was 38.1 ± 12.5.

Linkage factor values of live trees can be compared with those obtained in cut stem segments: 3 to 50 (avg. 20) in four conifers (Colorado blue spruce [*Picea pungens* Engelm.], white spruce [*Picea glauca* (Moench) Voss], lodgepole pine [*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelm.] and Scots pine [*Pinus sylvestris* L.] and 16.3 to 33.9 (avg. 22.6 ± 2.4) in six nonconifer native trees, Manitoba maple (*Acer negundo* L.) 16.1 ± 2.9, European mountain ash (*Sorbus scopulina* Greene) 19.5 ± 7.5, Bebb's willow (*Salix bebbiana* Sarg.) 28.3 ± 8.1, pin cherry (*Prunus pensylvanica* L. f.) 20.3 ± 6.3, paper birch (*Betula papyrifera* Marshall) 21.2 ± 6.1, caragana [*Caragana frutex* (L.) K. Koch] 33.9 ± 8.8, and trembling aspen (*Populus tremuloides* Michx.) 16.3 ± 3.6 under different mild water stresses (e.g., 0.014–0.034 mPa vacuum or 0.02–0.3 mPa pressure, Nadler and Tyree, 2008).

Considering the reported small experimental error in the control θ_{stem} and the small scatter in the even more prone shorter rod probes, we have to speculate that stem variability can explain this scatter. The observations of Lu et al. (2000) may explain our high LF scatter and support our suggested strategy of relying only on relative values from a single probe while strictly avoiding any comparison or averaging of results within a tree or among trees. With the present status of the method. absolute results may not be sufficient for scientific studies but have a potential for practical applications. For practical uses, we recommend not to compare or average values from even the same stem, let alone different trees, and use θ_{stem} and σ_{stem} changes relative to some initial values.

The economic advantages of resistivity measurements are improved accuracy, optional longer cables, flexible probe designs, shorter rods, simpler (direct current) multiplexing, and all for a lower price.

ACKNOWLEDGMENTS

We are grateful to Dr. Shabtai Cohen, Mr. Tibor Markovitz, and Mr. Meir Rosner for their help in constructing the irrigation systems, and to Dr. G. J. Levy for fruitful discussions. We acknowledge funding (304-0352-07) by the Chief Scientist of the Ministry of Agriculture.

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