Root to leaf electrical signaling in avocado in response to light and soil water content

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Summary

Phytomonitoring techniques for irrigation of avocado orchards indicate that plants respond very rapidly to fluctuations in soil water content. Root to leaf abscicic acid transport cannot fully explain the almost immediate response of stomata to either irrigation and/or sudden changes in climatic conditions. Therefore, we studied the existence of a fast conducting signal between roots and leaves, and the possible involvement of such a signal in the regulation of stomatal behavior. Two-year-old avocado trees were subjected to drying and re-watering cycles or changes in incident radiation (light or darkness). The difference in extracellular electrical potential between the leaf petiole and the base of stem (ΔV_{L-S}) was continuously recorded. Stomatal conductance (gs) was also recorded for the same leaves that were used for voltage difference measurements. A sudden change in soil water content induced by root drying and re-watering was accompanied by a slow, significant change in the recorded ΔV_{L-S} signal, which was fully developed at 52 and 32 min for root drying and re-watering, respectively. We found an inverse correlation ($r = -0.56$) between the change of ΔV_{L-S} and the gs difference measured before and after each soil-drying treatment. Plants that were girdled to disrupt the phloem and then irrigated tended to have lower ΔV_{L-S} differences over time than non-girdled irrigated plants, suggesting that the

Abbreviations: gs, stomatal conductance; PPF, photosynthetic photon flux; ΔV_{L-S}, voltage differences between the base of the stem and the leaf petiole; ω, gravimetric soil water content

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electrical signal was transmitted in the phloem. The existence of a fast signal transmitted from the root to the leaf that can be measured and correlated with stomatal control opens the possibility of developing a new phytomonitoring technique and/or artificially modifying plant responses by imposing agronomic management strategies aimed at rapid stomatal adaptation to changes in soil water content.

Introduction

Several possible routes exist for the communication of signals between the roots and the leaves of woody plants. Soil water deficits or excesses affect stomatal opening and closing, but the mechanism of stomatal regulation in response to soil stress is not fully understood. Giorio et al. (1999) observed that the soil water content and the root water status directly affected stomatal conductance (gs), which diminishes considerably before any observable change in leaf water potential occurs. Stomatal conductance generally decreases as the soil water content falls below an adequate level to sustain normal plant water uptake (Khalil and Grace, 1992). In dry soils, where gs is low, it generally increases immediately after the beginning of an irrigation event (Grantz and Meinzer, 1990). Stomata open and close very rapidly, in scales from minutes to hours, in response to changes in soil water conditions (Novak and Osmolovskaya, 1997; Kopyt et al., 2001; Meinzer, 2002; Gurovich and Gratacós, 2003; Zavala, 2004).

The effect of hydraulic and non-hydraulic signals between roots and shoots on stomatal closure during a period of water stress has been recently studied (Thomas and Eamus, 1999; Davies et al., 2000; Comstock, 2002; Liu et al., 2003). Significant variations in xylem hydraulic conductance have been measured in response to soil water deficits and hydraulic mechanisms have been proposed as signals arising from the roots that activate stomatal closure (Chazen and Neumann, 1994). In contrast, Davies and Zhang (1991) have reported the possible existence of non-hydraulic signals originating from the synthesis of phytohormones in the roots of some species. Partial closing of stomata in the absence of changes in leaf water potential has been observed in maize (*Zea mays* L.) (Blackman and Davies, 1985; Zhang and Davies, 1989), melon (*Cucumis melo* L.) (Melkonian and Wolfe, 1993), grapevine (*Vitis vinifera* L.) (Dry and Loveys, 1999), chestnut trees (*Castanea sativa* Mill.) (Maurel et al., 2004) and tomato (*Lycopersicon esculentum* Mill.) (Sobeih et al., 2004).

Plants can adjust to water stress without detectable changes in leaf water status due to osmotic and/or stomatal adjustment (Davies and Zhang, 1991). Thus, the stomata may receive a signal indicating the water status of the soil independently from the leaf water status. It has been postulated that changes in the concentrations of ABA generated in the roots and transported to the leaves induce stomatal closure (Zhang et al., 1987; Düring et al., 1997; Sauter et al., 2001; Hartung et al., 2002). However, Düring et al. (1997) found that a decrease of gs was correlated with an accumulation of the ABA synthesized in leaves and not in the roots. Furthermore, much higher (100 $\times$) ABA concentrations than those found in the roots are necessary to decrease gs (Munns and King, 1988). In *Pinus sylvestris* L. subjected to gradual soil desiccation, closing of stomata was observed before the arrival of ABA from the roots; thus, ABA translocation from root to leaves seems to be too slow to account for the stomatal closure in response to water stress, and closing of stomata was apparently not mediated by increases of ABA concentration in roots (Perks et al., 2002). Thus, it is likely that, in response to soil water deficit, ABA is neither the only nor the principal signal from the roots to the stomata (Munns and King, 1988). In addition, soil desiccation can induce an increase in the apoplastic pH of the leaf that causes rapid stomatal closure through the liberation of ABA to the symplast (Slovik and Hartung, 1992; Wilkinson and Davies, 1997). However, it is not known how the pH of leaf apoplast increases so rapidly after roots are water stressed.

These previous observations suggest that ABA is neither the only nor the principal signal traveling from the roots to the leaves which affects stomata opening and closing as a result of soil water stress. Therefore, other signaling mechanisms may exist. Another possible mechanism that has not been thoroughly investigated and may explain the response of stomata to soil water deficits is the presence of fast conducting electrical signals generated in the roots and conducted through the vascular system to the leaf. Stimulation of roots in *Salix viminalis* L. by the application of nutrients,

hormones or changes in pH caused changes in the electric potential difference recorded between the roots and leaves. These changes were followed by a modification of leaf respiration and photosynthetic rates within 3 min after treatments were applied, indicating that the changes in the electrical signals might reflect or be a mechanism of communication between the roots and the leaves (Fromm and Eschrich, 1993). Similarly, osmotic stress suddenly applied to maize roots generated an electrical potential difference between the roots and the leaves that accompanied the decreases in gs (Fromm and Fei, 1998). The role of changes of electrical potential in the regulation of leaf gas exchange has also been studied in maize subjected to drought cycles (Fromm and Fei, 1998). Additionally, the bioelectric potential in jute plants (*Corchorus capsularis* L.) was related to soil and air temperature, as well as photosynthetic photon flux (PPF) (Datta and Palit, 2004). A recent study of *Mimosa pudica* L. (Kaiser and Grams, 2006) showed that stomatal closure can be a response to heat-induced electrical signals. It has been postulated that electric signals could be transmitted in plants through sieve tubes of the phloem, serving as a communication pathway between roots and shoots under water stress (Fromm and Fei, 1998). These data indicate that several plant stressors may generate fast changes in the medium that can be recorded as changes in the extracellular potential difference between the roots and the leaves.

Avocado (*Persea americana*), an important commercial horticultural crop in Chile, is very sensitive to water stress and waterlogging. A phytomonitoring technique to define the plant water status and to calibrate the irrigation program has been used recently in Chile for irrigation scheduling of avocado orchards (Gurovich et al., 2006). This technique indicates that plants respond very rapidly to fluctuations in soil water content. The main goal of this study was to determine the existence of a root to shoot extracellular potential difference (variation potentials or slow wave potentials; see Stankovic et al., 1998; Stahlberg et al., 2006) in avocado plants and the possible role of this signal in regulating stomatal behavior in response to changes in soil water content and other environmental conditions.

Materials and methods

Plant material

Two-year-old 'Hass' avocado (*P. americana* Mill.) trees on clonal Duke 7 rootstock were used in this study. The plants were grown in a commercial nursery in a medium composed of peat, pearlite, compost and sand, and fertilized according to standard nursery practices. The plants ranged in height from 1.2 to 1.4 m, with a variable number of leaves (22–45) per plant.

Measurement of extracellular surface potential difference between the roots and the leaves

Extracellular surface potentials were measured in avocado plants. Surface contact electrodes (Fromm and Fei, 1998) were placed on the stem 20 cm above the soil surface and in the petiole of a leaf located in the lower third of the plant canopy. The electrodes consisted of a thick cotton thread saturated with KCl 0.1 M dipped in a 2.0 mL Eppendorf tube containing KCl 0.1 M. Ag/AgCl electrodes (0.4 mm in diameter) were immersed in the Eppendorf tubes and were connected to an amplifier with an input impedance of 10^{-11} ohm and DC-1 kHz bandwidth (M-707 Microprobe System; World Precision Instruments, Sarasota, FL, USA), and the output was recorded with a Power Lab analog–digital acquisition system at 2 Hz (AD Instruments, Castle Hill, Australia) (Figure 1). Prior to plant measurements, the electrodes were placed in KCl 0.1 M and calibrated to 0 mV to compensate for the junction potential. To record ΔV_{L-S}, the electrode located on the leaf petiole acted as the recording electrode while the electrode located on the stem served as the reference.

Control plants: baseline condition

Extracellular surface potentials were measured for about 80 min in 8 avocado plants (replications) under stable environmental conditions to determine the voltage differences between the base of the stem and the leaf petiole (ΔV_{L-S}) in the absence of environmental alterations (control or baseline).

Treatments: darkness, light, root drying and root wetting

The same plants were exposed to 4 different treatments: (1) exposure to darkness (0 μmol photons $m^{-2} s^{-1}$)

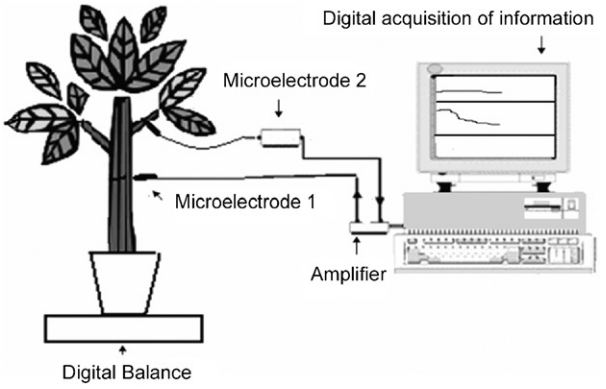

Figure 1. Schematic diagram of the setup for the digital acquisition of the recorded extracellular voltage difference between the leaf petiole and the base of the stem (ΔV_{L-S}).

for 20 min, (2) exposure to artificial light (85 μmol photons $m^{-2} s^{-1}$) for 20 min, (3) desiccation of the roots by exposure of the root system to a directed air current at ambient temperature (20 °C) for about 80 min and (4) re-wetting of desiccated plant roots by adding 500 cm^3 of distilled water to the soil and monitoring the ΔV_{L-S} response for 120 min. These treatments were chosen because they all were expected to influence stomatal behavior, but the light and dark treatments should have impacted the stomata directly at the leaf level, whereas the soil wetting and drying treatments would require communication (a signal) from the roots to the leaves to affect stomatal behavior. Also, times for signal registration were chosen according to the expected time of response of stomata to modification in light or soil water availability.

Air temperature during the measurement period was between 22.5 and 23.3 °C, and leaf temperature ranged from 22.4 to 23.7 °C. The PPF (Quantum sensor QSS-01 light meter, Lehle Seeds, Round Rock, TX, USA) directly above the adaxial leaf surface was about 85 μmol photons $m^{-2} s^{-1}$, which is above the light compensation point of this species, which is 30 μmol photons $m^{-2} s^{-1}$ (Whiley, 1994).

Measurement of stomatal conductance

Stomatal conductance was measured with a steady-state porometer (Li-Cor 1600, Lincoln, NE, USA) as described by Raviv et al. (2001) and Prive and Janes (2003). Stomatal conductance was measured on the same leaf on which the electrode was placed. Stomatal conductance was measured on each of the 8 replications before and after the voltage was recorded for each treatment (darkness, light, root drying and root wetting).

Measurement of soil moisture

Plants in each treatment were placed on a digital balance (Mettler Toledo, Hispanic Precision, Model Wildcat, Columbus, OH, USA), and the total weight of the plant, soil and pot was determined before and after each treatment. Plants were then excised at the soil surface, and pots and soil were re-weighed. Gravimetric soil water content (ω) was then determined by the formula:

$$\omega = \frac{\text{wet soil weight} - \text{dry soil weight}}{\text{dry soil weight}} \times 100.$$

Girdled plants

To detect whether changes in ΔV_{L-S} in response to changes in soil water content were transmitted through the phloem or xylem, 7 avocado plants were not irrigated for 4 days and then girdled to disrupt the flow of phloem sap. After girdling, plants were irrigated with 500 cm^3 of distillated water and ΔV_{L-S} was measured.

Data analysis

Data were expressed as means. The effects of treatment (darkness, light, drying and wetting) on the maximum ΔV_{L-S} − initial ΔV_{L-S} (ΔV_{L-S} difference) were analyzed by a one-way ANOVA and post-hoc comparison of means using Tukey's Studentized Range Test. ΔV_{L-S} differences arising after irrigation between girdled and non-girdled plants were analyzed by repeated measures two-way ANOVA and mean ΔV_{L-S} differences at specific points in time were analyzed by a Bonferroni test. The correlation between ΔV_{L-S} and Δgs was analyzed by linear regression analysis. Statistical analyses were performed with the SAS statistical package (SAS Institute, Cary, NC, USA).

Results

Control plants: baseline condition

Although control plants showed different initial ΔV_{L-S} values, they remained fairly constant during the experiments. The differences in baseline ΔV_{L-S} values were probably due to differences in size as well as numbers of branches and leaves among plants (height ranged from 1.2 to 1.4 m and the number of leaves ranged from 22 to 45 per plant). Therefore, small changes in resistance due to the size and number of branches may affect the measured potential. Notwithstanding, there was little modification in ΔV_{L-S} in control plants ($n = 8$) kept in stable environmental conditions for about 80 min. These values were relatively constant until the end of the measurement period (Table 1 and Figure 2), with a mean initial ΔV_{L-S} value of 27.3 mV and a mean end ΔV_{L-S} value of 21.1 mV; thus, the mean ΔV_{L-S} difference was −6.2 mV.

Plants subjected to cycles of light modification and water availability

The recorded ΔV_{L-S} was largely unaffected by most treatments (Table 1). Placing plants in the dark resulted in an increase in ΔV_{L-S} of 47.3 mV after 13.3 min, whereas illuminating plants previously in the dark resulted in only a decrease in ΔV_{L-S} of 0.5 mV after 13.3 min. However, the changes in maximum ΔV_{L-S} difference were not significantly different from those of the control treatment (one-way ANOVA, $P < 0.05$) (Table 1). Figure 3A and B shows the ΔV_{L-S} recorded during darkness and light treatments, respectively, in 8 plants.

Only the root desiccation treatment produced a statistically significant change in ΔV_{L-S} (maximum

Table 1. Effect of dark, light, soil drying and soil wetting on the root to leaf voltage difference in avocado plants

Treatments	Initial ΔV_{L-S} (mV)	Maximal difference ΔV_{L-S} (mV)	Time to maximal voltage difference (min)	Maximum ΔV_{L-S} difference (mV)
Control	27.3	21.1	58.0	−6.2a
Dark	262.2	309.5	13.3	47.3a
Light	328.9	329.7	13.3	0.5a
Drying	436.8	222.5	52.0	−214.3b
Wetting	77.4	162.6	32.0	85.3a

Each value of voltage difference represents the mean ($n = 8$ plants). Maximal difference ΔV_{L-S} is related to the initial value of the voltage curve for each replication within 80 min. The change in the maximum ΔV_{L-S} difference was calculated by subtracting the initial ΔV_{L-S} from the maximal different ΔV_{L-S}. Different letters (a, b) indicate significant differences ($P \leqslant 0.05$) among treatments (one-way ANOVA and Tukey's Studentized Range Test).

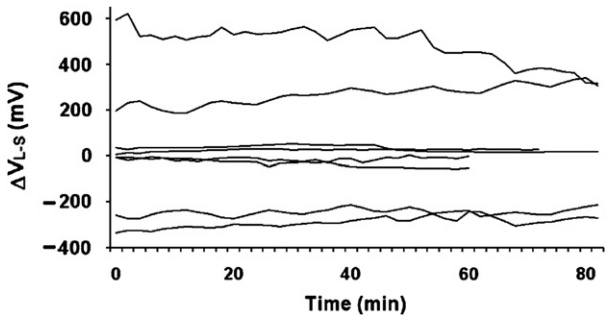

Figure 2. Voltage difference recorded between the leaf petiole and the base of the stem (ΔV_{L-S}) in 8 control plants during 80 min. Data were collected at 2 Hz and plotted at 2 min intervals.

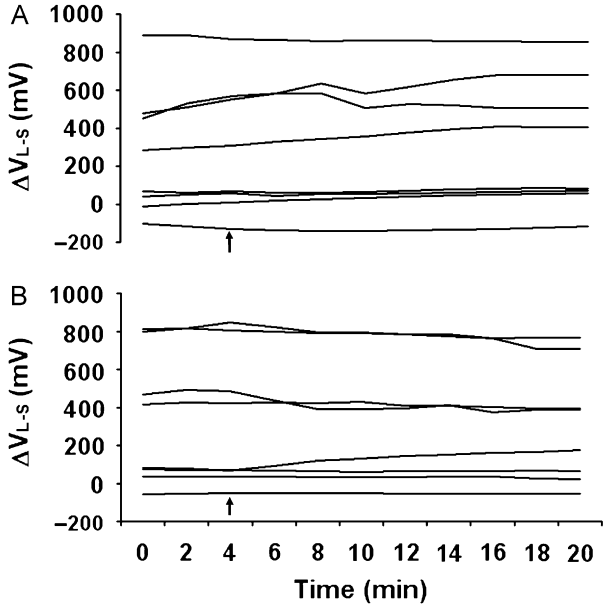

Figure 3. Voltage difference recorded between the leaf petiole and the base of the stem (ΔV_{L-S}) in 8 plants in darkness (0 μmol photons $m^{-2} s^{-1}$) for 20 min (A), and in 8 plants in artificial light (85 μmol photons $m^{-2} s^{-1}$) for 20 min (B). Data were collected at 2 Hz and plotted at 2 min intervals. The arrows indicate the beginning of each treatment.

voltage difference) compared with the control plants. Drying the soil just −1.3% ω from field capacity (1/3 atm) resulted in a significant reduction (one-way ANOVA, $P < 0.05$) in the ΔV_{L-S} (−214.3 mV) after 52 min (Table 1). In contrast, adding water to the dry soil resulted in an increase of 85.3 mV in the ΔV_{L-S} (maximum voltage difference) after 32 min of re-watering, but this value was not significantly different (one-way ANOVA, $P < 0.05$) from the control group. Figure 4A and B show the ΔV_{L-S} recorded during soil wetting and soil drying treatments, respectively, in 8 plants. Figure 5 shows a summary of the average curves of ΔV_{L-S} recordings for all treatments.

All the treatments produced changes in gs (Table 2), which were often directly related with stomatal opening and closing (Buckley et al., 2003; Tinoco-Ojanguren and Pearcy, 1992; Cowan, 1972). We found an inverse linear correlation ($r = -0.56$) between the change of ΔV_{L-S} and stomatal conductance difference measured before and after each treatment (Δgs) in the soil-drying treatment (Figure 6).

Girdled plants

When ΔV_{L-S} changes recorded from girdled plants were compared with non-girdled plants after both treatments were irrigated, there was a significant time and time × treatment interaction for the ΔV_{L-S} difference (repeated-measures two-way ANOVA, $P \leqslant 0.05$). The ΔV_{L-S} change was higher in the non-girdled plants than in the girdled plants throughout the 60 min measurement period. However, due to high between-plant variability, voltage differences were only statistically significant ($P \leqslant 0.05$, Bonferroni test after a two-way ANOVA) at 50 and 60 min of measurement (Figure 7).

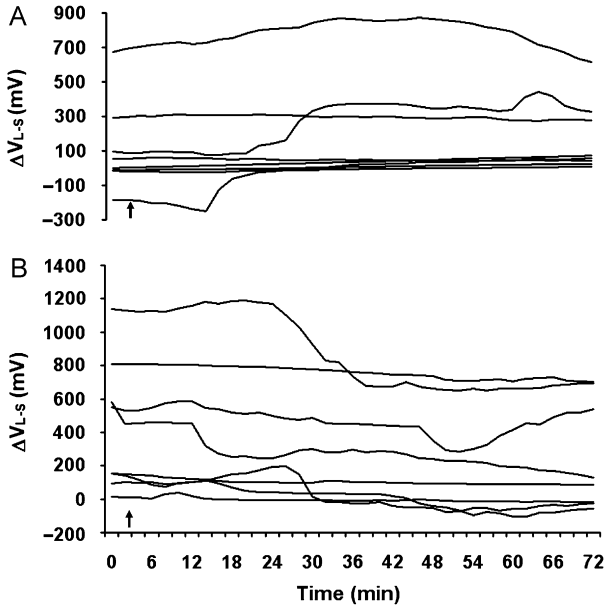

Figure 4. Voltage difference recorded between the leaf petiole and the base of the stem (ΔV_{L-S}) in 8 plants after irrigation (irrigation) for 72 min (A) and in 8 plants subjected to root desiccation (drying) for 72 min (B). Data were collected at 2 Hz and plotted at 2 min intervals. The arrows indicate the beginning of each treatment.

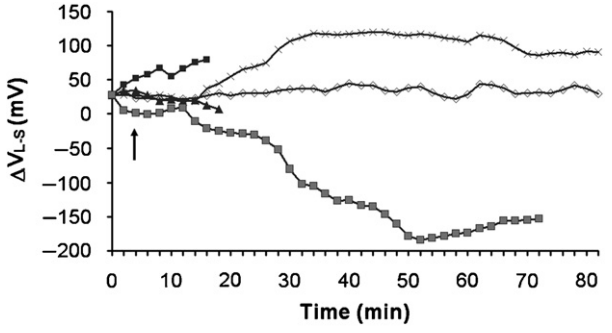

Figure 5. Effects of different treatments on the voltage difference recorded between the leaf petiole and the base of the stem (ΔV_{L-S}). Each data point represents the mean value ($n = 8$). –◇– Control, –■– Darkness, –▲– Light, – × – Irrigation, —■— Drying. The arrow indicates the beginning of each treatment. Data were collected at 2 Hz and plotted at 2 min intervals.

Discussion

The observed changes in ΔV_{L-S} between roots and leaves were concomitant with modifications in stomatal conductance. Changes in stomatal conductance are often directly related to stomatal opening and closing (Cowan, 1972; Tinoco-Ojanguren and Pearcy, 1992; Buckley et al., 2003). Thus, our results suggest a link between the recorded electrical signal and stomatal behavior. Previous experiments with *S. viminalis* L. (Fromm and Eschrich, 1993) and *Z. mays* (Fromm and Fei, 1998) showed that electrical potentials are generated in response to different stimuli in the roots

Table 2. Stomatal conductance difference after treatments were imposed

Treatments	Δgs (cm s^{-1})
Darkness	−0.023 ± 0.02
Light	0.022 ± 0.04
Soil drying	−0.021 ± 0.03
Soil wetting	0.017 ± 0.005

Positive numbers for the light and soil wetting treatments indicate stomatal opening, whereas negative numbers for the darkness and soil drying treatments indicate stomatal closure. Values represent means ± SE ($n = 8$).

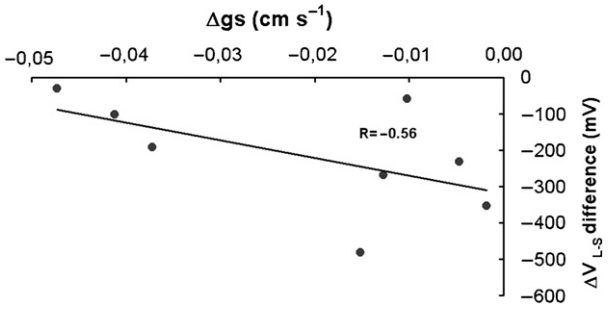

Figure 6. Linear correlation between ΔV_{L-S} maximum difference (ΔmV) and stomatal conductance difference (Δgs) in the soil-drying treatment.

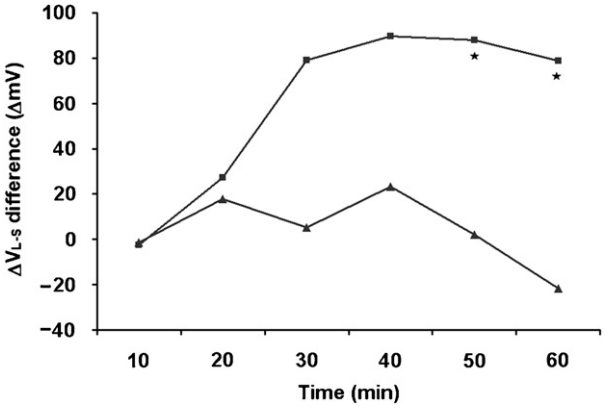

Figure 7. Comparison of ΔV_{L-S} differences in irrigated girdled plants and irrigated non-girdled plants. Values represent the ΔV_{L-S} differences (ΔmV) average (irrigated girdled treatement $n = 7$, irrigated non-girdled treatment $n = 8$) at times 10, 20, 30, 40, 50 and 60 (min) from the beginning of the treatment. Asterisks indicate a significant difference between girdled and non-girdled treatments according to a Bonferroni test after a two-way ANOVA ($P \leqslant 0.05$) at each time. –■– Irrigated non-girdled, –▲– Irrigated girdled.

(application of nutrients, hormones, changes in pH or drought) affecting leaf gas exchange. However, in previous studies action potentials were measured, whereas our study focused on variation potentials or slow wave potentials (Stankovic et al., 1998; Stahlberg et al., 2006). An action potential is defined as a transient change in the transmembrane difference of potential, which is triggered by a depolarizing stimulus at a given threshold, where the response becomes independent of the strength of the stimulus. On the other hand, a variation potential or slow electric potential referred to as a streaming potential (Stankovic et al., 1998), which is conducted electrotonically, decreases exponentially in magnitude as the distance from the point of generation increases.

Environmental changes generate bioelectric potentials in plants (Datta and Palit, 2004). In this study with avocado, the shape, magnitude and duration of ΔV_{L-S} was dependent upon the stimulus. In control plants that received no sudden environmental stimulation, changes in ΔV_{L-S} were small and not significant. However, drying the roots resulted in a large and significant decrease in ΔV_{L-S}. Similar changes in electrical signals were reported by Fromm and Fei (1998) after subjecting *Z. mays* plants to drought. The present results showed that, in avocado, soil drying of $-1.3\%\omega$ resulted in a change in ΔV_{L-S} that was observed within 28–56 min after forced-air soil drying was initiated, with an average maximum ΔV_{L-S} difference of -214.28 mV, which corresponds to a 96.3% variation of the initial value. Thus, as a result of plant stress induced by decreased soil water content, there was a significant modification of the variation potentials or slow wave potentials that appeared to be conduced at a speed of 2.4 cm min^{-1} or 144 cm h^{-1}. The modification of ΔV_{L-S} was correlated with reduced stomatal conductance, suggesting that there may be a cause and effect relationship between these two processes.

In contrast to the significant change in ΔV_{L-S} associated with soil drying, changing the light environment (from dark to light or light to dark) resulted in only a slight and non-significant change in ΔV_{L-S}. Changes in light intensity directly affect leaf and stomatal opening and closing and would not be expected to involve an inducible signal from the roots to the stomata. However, as a result of changes in the root zone, such as soil drying, a transmissible signal generated at the root and transported to the leaf would be expected to stimulate stomatal opening and closing. As expected, root drying or wetting resulted in a much greater voltage difference between the trunk and the leaf than changing the light environment. The response to desiccation was a decrease in ΔV_{L-S}, whereas a response to wetting was an increase in ΔV_{L-S}. Therefore, the magnitude and the duration of the recorded changes in ΔV_{L-S} were different for each condition.

Phytomonitoring techniques used for irrigation scheduling for fruit trees (Novak and Osmolovskaya, 1997; Kopyt et al., 2001; Gurovich and Gratacós, 2003; Gurovich et al., 2006) indicate that plant responses to changes in soil water availability are very fast processes. The transport of ABA from roots to shoots cannot explain the fast physiological response of the stomata (sometimes less than 15 min) to irrigation or to sudden increases or reductions of evapotranspiration. The rapid speed of the physiological changes in the leaves as a result of soil water changes suggests that communication from the root to the leaves is via hydraulic or electrical signals, such as a variation potential.

The sieve tubes of the phloem have been postulated to be a route of transmission of electrical signals between roots and shoots of several plant species (Fromm, 1991; Fromm and Eschrich, 1993; Fromm and Fei, 1998; Koziolek et al., 2003). After soil dessication, re-watering of *Z. mays* plants resulted in a voltage increase, which paralleled the increase in leaf gas exchange and water vapor exchange (Fromm and Fei, 1998). Moreover, a recent study of *M. pudica* (Kaiser and Grams, 2006) showed that stomatal closure is elicited by heat-induced electrical signals, suggesting a possible involvement of electrical signals in long-distance signaling for coordinating leaf gas exchange. The significant difference in ΔV_{L-S} after irrigation between non-girdled plants and plants that were girdled to disrupt the phloem indicated that the phloem is an important conduit for electrical signal transmission from the root to the shoot in avocado plants, as was reported previously for other species (Fromm, 1991; Fromm and Eschrich, 1993; Fromm and Fei, 1998; Koziolek et al., 2003). Girdled avocado plants tended to have lower ΔV_{L-S} differences than non-girdled plants, with statistically significant differences at 50 and 60 min from the beginning of the treatments. This suggests that the change in the electrical signal in response to a change in the soil moisture is occurring in the phloem.

Stahlberg et al. (2006) proposed that a variation potential can be induced by increasing xylem pressure or turgor. The ionic mechanism is as yet uncertain, but it has been postulated that it could be through a H^+-pump or ionic channels, such as a calcium channel or a transient shutdown of stretch-sensitive ATP-ases at the plasma membrane

(Stahlberg et al., 2006). Variation potential (or slow wave potential) characteristics (Stahlberg et al., 2006; Stankovic et al., 1998) match the shape, time and nature of the electrical signals recorded during these experiments. We originally hypothesized that the electrical signal in avocado plants was transmitted through the xylem because sap flow in avocado has been measured at speeds of 30–35 cm h^{-1} (Cantuarias, 1995), comparable to speeds at which we could see changes in the voltage. However, the comparison of changes in voltage differences between girdled and non-girdled avocado plants after irrigation indicated that the electrical signal was transmitted through the phloem.

In summary, our results suggest that changes in ΔV_{L-S} may play a role in root to shoot communication when avocado plants are water stressed. However, care must be taken when interpreting wave potential data in plants, because changes in extracellular voltage may be the result of true changes in the circulating extracellular current or modifications in extracellular resistance, which can be affected by water and/or by the ion content of the medium. Therefore, it is necessary to separate true electrical signaling phenomena from conductivity changes arising from water and/or ion handling by the plant tissue. However, even if the change in electrical potential was generated by a shift in the water or ionic balance in the roots and xylem resulting from soil drying, it does not negate the fact that changes in the extracelullar electrical potential may be the mechanism for root to leaf communication resulting in stomatal closure in response to soil drying. Also, the existence of a fast root to leaf signal that can be readily measured and related to stomatal control opens possibilities for developing a phytomonitoring technique for measuring plant response to soil water content or to artificially modifying plant responses by imposing agronomic management strategies aimed at rapid stomatal adaptation to changes in soil water content.

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