

DOI 10.7764/ijanr.v50i3.2552

RESEARCH NOTE

Stem electrical potential variations may aid in the early detection of drought stress in fruit-bearing trees

Pilar M. Gil¹ and Ana I. Vargas²

¹Pontificia Universidad Católica de Chile, Facultad de Agronomía e Ingeniería Forestal. Santiago, Chile.

²University of Florida, Tropical Research and Education Center. 18905 S.W. 280 Street, Homestead, FL 33031, USA.

Abbreviations: AP, action potential (mV); VP, variation potential (mV); EP, electrical potential (mV); d_{EP} , electrical potential deviation (mV); SWC, soil water content ($m^3 m^{-3}$); SF, sap flow rate ($g h^{-1}$); SWP, stem water potential (MPa); RWC, relative water content (%).

Abstract

P. M. Gil and A.I. Vargas. 2023. Stem electrical potential variations may aid in the early detection of drought stress in fruit-bearing trees. Int. J. Agric. Nat. Resour. 116-129.

Electrical plant signaling as a variation potential (VP) occurs in response to a wide range of stimuli, and it is associated with the induction of sudden changes in xylem pressure. Additionally, there is evidence that electrical potential (EP) of plants changes with changing soil water content. Therefore, the use of EP as a direct plant measurement of plant water status may have potential as water stress monitoring information. EP measurements within plant stems indirectly correlate with sap flow (SF), which is one possible variable for estimating plant water use. However, whether this relationship is stable under drought conditions is not known. The present work investigated the relationships between SF and EP variations during an 18-day drought period on three avocado trees to test the hypothesis that the relationships between SF and EP may be lost due to drought intensity. The results showed that short-term variations in EP were positively associated with vapor pressure deficit (VPD) and SF variations but negatively associated with soil water content (SWC). An increase in VP emissions was observed as drought advanced, which was negatively associated with stem water potential (SWP). After 18 days of drought, irrigation almost completely suppressed short-term variations in EP. The present work provides preliminary results that strongly suggest a relationship between drought stress and EP variations in plant stems. Further research is needed to confirm whether the EP trends observed during drought are due to cavitation events and emission of VP signals and/or linked to other physiological processes, e.g., pH changes in response to drought or embolism. Meanwhile, the present work indicates that short-term variations in EP (d_{EP}) are strongly associated with the intensity of drought stress, thus stem electrical potential variations may aid in the early detection of drought stress in fruit-bearing trees.

Keywords: Cavitation, electrical potential, embolism, *Persea americana*, plant water status monitoring, sap flow, variation potential.

Introduction

The increasing shortage of water resources for agricultural production in semiarid zones and the need for optimizing irrigation strategies to avoid an excess or lack of water in the root zone have led to an increased need for sensors to measure soil moisture and plant water status. The use of soil moisture sensors must consider the natural variability of soil properties and its effects on water distribution in the soil profile (Van Leeuwen et al., 2001). Spatial soil variability occurs in three dimensions, laterally and vertically, and it can become a major issue in drip and micro sprinkler irrigation systems where a great number of measurements or probes are needed for accurate representations of soil moisture in the root zone (Van Leeuwen et al., 2001). However, plant monitoring techniques, such as stem water potential (SWP) and trunk diameter change (TDC) data may be used to measure plant water status directly and may reduce errors due to soil moisture variability. The data provided by both types of sensors may be used with weather conditions and crop evapotranspiration data to allow the development of a more comprehensive irrigation management strategy.

Plant water stress indicators must be able to detect stress early and reliably for use in irrigation scheduling in avocado orchards. The midday SWP is a reliable stress indicator in many fruit trees, as described by Naor et al. (1995) for apples (*Malus domestica* Borkh. ‘Golden Delicious’), by Naor et al. (2001) for nectarines (*Prunus persica* L. ‘Fairlane’), and as described by Lampinen (1995; 2001) for prunes (*Prunus domestica* L. ‘French’). In avocado, SWP values of -1.0 to -1.2 MPa have been reported as a water stress indicator (Sterne et al., 1977; Bower, 1978; Scholefield et al., 1980). However, whether SWP detects water stress in avocado early enough to avoid its negative effects on fruit yield and roots is not clear. Digital dendrometers for measuring TDC have attracted the attention of researchers and growers. Other studies suggested that maximum daily trunk

shrinkage (MDTS), which is a parameter derived from the TDC, is a highly sensitive indicator of water stress in deciduous trees (Goldhamer et al., 1999; Cohen et al., 2001). MDTS has been used as a plant water status indicator for several crop species, including table and wine grapes (Gurovich, 1997; Gurovich & Saggé, 2005), peaches (*Prunus persica* L. Batsch., Sellés & Berger, 1990; Goldhamer & Fereres, 2001; Naor & Cohen, 2003), avocado (Celedón et al., 2012; Gurovich et al., 2006), and other fruit crops (Cohen et al., 2001; Moriana & Fereres, 2002; Fereres & Goldhamer, 2003). The high sensitivity of MDTS may provide an advantage for avocado irrigation scheduling, where the early detection of stress is critical. However, MDTS in apples was more variable than SWP, which made it a less reliable stress indicator (Naor & Cohen, 2003). Notably, the response of MDTS to environmental conditions and water availability is species dependent, which has been attributed to the water storage capacity of plant tissues surrounding the xylem and radial resistance to the water flow in xylem vessels (Huguet et al., 1992).

VPs (also called short-wave potential) correspond to transient changes in membrane potential and are distinguished from APs because they exhibit a longer, delayed repolarization phase on the order of 1-30 min (Stahlberg et al., 2006; Fromm & Lautner, 2007). VPs are propagated through the xylem (Stahlberg & Cosgrove, 1996) and are always coupled to pressure changes (Stahlberg et al., 2006). VPs generated in response to wounding are only generated under xylem tension (i.e., they are suppressed under non-transpiring conditions) (Mancuso, 1999). VP generation occurs in response to mechanical wounding (Frachisse et al., 1985), tissue burning (Stankovic & Davies, 1998) and insect bites (Alarcon & Malone, 1994), all of which trigger sudden changes in xylem tension (Stahlberg & Cosgrove, 1997).

Drought is one condition under which plants may be subjected to sudden changes in xylem tension. When the evaporative demand is high

and water availability is low, the water column in the xylem may be disrupted via cavitation, most likely by air seeding or heterogeneous nucleation (Rockwell et al., 2014). A link between cavitation and the generation of VPs has been mentioned in the literature (Huber & Bauerle, 2016), and there is at least one experimental report associating vacuum-induced xylem embolisms with VP emission (Stahlberg & Cosgrove, 1996). However, to the best of the authors' knowledge, there are no reports of an association between the occurrence of VP events and drought intensity.

Avocado (*Persea americana* Mill.) (Lauraceae) is an evergreen tree species that is grown commercially in tropical, subtropical and Mediterranean climates (Carr, 2013). Avocado plants are highly sensitive to low soil water availability. Although no experimental data are available on cavitation vulnerability, comparisons of avocado species and cultivars indicate that artificial selection has favored genotypes with fewer wider vessels, which increases the theoretical cavitation vulnerability index (Reyes-Santamaría et al., 2002). Avocado trees generate VPs in response to mechanical wounding (Oyarce & Gurovich, 2011) and osmotic stress (Gil et al., 2008b), and they exhibit electric potential (EP) changes in response to short and prolonged water withholding periods (Gil et al., 2008a; Gil et al., 2014; Ríos-Rojas et al., 2015). However, EP measurements have received increased attention as a tool for the development of irrigation scheduling sensors, the EP response patterns of avocado plants to drought have not been fully elucidated. EP data interpretation is often performed qualitatively, and the use of statistical procedures to link these signals to other environmental and physiological variables is rare (e.g., Gil et al., 2014). Cavitation probability is associated with water stress (Jackson et al., 1995; Tyree & Dixon, 1986). Therefore, stem EP measurements in avocado plants may become more erratic with increasing drought (Hypothesis 1) due to VP emission in response to sudden changes in xylem tension (Stahlberg & Cosgrove, 1996; Huber & Bauerle, 2016). In addition to the relationship of VPs to cavitation and water stress, daily

EP variations are strongly and inversely correlated with sap flow (SF). Although this correlation is well documented (Morat et al., 1994; Koppán et al., 2002; Gibert et al., 2006), there are no reports on whether this correlation exists under intense drought conditions. It is likely that this correlation is lost during periods of intense drought due to more intense variation in short-term EP measurements, and EP is not a reliable variable for estimating SF under drought conditions (Hypothesis 2).

To test these hypotheses, an exploratory assay linking EP measurements to SF, vapor pressure deficit (VPD) and volumetric soil water content (SWC) in avocado plants during an 18-day drought period was performed. Various statistical procedures were used to analyze these data, which were further linked to other physiological measurements, such as stomatal conductance (g_s), PSII quantum efficiency (Fv/Fm), midday stem water potential (SWP) and relative leaf water content (RWC).

Materials and methods

Plant material and experimental setup

The experiment was performed in the greenhouse area of the Faculty of Agriculture and Natural Resources, Pontificia Universidad Católica de Chile, in Santiago, Chile. Three potted 2 year-old avocado plants (*Persea americana* Mill. cv. 'Hass' grafted on clonal Duke 7 rootstock) were placed in a grounded Faraday cage to isolate them from environmental electromagnetic fields. All three plants were grown in a compost substrate in 20-L containers and had a recent cohort of new leaves but did not flower, which indicated phenological synchronicity. An irrigation system consisting of two adjustable flow drippers per plant was installed, and the emission rates were adjusted so that each plant received the same water volume per unit time. At the onset of the experiment (October 24th, springtime in the Southern hemisphere), plants were irrigated to reach a water content near field capacity (FC,

-0.3 bar) then left unwatered for a period of 18 days, after which they were again irrigated to FC. The experiment ended on November 14th.

Electrical potential

Two sets of three measuring electrodes were placed on each plant in the Faraday cage. Each set consisted of a ground electrode (e0) placed at the base of the trunk and three measuring electrodes (e1, e2 and e3) placed at regularly spaced intervals along the stem, at the base, center and top of the canopy, respectively. The decision to use 2 sets of measuring electrodes was conceived as a security measure in case the electrodes failed to record the EP or were unintentionally disconnected.

Electrodes were constructed by inserting a 99% silver 0.1-mm wire into a 21G (0.8 mm) scalp-vein needle filled with a 1 M KCl solution. Prior to insertion, the silver wires were chlorinated via submersion in a 0.1 M HCl solution under a current of 3 V for 2 min. Scalp-vein needles were filled with the KCl solution then sealed at the tips using a small amount of epoxy glue. Once sealed,

electrodes were inserted 3 mm into the stem according to Gil et al. (2014), which determined that this was the optimum depth for measuring the xylematic EP.

Data acquisition for EP measurements was performed at 1-min intervals using an amplifier-multi-voltmeter Model 2701 (Keithley Instruments, Inc., Cleveland, OH, USA) with a 20-channel multiplexer Model 7700 (Keithley Instruments, Inc.). A dedicated computer was used for the continuous monitoring of EP data via ExceLINX-1A software.

Sap flow

Sap flow was measured using a Dynagage Flow32-1K system (Dynamax, Inc., Houston, TX, USA) and the heat balance method. One sensor (model SGB16, Dynamax, Inc.) was installed just over the rootstock of each plant after cleaning and an oil application, and it was later covered with an insulating layer film to prevent heat exchange with the environment. The sap flow data were computed in g h^{-1} according to the sensor resistances and stem area at the point of installation according to the model provided by Dynamax.

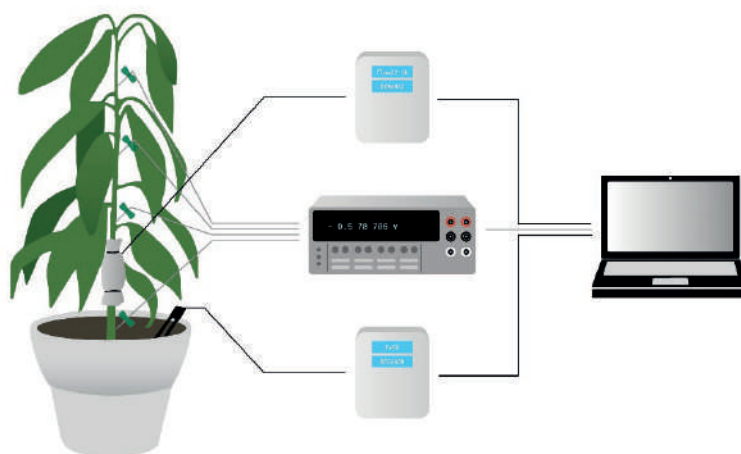


Figure 1. Schematic depiction of the experimental setup. Each avocado plant was connected with two sets of 4 electrodes (e0-e3) to measure EP using a Keithley 2701 amplifier-multi-voltmeter. An FDR probe was inserted 15 cm into the substrate to measure the SWC. A Dynagage sensor was installed over the rootstock of each plant to measure SF. All data were downloaded via direct connection to a computer.

Soil water content

In each plant, the volumetric SWC ($\text{m}^3 \text{m}^{-3}$) was measured via the installation of one frequency domain reflectometry (FDR) probe (Decagon Devices, Inc., Pullman, WA, USA) in each potting medium, which was connected to an EM-50 Datalogger (Decagon Devices, Inc.). The data were obtained using DataTrac3 software (Decagon Devices, Inc.) at 10 min intervals, with FDR probes installed 15 cm into the potting medium. A schematic figure of the experiment set up is available in Figure 1.

Environmental variables

Temperature and relative humidity were measured using a Hobo datalogger (Onset Computer Corporation, Pocasset, MA, USA) installed at one border of the Faraday cage at 10-min intervals. These variables were subsequently used to compute the VPD.

Plant physiological variables

Stomatal conductance (gs) and Fv/Fm were measured every other day on three randomly selected leaves from each plant at midday (1200-1400 HR). The gs was measured using a leaf porometer (SC-1, Decagon Devices, Inc., Pullman, WA, USA), and PSII efficiency was measured on 30-min pre-darkened leaves using a leaf fluorimeter (Pocket Pea, Hansatech, Norfolk, UK).

SWP and RWC were measured at four different times during the experiment: on days 0 (October 24), 14, 18 and 21, always at midday (1200-1400 HR). The SWP (MPa) was measured by placing a pre-enclosed, pre-darkened leaf (30 min) from each plant into an N₂-pressurized Scholander pump and determined by direct observation under a magnifying glass (Scholander et al., 1965). For RWC calculations, each of the leaves used for SWP was weighed before placement into the Scholan-

der pump (fresh weight), after a 24-h submersion under distilled water (turgid weight) and a 48-h drying period at 70°C (dry weight). The RWC was subsequently calculated as the ratio between the difference in fresh weight and turgid weight with respect to leaf dry weight (Smart & Bingham, 1974).

Data analyses

Several different data analyses were performed to determine the relationships between EP, SF, SWC and VPD. Prior to any analysis, EP measurements were corrected by eliminating noise ($\text{EP} > 1 \text{ V}$). Data from plants with failed EP measurements, due to prolonged noise periods ($> 1 \text{ day}$) or electrode disconnection, were excluded from the analyses. EP measurements at each insertion point were averaged at 10-min intervals and used for the computation of Equation 1 the electrical potential difference between the electrodes (ΔEP) and (2) the 10-min average absolute difference of each of the 1-min measurements from the continuous 10-min average EP (d_{EP}) (Equation 1).

$$d_{\text{EP}} = \frac{\sum_{i=1}^{10} |\bar{x} - x_i|}{10} \quad (\text{Equation 1})$$

where x represents each of the 1-min measurements. The latter was used as a measure of short-term EP variations, which were hypothesized to positively correlate with drought stress intensity.

As an exploratory approach, EP, ΔEP , d_{EP} , SF, SWC and VPD data were analyzed using principal component analysis (PCA) to determine the association between the variables. After PCA, multiple regressions were performed to determine whether differences in SF, SWC and VPD (all related to water stress) were associated with changes in d_{EP} . To test the hypothesis that VP emission increases with drought intensity, the number of VP events per hour (i.e., the VP emission rate) was calculated as the sum of the number of cases in which the difference between the 1-min measurements

and the 10-min average fell below -10 mV at all 3 electrodes, which indicated that a short-term negativity wave consistently occurred along the stem. Although no experimental data allowed us to define a clear threshold for VP emission, whose amplitude is dependent on the intensity and nature of the stimulus (Stahlberg et al., 2006), the threshold used herein was taken from VP amplitudes reported for this species in response to mechanical wounding (Oyarce & Gurovich, 2011). Linear multiple regressions were also performed to determine to what extent the EP-derived variables, with and without VPD and SWC, predicted sap flow during the experimental period. Considering the hypothesis that EP measurements may become more erratic and less reliable for estimating SF as drought progresses, regressions were performed for different periods defined according to SWC measurements. For the latter, changes in the determination coefficient (R^2) for each period are

presented. All of the data analyses were performed using XLSTAT 2014 software (XLSTAT, Addinsoft FRANCE, Paris, France). Graphs were generated using Origin Pro 8.0 software (OriginLabs Corp., Wellesley, MA, USA).

Results

Plant physiological variables

During the experimental period, consistent decreases in SWP, RWC and stomatal conductance were observed for all plants after the first irrigation event. Irrigation on day 18 led to full recovery of the initial SWP and RWC values after 3 days, but stomatal opening was not observed after 3 days of irrigation (Figure 2). Although PSII efficiency exhibited significant variations during the experimental period, the changes in Fv/Fm were

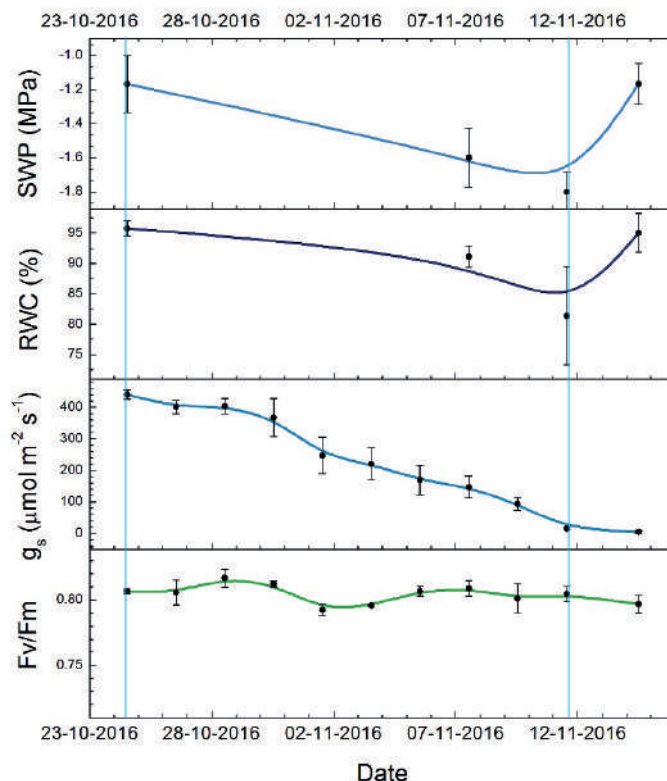


Figure 2. Results for plant physiological variables during the course of the experiment. The points represent the mean values for three plants. The error bars indicate SEs. The vertical lines denote irrigation events.

mild, with variations smaller than 3% compared with to the initial values (Figure 2).

EP relationship to SF, VPD and SWC

The plants exhibited daily patterns of EP, ΔEP or d_{EP} during the drought period (Figure 3, Figure 4). Although two electrode sets were installed on each plant, the results for all three

electrodes at all times were only available for plant 1 (Figure 3) due to unintentional disconnection or prolonged noise periods (>1 day) for the other plants. Variations in EP, ΔEP or d_{EP} measurements available for plant 3 are shown in Figure 4, but these data were incomplete and excluded from the analyses.

Of all variables obtained from the EP measurements, d_{EP} most strongly correlated with SF and

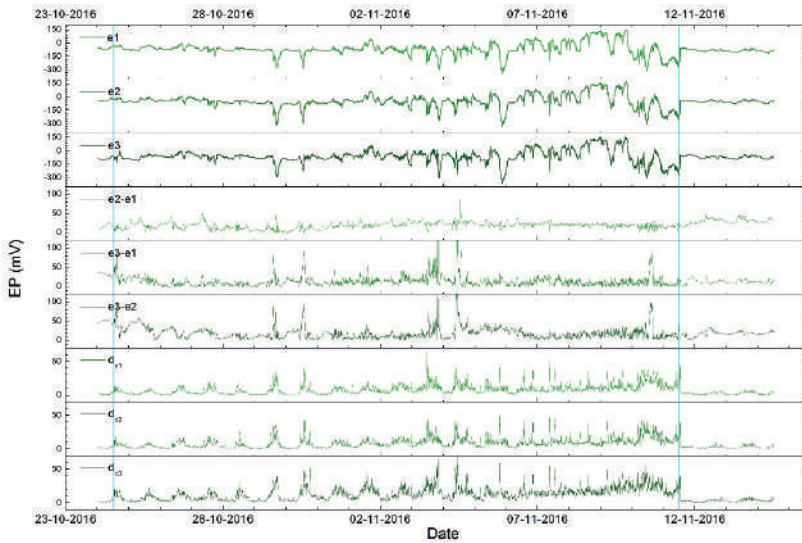


Figure 3. EP results for plant 1. e1, e2 and e3 correspond to electrodes installed at the base, center and top of the canopy, respectively. Differences between the electrodes and mean deviations from the 10-min average (d_{EP}) are also shown. The vertical lines denote irrigation events.

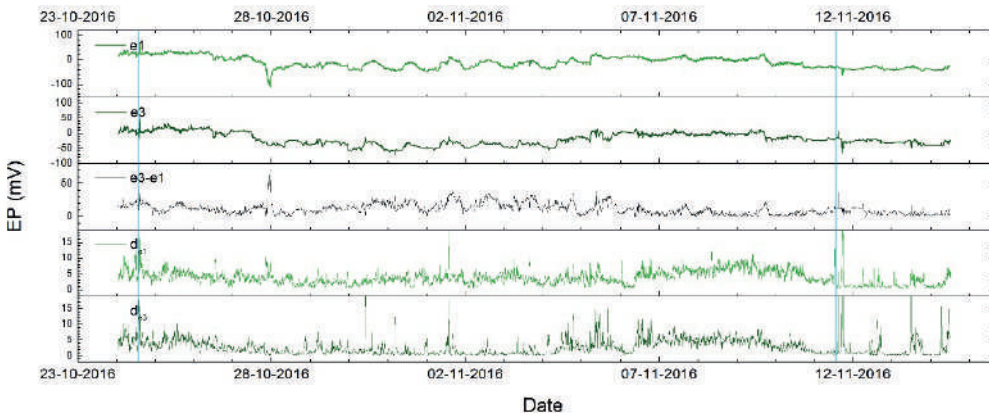


Figure 4. EP results for plant 3. e1, e2 and e3 correspond to electrodes installed at the base, center and top of the canopy, respectively. Differences between the electrodes and mean deviations from the 10-min average (d_{EP}) are also shown. The vertical lines denote irrigation events.

VPD, as indicated in the PCA loading plot (Figure 5). This relationship was greater during the initial period of the experiment, when d_{EP} showed a clear daily pattern, with the lowest values occurring at night. As drought advanced, a consistent increase in d_{EP} was observed until the plants were irrigated (Figure 6). Other EP variables exhibited some daily variations, albeit with a less evident pattern (Figure 3, Figure 4). The d_{e3} variable was most closely associated with SF and VPD (Figure 5, Figure 6) and corresponded to the variable that was best explained by multiple regression mod-

els ($R^2=0.456$) (Table 1). In all of the regression models, SF and VPD were positively associated with d_{EP} , but SWC exhibited a negative relationship with d_{EP} and contributed most to the regression models, as indicated by the model standardized coefficients (Table 1).

VP emission rate

An increase in the VP emission rate was observed during the drought period, with most VP events occurring during the daytime (Figure 7). The maximum VP emission rate was observed one day before irrigation, when the SWP reached its minimum (i.e., maximum xylem tension) value (Figure 8). After irrigation, the VP emission ceased almost completely (Figure 7, Figure 8). The average VP emission rate positively correlated with the average daily VPD ($r=0.54$) and negatively correlated with the average daily SWC ($r=-0.77$) (data not shown).

SF estimation using EP

Sap flow estimations using EP, SWC and VPD data as independent variables in linear multiple regression models exhibited moderate accuracy ($R^2\sim 0.8$) for the first nine days of the experimental period (i.e., when $SWC > 0.2 \text{ m}^3 \text{ m}^{-3}$) (Figure 9). All regression models that considered all variables or

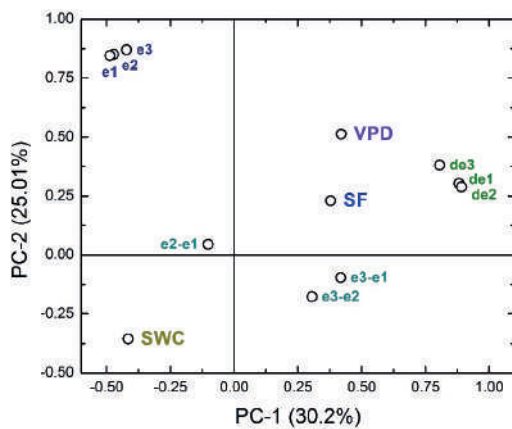


Figure 5. Principal component analysis (PCA) loading plot for SWC, SF, VPD and all EP-derived variables. Loading plots for other principal components are not shown due to the low variability accounted for (<10%).

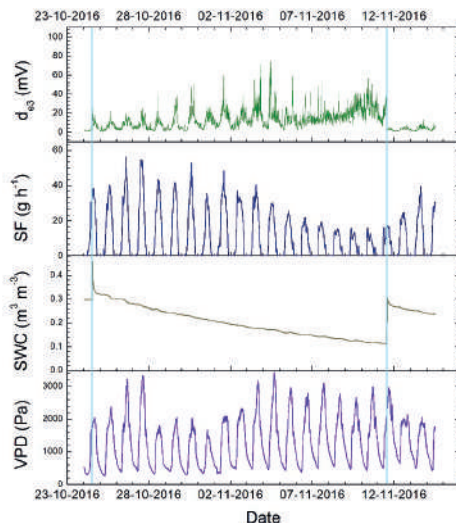


Figure 6. d_{e3} , SF, SWC and VPD measurements obtained during the experiment for Plant 1. The vertical lines indicate irrigation events.

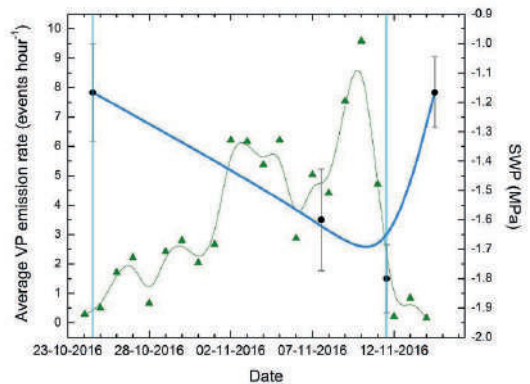


Figure 7. Average (1 day) hourly VP emission rates for plant 1 (triangles) associated with changes in the SWP (black dots) during the course of the experiment. The vertical lines indicate irrigation events.

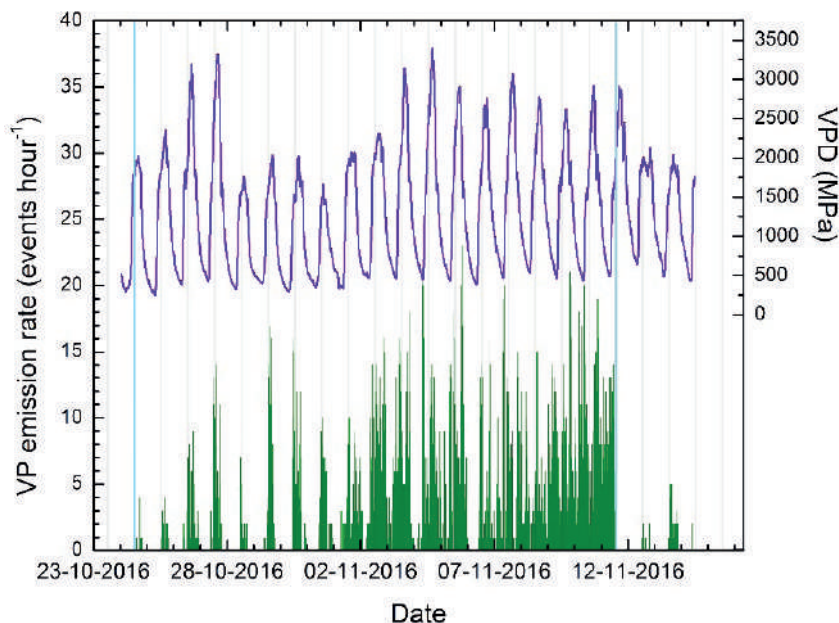


Figure 8. Hourly VP emission rates for plant 1 (lower bars) associated with changes in VPD.

exclusively considered environmental (e.g., VPD and SWC) or EP variables exhibited a decreased predictability of SF as drought advanced (Figure 9). Overall, SWC and VPD were better predictors of SF than EP-derived variables, and their models showed higher R^2 values than EP-based models for most days of the experimental period (Figure 9) and higher standardized coefficients in the combined models (data not shown).

Although the decreasing pattern of the determination coefficient was similar for the three models, irrigation led to important differences in the R^2 values between the SWC-VPD-based model and the EP-based model. The changes in SF in response to irrigation were better explained by the EP-based model ($R^2=0.496$), and the SWC-VPD-based model exhibited poor predictability ($R^2=0.175$).

Discussion

Numerous authors have established a negative correlation between SF and EP differences along plant stems (Morat et al., 1994; Koppán et al., 2002;

Gibert et al., 2006), which may be due to so-called streaming potentials (Labady et al., 2002). However, the latter explanation has been questioned recently, and an alternative hypothesis that EP differences between the plant and its surrounding soil are primarily due to medium pH differences has been favored (Love et al., 2008). The present work showed that avocado EP differences along the stem did not strongly correlate with SF (Figure 5), and daily patterns of EP variation were lost during drought (Figure 3), which may be due to other physiological processes inducing changes in EP. The latter provides additional evidence that the streaming potential theory does not sufficiently explain the daily patterns of EP variations along plant stems. However, the EP values exhibited an immediate and substantial (~ 50 mV) change after irrigation (Figure 3) that was accompanied by an increase in SF (Figure 6). Because the reference electrode in the present work was placed at the base of the plant and not in the soil (as in Love et al., 2008), the observed change in EP was not due to a change in soil pH in response to irrigation. Due to pH differences, the xylem sap at the scion (3 measuring electrodes) and at the rootstock (reference electrode) must have different pH values.

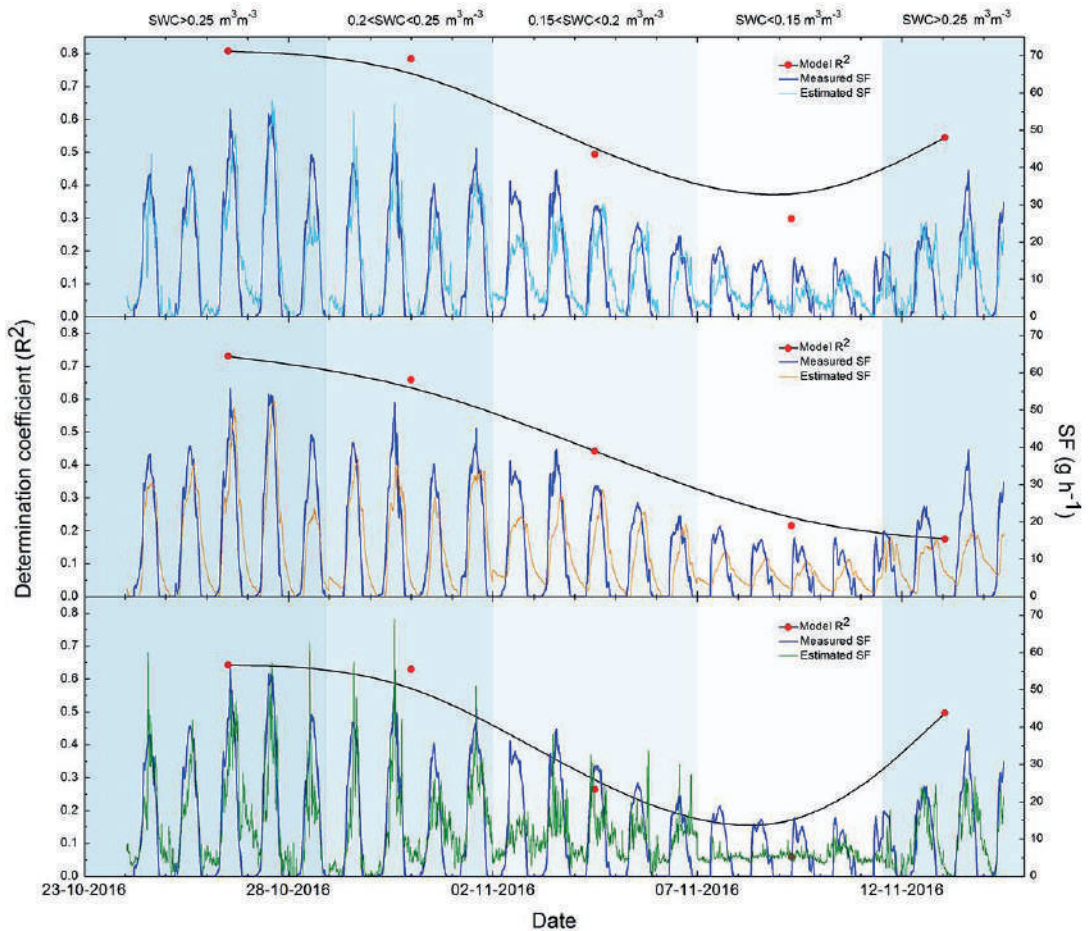


Figure 9. Periodic regression models represented by their estimated values and determination coefficients. Top: SF/VPD/EP-based models (all variables included); center, SF-VPD-based models; bottom: EP-based models. The background color denotes the SWC (labels on top).

Xylem sap becomes more alkaline under drought conditions by 1 pH unit (reviewed in Wilkinson, 1999), but this change has been interpreted as a root-sourced signal to leaves (Wilkinson & Davies, 1997), which reduces the stomatal aperture in an ABA-dependent manner. However, if EP differences are due to a variation in pH within the xylem, this difference must originate from the aerial part of the plant and not from the roots. Further interpretations of this behavior in relation to changes in xylem sap pH are limited by the unknown nature of how apoplastic pH changes in response to drought (Gloser et al., 2016) and by the recently documented fact that transient opposite pH changes (e.g., xylem acidification) arise in response to embolism (Secchi & Zwieniecki,

2012; Secchi & Zwieniecki, 2016).

Although daily patterns were rapidly lost in the EP and ΔEP measurements, a clear diurnal cycle was observed for d_{EP} . This pattern ultimately vanished as drought proceeded but was quickly reestablished after irrigation. The almost immediate reestablishment of normal EP behavior after irrigation contrasts with the results of Ríos-Rojas et al. (2015), in which avocado plants took several days to recover their initial EP values after irrigation.

The immediate change in EP after irrigation led to a significant change in SF, as indicated by the increase in the R^2 value of the EP-based model after

rewatering (Figure 9). In contrast, the VPD-SWC model performed poorly. This finding indicates that the sudden change in EP after a drought period was strongly associated with a change in SF, which suggests that EP variations are associated with streaming potentials (i.e., surface charge generation via the flow of an electrically charged fluid).

The present work indicated that short-term variations in EP (d_{EP}) were strongly associated with drought stress intensity. This result leads to two basic conclusions: (1) drought is associated with the emission of VP-like electrical pulses, and (2) an increasing number of electrical pulses strongly restrains the possibility of estimating SF using EP data. Although it is not possible to determine whether these short-term variations in EP are due to changes in electrical current (i.e., a “genuine signal”) or rather a consequence of changes in the medium (i.e., the plant’s) electrical conductivity, the latter seems unlikely because electrical impedance in avocado scales linearly with water potential (Dixon et al., 1978). Therefore, the VP emission rate should actually decrease with the SWP under the same electrical current because signal attenuation would increase when traveling along the stem. Therefore, the results obtained herein suggest that EP variations are due to changes in electrical current rather than (but not exempt of) changes in the medium resistance.

The emission of VP is associated with cavitation events induced by pressure steps (Stahlberg & Cosgrove, 1996). Although the sampling rate used in the present work did not permit confirmation of each of the estimated VP events (defined herein as events in which $d_{EP} < -10$ mV in all three electrodes) due to the possibility of aliasing (Labady et al., 2002), the results of both multiple regression models (Table 1) and the daily occurrence of VP events (Figure 8) throughout the experiment strongly favor the hypothesis that d_{EP} and VP emissions increase with drought intensity. The regression models revealed that d_{EP} at all electrodes was

positively associated with VPD and SF and negatively associated with SWC. All of these variables are related to cavitation vulnerability (Jackson et al., 1995), and the observed EP behavior may be linked to sudden changes induced in xylem tension via cavitation. VP signals occur in response to changes in hydraulic pressure, particularly positive xylem pressure steps (Stahlberg et al., 2006), which are observed during cavitation events (Wei et al., 1999).

Conclusions

The present work provides preliminary results that strongly suggest a relationship between drought stress and EP variations in plant stems. Further research is needed to confirm whether the observed EP trends observed during drought are due to cavitation events and the emission of VP signals (e.g., as in Stahlberg & Cosgrove, 1996) and/or linked to other physiological processes, e.g., pH changes in response to drought (Wilkinson, 1999) or embolism (Secchi & Zwieniecki, 2016). VPs are associated with hydraulic events, suggesting that the function of VP signals may be associated with drought adaptation in plants. However, additional research is needed to assess how xylematic EP trends relate to changes in the solution pH, which changes in response to SWC and cavitation events. Although VPs are related to hydraulic events, no previous research has postulated that their function is associated with adaptation to drought because this condition induces embolism in plants. Meanwhile, the present work indicates that short-term variations in EP (d_{EP}) are strongly associated with the intensity of drought stress, thus stem electrical potential variations may aid in the early detection of drought stress in fruit-bearing trees.

Acknowledgments

We highly thank and appreciate Tomás I. Fuenzalida’s (PUC) for all his intellectual and

data collection contribution. We also thank Patricio Candia for his help with the experimental setup and Javier Merrill for his aid in the data analyses. This research was financed

by the funds of the Water and Irrigation Lab at the Faculty of Agronomy and Natural Systems at Universidad Católica de Chile.

Resumen

P. M. Gil y A.I. Vargas. 2023. Las variaciones del potencial eléctrico del tallo pueden ayudar en la detección temprana del estrés hídrico en árboles frutales. Int. J. Agric. Nat. Resour. 116-129. La señalización eléctrica en plantas, conocida como potencial de variación (VP), ocurre en respuesta a una amplia gama de estímulos y se asocia con la inducción de cambios repentinos en la presión del xilema. Además, hay evidencia de que el potencial eléctrico (EP) de las plantas cambia con el contenido de agua del suelo. Por lo tanto, el uso del EP como una medida directa del estado hídrico de la planta puede tener potencial como información para el monitoreo del estrés hídrico. Las mediciones de EP dentro de los tallos de las plantas se correlacionan indirectamente con el flujo de savia (SF), una variable que se utiliza para estimar el uso del agua en las plantas. Sin embargo, si esta relación es estable bajo condiciones de sequía no es información conocida. El presente trabajo investigó las relaciones entre SF y las variaciones de EP durante un período de sequía de 18 días en tres árboles de aguacate para probar la hipótesis de que las relaciones entre SF y EP pueden perderse debido a la intensidad de la sequía. Los resultados mostraron que las variaciones a corto plazo en el EP estaban positivamente asociadas con el déficit de presión de vapor (VPD) y las variaciones de SF, pero negativamente asociadas con el contenido de agua del suelo (SWC). Se observó un aumento en las emisiones de VP a medida que avanzaba la sequía, lo cual estaba negativamente asociado con el potencial hídrico del tallo (SWP). Después de 18 días de sequía, luego de la aplicación de un evento de riego, se suprimieron casi por completo las variaciones a corto plazo en el EP. El presente trabajo proporciona resultados preliminares que sugieren fuertemente una relación entre el estrés por sequía y las variaciones de EP en los tallos de las plantas. Es necesaria más investigación para confirmar si las tendencias de EP observadas durante la sequía se deben a eventos de cavitación y emisión de señales de VP y/o están vinculadas a otros procesos fisiológicos, por ejemplo, cambios de pH en respuesta a la sequía o embolia. Mientras tanto, el presente trabajo indica que las variaciones a corto plazo en el EP (dEP) están fuertemente asociadas con la intensidad del estrés por sequía, por lo cual, las variaciones del potencial eléctrico del tallo podrían ser útiles en la detección temprana del estrés hídrico en árboles frutales.

Palabras clave: Cavitación, embolia, flujo de savia, monitoreo del estado hídrico de la planta, *Persea americana*, potencial eléctrico, potencial de variación.

References

- Alarcon, J. J. & Malone, M. (1994). Substantial hydraulic signals are triggered by leaf-biting insects in tomato. *Journal of Experimental Botany*, 45(7), 953-957. <https://doi.org/10.1093/jxb/45.7.953>
- Carr, M. K. V. (2013). The water relations and irrigation requirements of avocado (*Persea americana* Mill.): a review. *Experimental Agriculture*, 49(02), 256-278. <https://doi.org/10.1017/S0014479712001317>
- Dixon, M., Thompson, R. G. & Fensom, D. S. (1978). Electrical resistance measurements of water potential in avocado and white spruce. *Canadian Journal of Forest Research*, 8(1), 73-80. <https://doi.org/10.1139/x78-013>

- Frachisse, J. M., Desbiez, M. O., Champagnat, P. & Thellier, M. (1985). Transmission of a traumatic signal via a wave of electric depolarization, and induction of correlations between the cotyledonary buds in *Bidens pilosus*. *Physiologia Plantarum*, 64(1), 48-52. <https://doi.org/10.1111/j.1399-3054.1985.tb01211.x>
- Fromm, J. & Lautner, S. (2007). Electrical signals and their physiological significance in plants. *Plant, Cell & Environment*, 30(3), 249-257. <https://doi.org/10.1111/j.1365-3040.2006.01614.x>
- Gibert, D., Le Mouél, J. L., Lambs, L., Nicollin, F. & Perrier, F. (2006). Sap flow and daily electric potential variations in a tree trunk. *Plant Science*, 171(5), 572-584. <https://doi.org/10.1016/j.plantsci.2006.06.012>
- Gil, P.M., Saavedra, J., Schaffer, B., Navarro, R., Fuentealba, C. & Minoletti, F. (2014) Quantifying effects of irrigation and soil water content on electrical potentials in grapevines (*Vitis vinifera*) using multivariate statistical methods. *Scientia Horticulturae*, 173, 71-78. <https://doi.org/10.1016/J.SCIENTA.2014.04.014>
- Gil, P. M., Gurovich, L., Schaffer, B., Alcayaga, J., Rey, S. & Iturriaga, R. (2008a). Root to leaf electrical signaling in avocado in response to light and soil water content. *Journal of Plant Physiology*, 165(10), 1070-1078. <https://doi.org/10.1016/J.JPLPH.2007.07.014>
- Gil, P. M., Gurovich, L. & Schaffer, B. (2008b). The electrical response of fruit trees to soil water availability and diurnal light-dark cycles. *Plant Signaling & Behavior*, 3(11), 1026-1029. <https://doi.org/10.4161/psb.6786>
- Gloser, V., Korovetska, H., Martín-Vertedor, A. I., Hájíčková, M., Prokop, Z., Wilkinson, S. & Davies, W. (2016). The dynamics of xylem sap pH under drought: a universal response in herbs? *Plant and Soil*, 409(1-2), 259-272. <https://doi.org/10.1007/s11104-016-2962-6>
- Huber, A. E. & Bauerle, T. L. (2016). Long-distance plant signaling pathways in response to multiple stressors: the gap in knowledge. *Journal of Experimental Botany*, 67(7), 2063-2079. <https://doi.org/10.1093/jxb/erw099>
- Jackson, G. E., Irvine, J. & Grace, J. (1995). Xylem cavitation in Scots pine and Sitka spruce saplings during water stress. *Tree Physiology*, 15(12), 783-790. <https://doi.org/10.1093/treephys/15.12.783>
- Koppán, A., Fenyvesi, A., Szarka, L. & Wesztergom, V. (2002). Measurement of electric potential difference on trees. *Acta Biologica Szegediensis*, 46(3-4), 37-38.
- Labady, A., Thomas, D. J., Shvetsova, T. & Volkov, A. G. (2002). Plant bioelectrochemistry: effects of CCCP on electrical signaling in soybean. *Bioelectrochemistry*, 57(1), 47-53. [https://doi.org/10.1016/S1567-5394\(01\)00175-X](https://doi.org/10.1016/S1567-5394(01)00175-X)
- Love, C. J., Zhang, S. & Mershin, A. (2008). Source of sustained voltage difference between the xylem of a potted *Ficus benjamina* tree and its soil. *PLoS one*, 3(8), e2963. <https://doi.org/10.1371/journal.pone.0002963>
- Mancuso, S. (1999). Hydraulic and electrical transmission of wound-induced signals in *Vitis vinifera*. *Functional Plant Biology*, 26(1), 55-61. <https://doi.org/10.1071/PP98098>
- Morat, P., Le Mouél, J. L. & Granier, A. (1994). Electrical potential on a tree. A measurement of the sap flow? *Comptes rendus de l'Académie des sciences. Série 3, Sciences de la vie*, 317(1), 98-101.
- Oyarce, P. & Gurovich, L. (2011). Evidence for the transmission of information through electric potentials in injured avocado trees. *Journal of Plant Physiology*, 168(2), 103-108. <https://doi.org/10.1016/j.jplph.2010.06.003>
- Reyes-Santamaria, I., Terrazas, T., Barrientos-Priego, A. F. & Trejo, C. (2002). Xylem conductivity and vulnerability in cultivars and races of avocado. *Scientia Horticulturae*, 92(2), 97-105. [https://doi.org/10.1016/S0304-4238\(01\)00284-9](https://doi.org/10.1016/S0304-4238(01)00284-9)
- Rios-Rojas, L., Morales-Moraga, D., Alcalde, J. A. & Gurovich, L. A. (2015). Use of plant woody species electrical potential for irrigation scheduling. *Plant Signaling & Behavior*, 10(2), e976487. <https://doi.org/10.4161/15592324.2014.976487>
- Rockwell, F. E., Wheeler, J. K. & Holbrook, N. M. (2014). Cavitation and its discontents: opportunities for resolving current controversies. *Plant*

- Physiology*, 164(4), 1649-1660. <https://doi.org/10.1104/pp.113.233817>
- Scholander, P. F., Hammel, H. T., Bradstreet, E. D. & Hemmingsen, E. A. (1965). Sap pressure in vascular plants. *Science*, 148(3668), 339-346. <https://doi.org/10.1126/science.148.3668.339>
- Secchi, F. & Zwieniecki, M. A. (2016). Accumulation of sugars in the xylem apoplast observed under water stress conditions is controlled by xylem pH. *Plant, Cell & Environment*, 39(11):2350-2360. <https://doi.org/10.1111/pce.12767>
- Smart, R. E. & Bingham, G. E. (1974). Rapid estimates of relative water content. *Plant Physiology*, 53(2), 258-260. <https://doi.org/10.1104/pp.53.2.258>
- Stahlberg, R., Cleland, R.E., Van Volkenburgh, E. (2006). Slow Wave Potentials — a Propagating Electrical Signal Unique to Higher Plants. In: Baluška, F., Mancuso, S., Volkmann, D. (eds) *Communication in Plants*. Springer, Berlin, Heidelberg. <https://doi.org/10.1007/978-3-540-28516-8>
- Stahlberg, R. & Cosgrove, D. J. (1996). Induction and ionic basis of slow wave potentials in seedlings of *Pisum sativum* L. *Planta*, 200(4), 416-425. <https://doi.org/10.1007/BF00231397>
- Stahlberg, R. & Cosgrove, D. J. (1997). The propagation of slow wave potentials in pea epicotyls. *Plant Physiology*, 113(1), 209-217. <https://doi.org/10.1104/pp.113.1.209>
- Stanković, B. & Davies, E. (1998). The wound response in tomato involves rapid growth and electrical responses, systemically up-regulated transcription of proteinase inhibitor and calmodulin and down-regulated translation. *Plant and Cell Physiology*, 39(3), 268-274. <https://doi.org/10.1093/oxfordjournals.pcp.a029367>
- Tyree, M. T. & Dixon, M. A. (1986). Water stress induced cavitation and embolism in some woody plants. *Physiologia Plantarum*, 66(3), 397-405. <https://doi.org/10.1111/j.1399-3054.1986.tb05941.x>
- Wei, C., Tyree, M. T. & Steudle, E. (1999). Direct measurement of xylem pressure in leaves of intact maize plants. A test of the cohesion-tension theory taking hydraulic architecture into consideration. *Plant Physiology*, 121(4), 1191-1205. <https://doi.org/10.1104/pp.121.4.1191>
- Wilkinson, S. & Davies, W. J. (1997). Xylem sap pH increase: a drought signal received at the apoplastic face of the guard cell that involves the suppression of saturable abscisic acid uptake by the epidermal symplast. *Plant physiology*, 113(2), 559-573. <https://doi.org/10.1104/pp.113.2.559>
- Wilkinson, S. (1999). pH as a stress signal. *Plant Growth Regulation*, 29(1-2), 87-99. <https://doi.org/10.1023/A:1006203715640>

