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Electrophysiology of Woody Plants

Luis A. Gurovich
Universidad Católica de Chile
Chile

1. Introduction

A fundamental property of all living organisms is related to the continuous gathering of environmental information and the expression of physiological responses aimed to optimize its performance under new environmental conditions. In order to keep homeostasis, plants need to continuously gather information about its environment and to react physiologically, in order to synchronize its normal biological functions. Plant cells become bio - electrochemically excited under the influence of environmental changes and the conduction of these electric potential modifications to distant plant organs have been widely reported. Electrochemical phenomena in plants have attracted researchers since the eighteenth century (Bertholon, 1783; Burdon-Sanderson, 1873; Darwin, 1875; Lemström, 1904; Bose, 1926); however, only in the last decade numerous papers related to plant electrophysiology have been published (for a comprehensive review on the subject see Volkov's book "*Plant Electrophysiology, Theory and Methods*", 2006). Detection of electrical potentials in plants indicates that electrical signaling is a major system to transmit information over long distances throughout its organs. The reason why plants have developed pathways for electrical signal transmission is probably related to its need to respond rapidly to environmental stress factors (Fromm & Lautner, 2007). Electrophysiological studies of long-distance signals in plants and animals contribute to our knowledge of the living world by revealing important similarities and crucial differences between plants and animals, in an area that might be directly related to their different capacities to respond to environmental change.

The existence of electrophysiological mechanisms for information perception, transmission and processing between different plant organs and tissues, allowing the expression of fast and accurate physiological reactions to specific biotic or abiotic stimuli, is expressed by means of real-time detectable *action* (APs) and *variation* (VPs) potentials (Datta & Palit, 2004; Gil et al., 2008; Lautner et al., 2005; Oyarce & Gurovich, 2010; Volkov et al., 2009; Wang et al., 2009). An additional type of electric potential in plants has been proposed by Zimmermann et al. (2009), to be called *system* potential. In addition to APs that occur also in animals and lower plants (Trebacz et al., 2005) higher plants feature an additional, unique, hydraulically propagated type of electric signals VPs, called also *slow wave potentials* (Stahlberg et al., 2005).

Several models have been proposed to explain the onset of plant cell electric excitation, resulting from external stimuli (Wayne, 1993; Fromm & Lautner, 2007). All plant cells are

surrounded by a plasma membrane (Murphy et al., 2010), composed of a lipid bilayer, with a variety of molecular structures embedded in it, known generically as *ion channels* and *electrogenic pumps* (Hedrich & Schroeder, 1989). Electrochemical excitation is caused by ionic fluxes through the cell plasma membrane (Knudsen, 2002; Blatt, 2008), creating an electric charge modification in the membrane itself, as well as a differential charge on either side. This trans - membrane potential is the difference in voltage (or electrical potential difference) between the interior and exterior of a cell ($V_{\text{interior}} - V_{\text{exterior}}$). Plant plasma membranes always maintain a potential, the cell interior being more negative than the exterior, arising mainly from the activity of electrogenic pumps. As an example, H^+ -transporting ATPases (Sze et al., 1999) pump protons out of the cell, thus maintaining a pH gradient across the plasma membrane. This process is involved in the simultaneous symport of carbohydrates and amino acids into the cell, which are produced at different plant tissues as photosynthetic derivatives. Other electrogenic ion pumps described for plant cell plasma membranes are related to ion and solute fluxes, underpinning inorganic mineral nutrient uptake; they trigger rapid changes in secondary messengers such as cytosolic-free Ca^{+2} concentrations, and also power the osmotic gradients that drive cell expansion (Schroeder & Thuleau 1991; Gelli & Blumwald, 1997; Zimmermann et al., 1997; Bonza et al., 2001; Sanders, 2002; Blatt, 2008; Lautner & Fromm, 2010). The K^{+1} -transporting ATPase, also embedded in the cell plasma membrane, enables the onset of different ion concentrations (and therefore electrical charge) on the intracellular and extracellular sides of the membrane (Maathuis & Sanders, 1997).

Ion channels, when active, partially discharge the plasma membrane potential, while the electrogenic pumps restore and maintain it (Fromm & Spanswick, 1993; Neuhaus & Wagner, 2000). The plasma membrane potential has two basic functions. First, it allows a cell to function as a *battery*, providing power to operate the variety of electrogenic pumps embedded in its lipid bilayer. Second, in electrically excitable cells, it is used for transmitting signals between different parts of a cell or to other plant cells, tissues or organs. Opening or closing of ion channels at one point in the membrane produces a local and transient change in the membrane potential, which causes an electric current to flow rapidly to other points in the membrane and eventually, to the plasma membrane of surrounding cells. In non-excitable cells, and in excitable cells in their baseline state, the membrane potential is held at a relatively stable value, called the *resting potential*, characterized by its absence of fluctuations; the resting potential varies from -20 mV to -200 mV according to cell type. Opening and closing of ion channels can induce a departure from the resting potential, called a *depolarization* if the interior voltage rises, or a *hyperpolarization* if the interior voltage becomes more negative. In excitable cells, a sufficiently large depolarization can evoke an action potential (AP), in which the membrane potential very rapidly undergoes a significant, measurable change, often briefly reversing its sign; AP are short-lasting, all-or-nothing events.

Change in trans - plasma membrane potential creates a *wave of depolarization*, which affects the adjoining resting plasma membranes, thus generating an *impulse*. Once initiated, these impulses can propagate to adjacent excitable cells. Electrical signals can propagate along the plasma membrane (Van Bel & Ehlers, 2005; Volkov et al., 2011) on short distances through plasmodesmata and on long distances in plant phloematic tissue (Ksenzhek & Volkov, 1998; Volkov, 2000; Volkov, 2006; Volkov et al., 2011).

Research on the subject of electrochemical phenomena in plants is generically known as *plant electrophysiology* (Volkov, 2006); this knowledge is the basis of a newly developed discipline in the field of plant physiology: *plant neurobiology* (Brenner et al, 2006; Stahlberg, 2006; Baluška & Mancuso, 2008; Barlow, 2008). Plant neurobiology is aimed at establishing the structure of information networks that exist within the plant, which is expressed as responses to environmental stimuli by means of electrochemical signals (Baluška et al., 2004; Trewavas, 2005). These signals seem to complement other plant signals: hydraulic, mechanical, volatile and hormonal, already well documented in plant science (Fromm & Lautner, 2007; Gil et al., 2009; Dziubinska et al., 2003).

Research on plant electrophysiology specifically focused on woody plants like poplar and willow trees, have been seldom reported (Fromm & Spanswick, 1993; Lautner et al, 2005; Gibert et al., 2006). In fruit bearing deciduous and perennial plant species, electrophysiology studies are very limited as well, although it is in such plants that the need for rapid and efficient signals other than chemical and hydraulic signaling becomes more obvious (Gil et al., 2008; Nadler et al. 2008; Gurovich & Hermosilla, 2009; Oyarce & Gurovich, 2011). These studies have associated the effect of water stress, deficit irrigation, light cycles and mechanical or heat injury with electrical signaling in several fruit bearing tree species. Electrical signaling has been also associated to conditions of differential soil water availability; the use of real-time information on tree electrochemical behavior, as early indicator of biotic or abiotic induced water stress conditions, can provide a strategy to quantitatively relate plant physiological reactions to environmental changes and eventually, for the auto-programmed operation of pressurized irrigation systems, aimed to prevent water stress conditions in irrigated trees (Oyarce and Gurovich, 2010).

Additional applications of electrical signals in plants have been postulated, including its eventual use as environmental biosensors (Davies, 2004; Volkov & Brown, 2006) as well as to correlate sap flow based ET measurements with plant electrical behavior has been proposed (Gibert et al., 2006). Artificially applied electric potential differentials between plant organs under field conditions may enhance water use efficiency in woody plants, through its controlled influence on stomata conductance and plant internal water flux (Gil et al., 2008; Jia & Zhang, 2008; Gil et al., 2009; Gurovich, 2009).

2. History of plant electrophysiology

For a long time, plants were thought to be living organisms whose limited ability to move and respond was related to its relative limited abilities of sensing (Trewavas, 2003), with the exception only for plants with rapid and/or purposeful movements such as *Mimosa pudica* (also called *the sensitive plant*), *Drosera* (sundews), *Dionea muscipula* (flytraps) and tendrils of climbing plants. These sensitive plants attracted the attention of outstanding pioneer researchers such as Burdon-Sanderson (1873, 1899), Pfeffer (1873), Haberlandt (1914), Darwin (1896) and Bose (1926). They found plants not only to be equipped with various mechano-receptors that exceeded the sensitivity of a human finger, but also its ability to trigger action potentials (APs) that implemented these movements.

The discovery that common plants had propagating APs just as the “sensitive” plants (Gunar & Sinykhin 1962, 1963; Karmanov et al., 1972) was a scientific breakthrough with important consequences, correcting the long-held belief that normal plants are less sensitive

and responsive as compared to the so-called “sensitive plants.” Also, it led to studies aimed to understand the meaning of the widely distributed electrical signals in different plant tissues (Pickard, 1973), which carry important messages with a broader relevance than the established induction of organ movements in “sensitive plants”.

The first known recording of a plant AP was done on leaves of the Venus flytrap (*Dionea muscipula* Ellis) in 1873 by Burdon-Sanderson, measuring the voltage difference between adaxial and abaxial surfaces of a *Dionea* leaf half, while stimulating the other half mechanically by touching the hairs (Burdon-Sanderson 1873, 1899). The trap closure in *Dionea* has been considered as a model case, showing comparable roles of APs in plants and nerve-muscle preparations of animals (Simons, 1992). Bose (1926) proposed that vascular bundles act analogous to nerves, by enabling the propagation of an excitation that moved from cell to cell. A comprehensive review of the early development of plant electrophysiology is provided by Stahlberg (2006).

For many years, the application of external electrodes to the surface of plant and animal organs was the only available technique for measuring potentials. The introduction of microelectrodes, like KCl-filled glass micropipettes with a tip diameter small enough to be inserted into living cells (Montenegro et al., 1991), enabled to record intracellular, *i.e.* real, membrane potentials (Vm). This technique was first adopted for giant cells from charophytic algae such as *Chara* and *Nitella*. Later on, it was complemented with precise electronic amplifiers and voltage clamp circuits, monitoring the activity of ion channels by direct measurement of ion currents instead of voltages. Parallel voltage (V) and current (I) measurements allowed I-V-curves, used to differentiate between the action of an ion channel (ohmic or parallel changes in I and V) or ion pump (non-ohmic relation between V and I changes) (Higinbotham, 1973).

As a next step to improve recording possibilities, the *patch clamp* technique was developed; by going from single cells to isolated membrane patches, one can record the current of as small a unit as a single ionic channel. Initially developed for animal cells, this technique was rapidly adopted for plant cell studies (Hedrich & Schroeder 1989). Voltage clamp techniques were introduced to demonstrate the contribution of various ion currents involved in the AP in *Chara* cells (Lunevsky et al. 1983; Wayne 1994). To this day, charophytic algae have served as important research models for higher plant cells electric behavior studies.

Additional studies made considerable progress in linking electrical signals with respiration and photosynthesis (Lautner et al, 2005; Koziol et al. 2003), phloem transport (Fromm & Eschrich, 1988; Fromm & Bauer, 1994) and the rapid, plant-wide deployment of plant defenses (Wildon et al. 1992; Malone et al. 1994; Herde et al. 1995, 1996; Volkov & Haak 1995; Stankovic & Davies, 1996, 1998; Volkov, 2000). The significant development of plant neurobiology in the last decade is mostly related to electrophysiology based research, as an integrated view of plant signaling and behavior (Brenner et al., 2006; Baluška & Mancuso 2008; Barlow, 2008).

3. Hormonal and hydraulic physiological signals in woody plants

Hydraulic and hormonal signals in woody plants complement signaling electrophysiology in plants, playing a significant role in the dynamics of information processes integrating the plant responses to the environment.

Hydraulic pressure signals are propagating changes in water pressure inside plant tissues (Malone, 1996); plant tissues have plenty of hydraulic connections (mainly xylematic vessels) which provide a pathway for long-distance transmission of hydraulic signals. Pressure waves can be relatively quick and fast, as they can diffuse through the plant at the speed of sound ($\sim 1500 \text{ m s}^{-1}$ in water), but, to be physiologically important, a hydraulic signal must cause a significant change in turgor pressure inside a cell. As plant cells can be elastic, their turgor will change only when a significant influx (or efflux) of water occurs: the needed flux is strictly linked with the hydraulic capacitance of the cell, a widely variable property related to plant water potential and plant cell wall elasticity. Thus, hydraulic signals must involve massive water mass flow; for example, to increase the turgor pressure in leaf cells by 1 bar, a net water influx equivalent to 1–5% of the total volume of a leaf must occur (Malone 1996). For a detailed review on plant hydraulic signaling, see Mancuso & Mugnai (2006).

Many chemicals are critical for plant growth and development and play an important role in integrating various stress signals and controlling downstream stress responses, by modulating gene expression machinery and regulating various transporters/pumps and biochemical reactions. These chemicals include calcium (Ca^{+2}), cyclic nucleotides, polyphosphoinositides, nitric oxide (NO), sugars, abscisic acid (ABA), jasmonates (JA), salicylic acid (SA) and polyamines. Significant research in chemical signaling in plants has been aimed to understand the ability of plants respond to abscisic acid (ABA), often called the *stress hormone*. This hormone controls many of the adaptive responses that plants have evolved to conserve water when they perceive a reduced supply of this commodity. Stomata closure, reduced canopy area, and increased root biomass are three of the major adaptive processes regulated by ABA that can potentially be manipulated to improve crop water use efficiency (Wilkinson & Hartung, 2009; Jiang & Hartung, 2008). A comprehensive review on chemical signaling under abiotic stress environment in plants has been recently published by Tuteja & Sopory (2008).

4. Facts and hypothesis about electrical signals in woody plants

Rapid plant and animal responses to environmental changes are associated to electrical excitability and signaling, using the same electrochemical pathways to drive physiological responses, characterized in animals by movement (physical displacement) and in plants by continuous growth. In plants and animals, signal transmission can occur over long and short distances and correspond to intra and intercellular communication mechanisms, which determine the physiological behavior of the organism. Electrical pulses can be monitored in plants as *signals*, which are transmitted through excitable phloematic cell membranes, enabling the propagation of electrical pulses in the form of a depolarization wave or “action potential” AP. (Dziubinska et al., 2001; Fromm & Spanswick, 2007). At the onset of a change in the environmental conditions, plants respond to these stimuli at the site of occurrence and bioelectrical pulses are distributed throughout the entire plant, from roots to shoots and vice versa. A working model (Figure 1) to define plant behavior has been adapted from work published by Volkov & Ranatunga, 2006 and Gibert et al., 2006.

Two different types of electrical signals have been reported in plants: AP (Fromm, 2006), which is a rapid propagating electrical pulse, travelling at a constant velocity and maintaining a constant amplitude, and VP (slow wave or “variation potential”),

corresponding to a long range of a variation pulse (Stahlberg et al., 2006), which varies with the intensity of the stimulus, and its amplitude and speed decrease with increasing distance from its generation site (Davies, 2004, 2006). AP is an all-or-none depolarization that spreads passively from the excited cellular membrane region to the neighboring non-excited region. Excitation in plant cells depends on Ca^{+2} depolarization and Cl^- and K^+ repolarization, that spreads passively from the excited cellular membrane region to the neighboring non-excited region (Brenner et al., 2006). A similitude on electrical signal transmission between animal and plant organs has been postulated by Volkov & Ranatunga (2006), using the model presented in Figure 2.

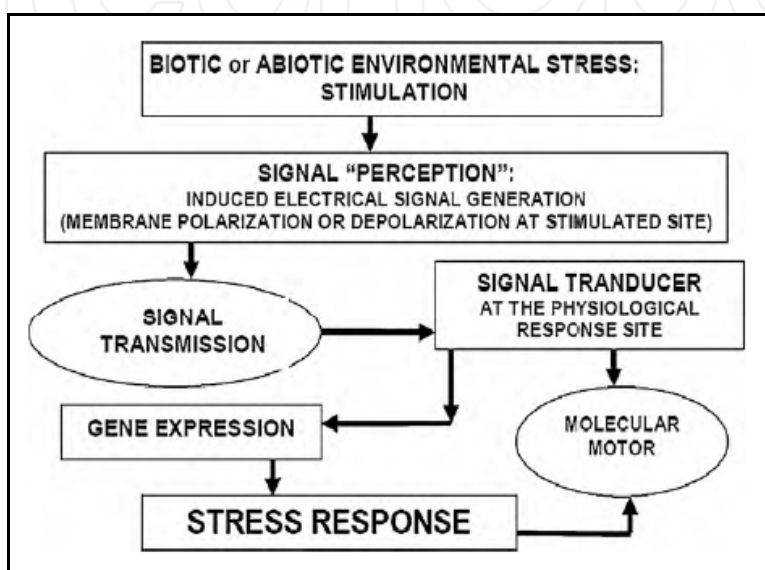


Fig. 1. Proposed mechanism of electric potential signals in plants (Adapted from Volkov & Ranatunga, 2006 and Gibert et al., 2006).

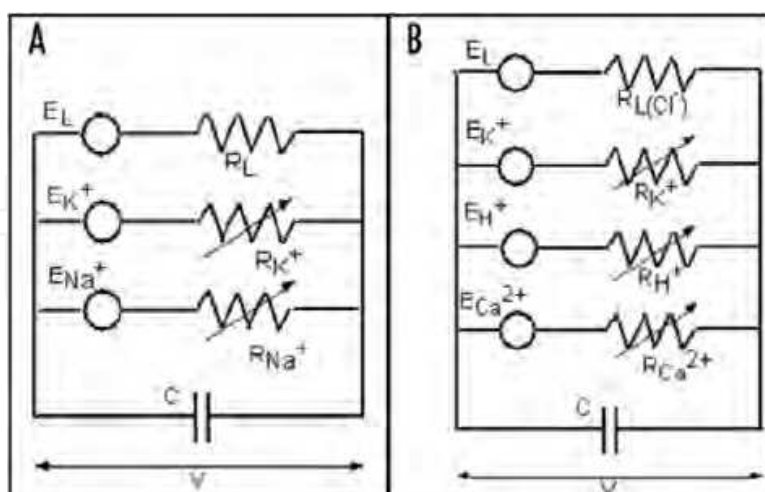


Fig. 2. The Hodgkin-Huxley (HH, 1952) equivalent circuit for an axon (A) and the modified HH circuit for sieve tubes in phloem (B) (Volkov & Ranatunga, 2006).

Electrical conduction rate of most of the plant action potentials studied so far is in the range of $0.01\text{--}0.2\text{ m s}^{-1}$, i.e. much slower than the conduction velocity of action potentials in animal nerves, which is between 0.4 and 42 m s^{-1} (van Bel & Ehlers 2005). Usually, the receptor

potential lasts as long as the stimulus is present, being an electrical replica of the initial stimulus. If the stimulus is sufficiently large to cause the membrane potential to depolarize below a certain threshold, this will cause an action potential to be generated. It shows a large transient depolarization which is self-perpetuating and therefore allows the rapid transmission of information over long distances.

Action potentials can propagate over short distances through plasmodesmata, and after it has reached the sieve element/companion cell (SE/CC) complex (Figure 3), it can travel over long distances along the SE plasma membrane in both directions.

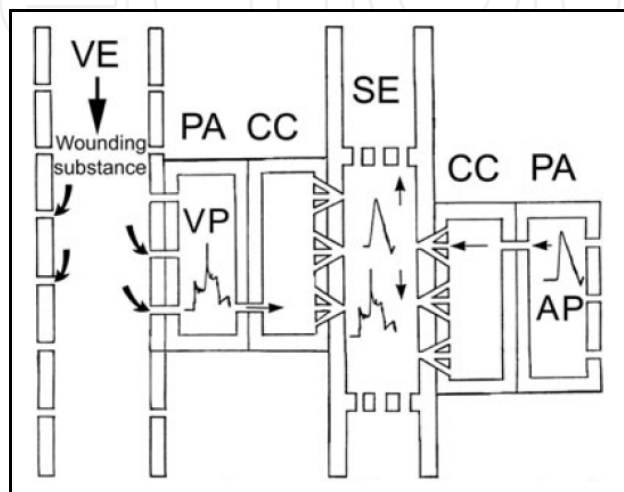


Fig. 3. Action and variation potentials in plants. (After Lautner et al. 2005; Fromm & Lautner, 2007).

In contrast, a VP is generated at the plasma membrane of parenchyma cells (PAs) adjacent to xylem vessels (VEs) (Figure 3) by a hydraulic wave or a wounding substance. Because VPs were measured in SEs, it is suggested that they also can pass through the plasmodesmal network and can reach the phloem pathway. However, in contrast to APs, their amplitude will be reduced with increasing distance from the site of generation.

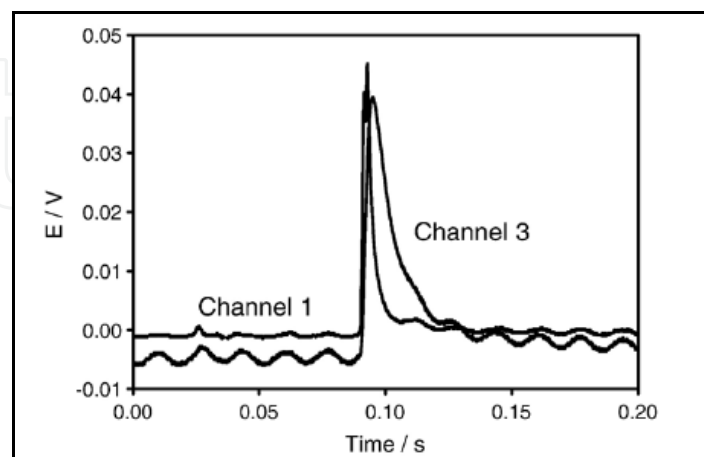


Fig. 4. An action potential recorded in *Aloe vera* spp. (After Volkov et al., 2007).

Action potentials (AP) induced in leaves of an *Aloe vera* spp. plant by thermal shock (flame) are described by Volkov et al., 2007 (Figure 4). Measurements were recorded at 500,000

scans/second and 2,000,000 scans/sample. Channel 1 is located on the leaf treated by thermal shock and channel 2 is located on a different leaf of the same plant. Distance between Ag/AgCl electrodes for each channel was 1 cm.

Stankovic et al. (1998) provide data on APs and VPs measured in *Helianthus annuus* stems by extracellular electrodes (Figure 5). The AP was elicited by electrical stimulation (\pm), and the VP by wounding (W).

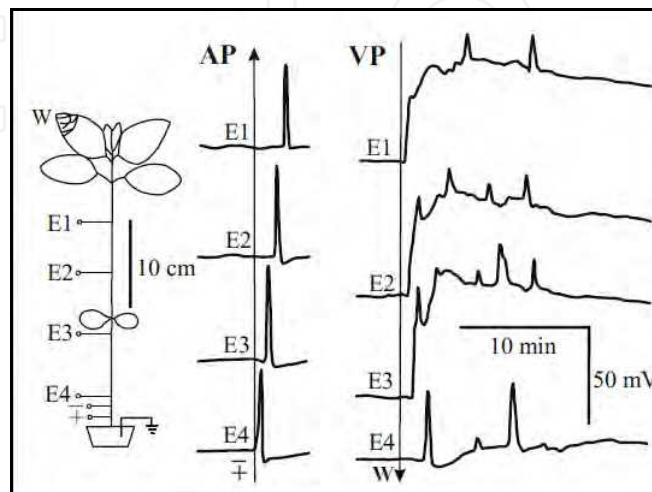


Fig. 5. Action potentials (APs) and variation potentials (VPs) recorded in the stem of *Helianthus annuus* by extracellular electrodes, E1–E4. Vertical arrows indicate the moment of stimulation. Arrowheads point to the direction of propagation. (After Stankovic et al., 1998).

After a transient change in the membrane potential of plant cells (depolarization and subsequent repolarization), VPs and APs make use of the vascular bundles to achieve a potentially systemic spread through the entire plant. The principal difference used to differentiate VPs from APs is that VPs show longer, delayed repolarizations, as shown in Figure 6.

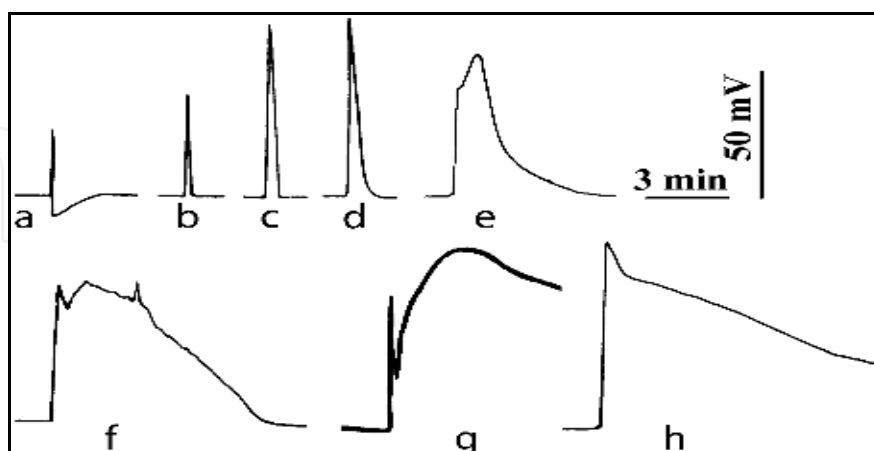


Fig. 6. APs (a to e) and VP (f to h) in plants (After Stahlberg et al., 2006).

VPs repolarizations show a large range of variation that makes a clear distinction to APs difficult; however, VPs and APs do differ more clearly in two aspects: a. the causal factors stimulating their appearance - the ionic mechanisms of their depolarization and

repolarization phases – and b. the mechanisms and pathways of signal propagation. The generation of APs occurs under different environmental and internal influences, like touch, light changes, cold treatment or cell expansion that trigger a voltage-dependent depolarization spike in an all-or-nothing manner. The depolarizations of a VP arise with an increase in turgor pressure cells experience as a result of a hydraulic pressure wave, that spreads through the xylem conduits after rain, embolism, bending, local wounds, organ excision or local burning. While APs and VPs can be triggered in excised organs, VPs depend on the pressure difference between the atmosphere and an intact plant interior. High humidity and prolonged darkness will also suppress VP signaling.

The ionic mechanism of the VP is thought to involve a transient shutdown of a P-type H⁺-ATPase in the plasma membrane and differs from the mechanism underlying APs. Another defining characteristic of VPs is the hydraulic mode of propagation, that enables them – but not APs – to pass through killed or poisoned areas. Unlike APs they can easily communicate between leaf and stem. VPs can move in both directions of the plant axis, while their amplitudes show a decrement of about 2.5% cm⁻¹ and move with speeds that can be slower than APs in darkness and faster in bright light. The VPs move with a rapid pressure increase, establishing an axial pressure gradient in the xylem. This gradient translates distance (perhaps via changing kinetics in the rise of turgor pressure) into increasing lag phases for the pressure-induced depolarizations in the epidermis cells. VPs are not only ubiquitous among higher plants but represent a unique, defining characteristic without parallels in lower plants or animals (Stahlberg et al., 2005; Baluska, 2010).

Electric signals in different fruit bearing trees and other plants species are evaluated at the present, and the effects of different environmental stimuli on its magnitudes and interpretation is a major subject of research. Also, the large number of experiences, yet to be published and now on the peer review referral process in several scientific journals is indicative of a major breakthrough in our knowledge of plant electrical physiology. As an example, data on the effects of tipping and shoot removal in apple trees (Gurovich, Rivera & García, 2011, Figure 7), and dark – light cycles in olive trees (Gurovich and Cano, 2011, Figure 8) are presented below.

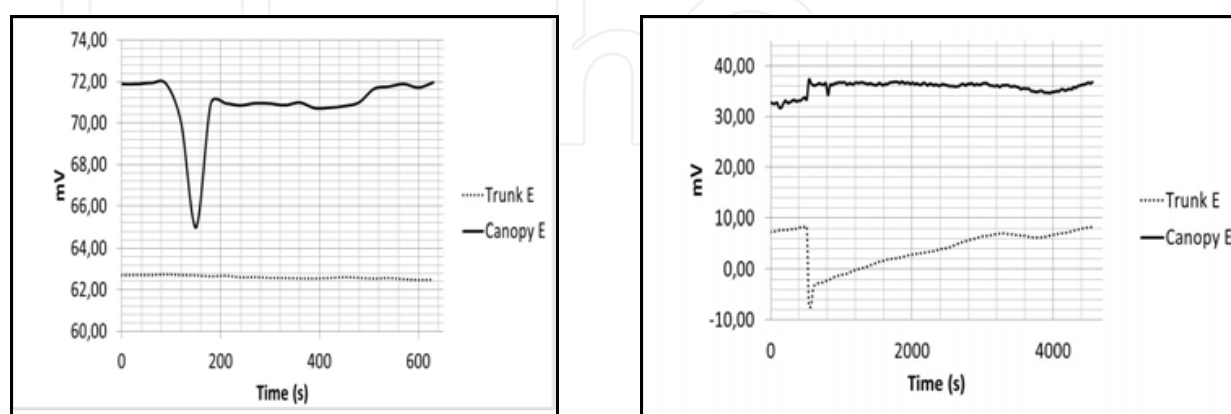


Fig. 7. Apple tree (*Malus domestica* Borkh), cv. Granny Schmidt electric behavior after tipping (A) and basal shoot removal (B). Electrodes are separated by 35 cm. (After Gurovich, Rivera & García, 2011, unpublished data).

In Figure 7A an electrical pulse is transmitted from the tree distal upper tipped point down to the microelectrode located 50 cm in the trunk, within the canopy, with a 3 s delay, and led to a maximal EP reduction of 6.93 ± 1.2 mV in 15 s, with an almost complete EP recovery in 90 s; however, no changes in the EP were measured at the base of the trunk. Elimination of a basal shoot from the rootstock (Figure 7 B) resulted in a EP 15.76 mV reduction, measured with a microelectrode located 5 cm above the rootstock – tree grafting area and a slight increase of 3.88 mV measured at the canopy.

Olive plants kept for 48 hr in total darkness were cyclically illuminated every 5 min for 1000 s periods and EP was measured at the root, rootstock, grafted tree and 2 shoots (Figure 8). A sharp reduction in EP values (on average 50 mV, with a polarity change) take place 3 to 5 s after each illumination cycle, with a slow EP recovery when dark conditions are restored. This behavior is much intense in shoots than in roots, grafted tree and rootstock, and each electric impulse travels throughout the whole plant with similar patterns and velocities.

5. Plant electrophysiology research technology and applications

Two techniques for the measurement of electrical currents in plant studies have been developed: a. non invasive surface recording and b. measurements using inserted thin metal electrodes (Fromm & Lautner, 2007). At different positions of the plant, from roots to fruits, electrodes are connected by insulated cables to a high – input impedance multichannel electrometer and a reference electrode is inserted in the soil. When all channels are stabilized electrically, the effect of many treatments on plant electric behavior can be evaluated, such as electrical stimulation at different organs in the symplastic continuum, to study its transmission dynamics within the plant, resulting from environmental stimuli like light – darkness sequences, drought - irrigation cycles, heat pulses at a specific leaf, localized chemical product applications, variable wind speed and air relative humidity conditions, or plant organ mechanical wounding, like trunk girdling, pruning, leaf and fruit thinning or root excision by underground tillage.

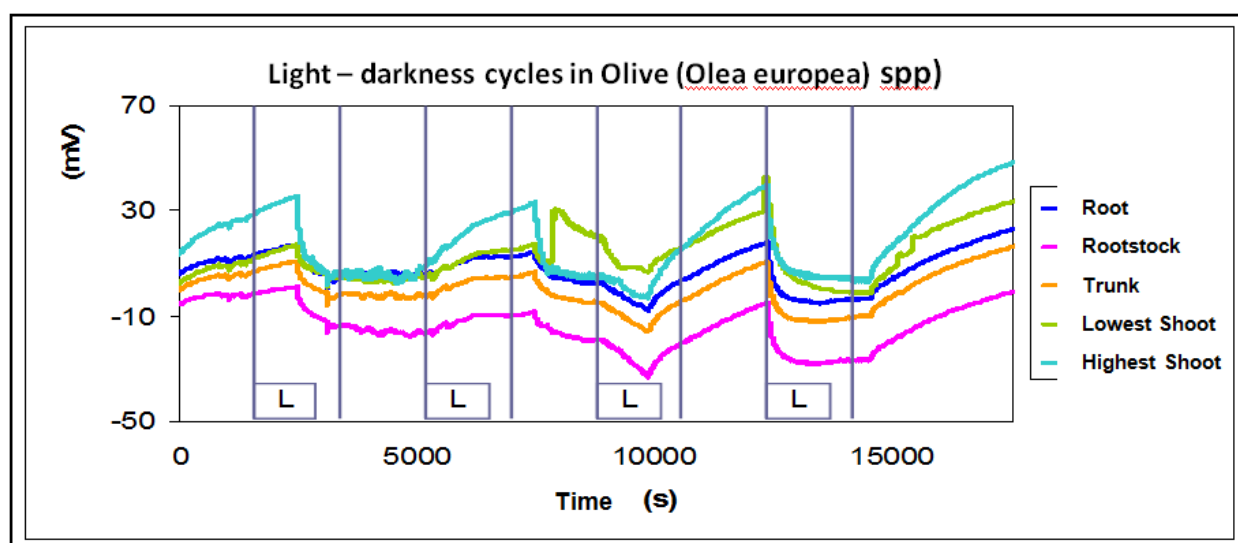


Fig. 8. Electrical behavior of Olive (*Olea europea*) trees) in alternate dark – light cycles (average values from 10 plants) (After Gurovich & Cano, 2011, unpublished data). L = light period at constant 45 watt m⁻², at the canopy top).

Several micro-electrodes have been used for electrophysiological studies in plants. In most of our publications, electrical potentials are monitored continuously using own designed nonpolarizable Ag/AgCl microelectrodes inserted into different positions along the trunk; microelectrode characteristics have been reported by Gurovich & Hermosilla (2009), Gil et al. (2009), Oyarce & Gurovich (2011), and consist on a 0.35 mm-diameter silver wire (99.99% Ag), chlorated in a solution of HCl 0.1N for 30 s using a differential voltage of 2.5 V, to obtain an Ag/AgCl coating, which is inserted in a stainless steel hypodermic needle, 0.5 mm in diameter, filled with a KCl 3M solution; both needle ends are heat-sealed with polyethylene. Electrodes were inserted into the trunk using a low velocity electric microdriller, with a barbed microreel, penetrating the phloematic and cambium tissue; needle tip was further inserted into the xylematic tissue, 0.5–0.75 cm, by mechanical pressure. Each Ag/AgCl microelectrode was referenced to an identical microelectrode installed in the sand media, within the root system (Figure 9).

In our work on electrophysiology, EP real time measurements are implemented using a multi channel voltmeter (Model 2701, Keithley Instruments, including a 20 channel switch module Keithley, model 7700), measuring DC and AC voltage in the range from 100 mV to 1000 V, in testing intervals from 1 to 100 ms. Signals obtained are analyzed with the software ExceLINX-1, an utility provided by Microsoft Excel. All EP measurements are made by keeping the trees within a Faraday-type electromagnetic insulation cage, installed in the laboratory to control constant light and temperature conditions (Figure 10).

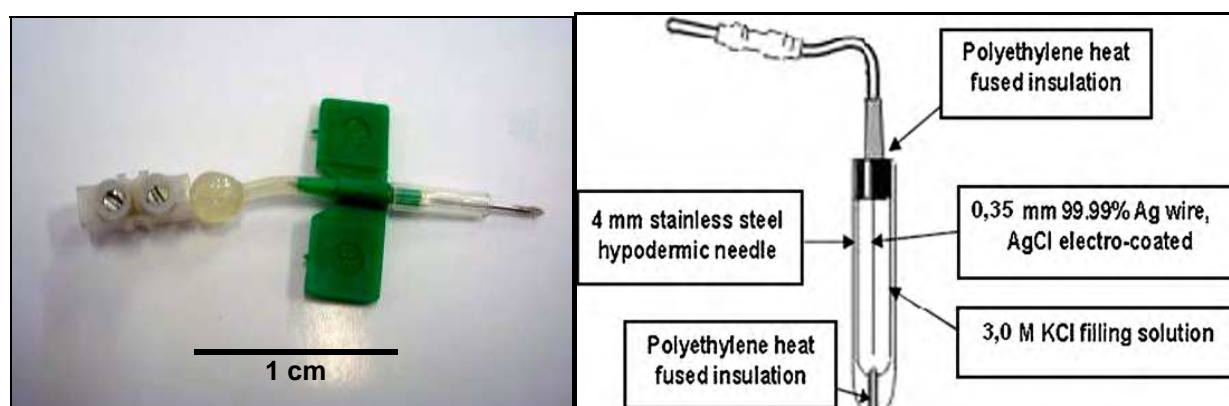


Fig. 9. The Ag/AgCl microelectrode construction.

6. Research on plant electrophysiology of woody plants

Trees live in a continuously changing environment and although not all parts of the tree are exposed to the same stimuli at the same time, tree organs respond in a coordinated fashion, for example, by fast stomata closing under even mild water stress buildup, demonstrating the existence of communication between various regions of the tree. For years, researchers have concentrated their efforts on the study of chemical (hormonal) signals in trees, and very seldom considering that plants simultaneously show distinct electrical and hydraulic signals, which correlate to water stress conditions and other physiological stimuli as well. Considering the large leaf area of a tree, very large amounts of chemicals would need to be synthesized, transported and be perceived at the canopy, in order to respond to a signal coming from the roots.

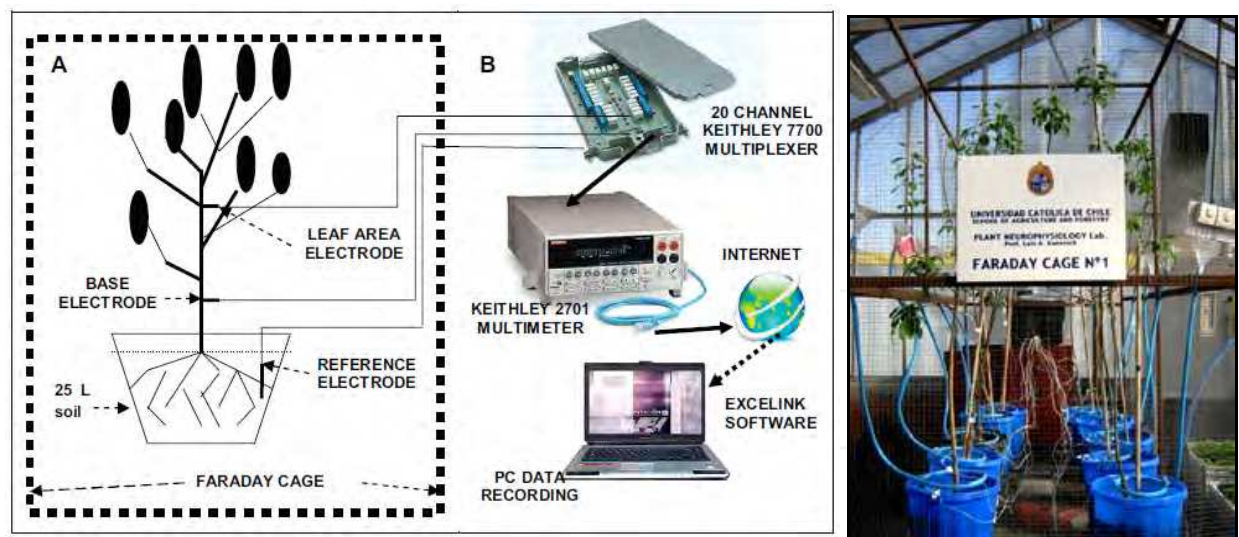


Fig. 10. Schematic diagram of the digital acquisition system for recording voltage differences between the base of the trunk and the canopy. (After Gurovich and Hermosilla, 2009).

Limited research has been reported on signaling in woody trees (*Tilia* and *Prunus*, Boari & Malone 1993; *Salix*, Fromm & Spanswick 1993; Grindl et al., 1999; Oak, Morat et al., 1994; Koppan et al., 2000, 2002; *Vitis*, Mancuso,1999; *Poplar*, Gibert et al., 2006) although it is in such plants that the need for rapid and efficient signals other than chemicals becomes more obvious.

Gibert et al., 2006 present relevant information on the electric long term (2 year) behavior of a single poplar tree, focused on the spatial and temporal variations of the electric potential distribution (Figure 11), with its correlation to air temperature, concluding that seasonal fluctuations of EP trends may be correlated to sap flow patterns, largely influenced by seasonal sap constituents and concentrations.

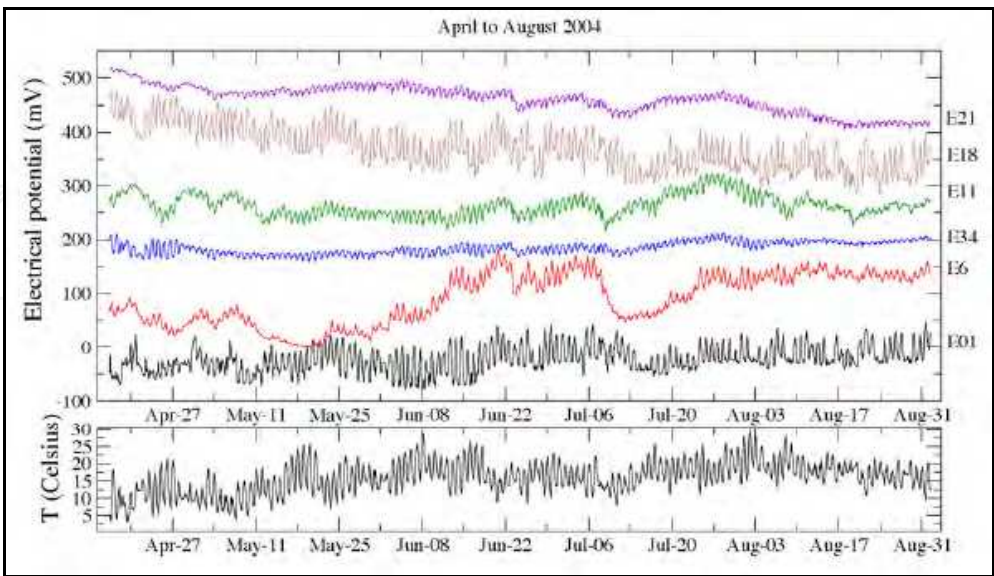


Fig. 11. Top: potential signals for the December 2003–April 2004 period, expressed as relative potential values (see Gibert et al., 2006, Fig. 1 for electrode location). Bottom: outdoor temperature measured near the tree. Tick marks fall at midday.

Recent studies have associated the effect of water stress build-up, irrigation and light with electrical signaling in fruit bearing tree species including avocado (*Persea americana* Mill.), blueberry (*Vaccinium spp.*), lemon (*Citrus limon* (L.) Buró) and olive (*Olea europaea* L.) (Gil et al., 2008; Gurovich & Hermosilla, 2009; Oyarce & Gurovich, 2010, 2011). Some results are included below as examples on this research line, aimed to develop new real - time plant stress sensors based on tree electric behavior, for the automation of irrigation systems operation, optimizing water and energy efficiency in fruit production.

Electric potential (EP) differences have been detected between the base of the stem and leaf petiole and between the base of the stem and the leaf area, located in the upper half of the tree canopy, in response to drought, irrigation and diurnal light and dark cycles (Figure 12). Orders of magnitude of the observed EP variation in those studies were similar to values observed by other authors (Fromm, 2006; Davies, 2006). Electric potential variations observed in avocado trees in response to decreased soil water content have been associated with a decrease in stomata conductance (g_s) (Gil et al., 2009), indicating that stomata closure might be induced or at least associated with an electrical signal that travels through the phloem at a speed of 2.4 cm min^{-1} . Larger changes in electric potential behavior have been detected in response to drought compared to watering. Thus, an extra-cellular electrical signal appears to be involved in root to leaf communication, initiating stomata closure at a very early stage of drought stress. These drought-induced electrical signals were also related to changes in g_s , in concordance to other studies published by Fromm & Fei (1998).

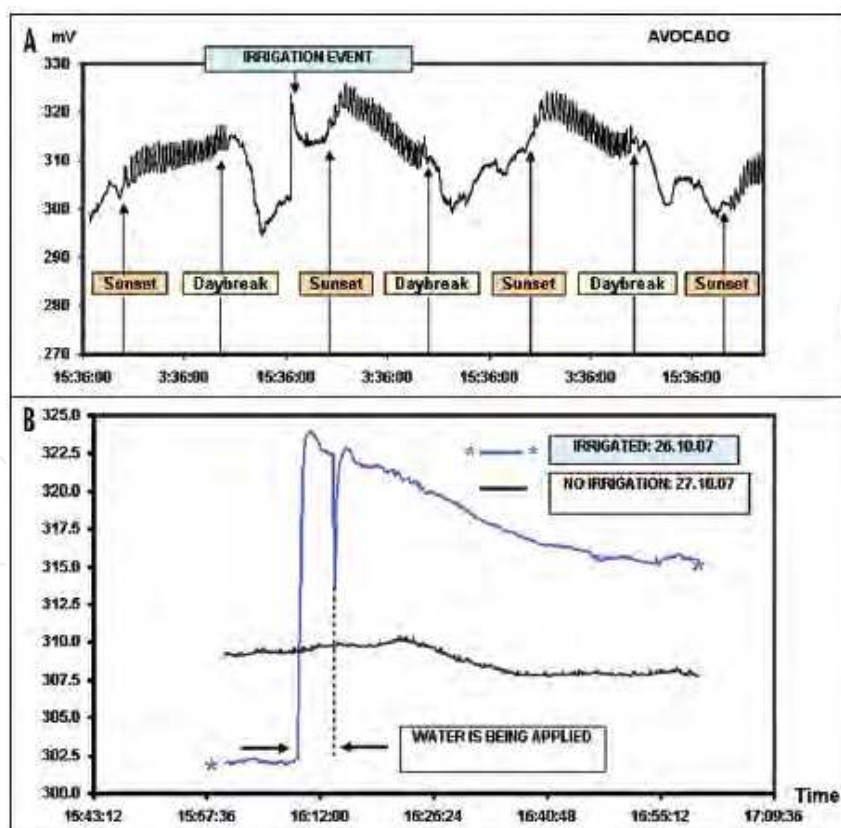


Fig. 12. Electrical potential responses of avocado plants to light and dark and irrigation. (A) EP responses according to the day time. (B) Effect of irrigation on EP behavior (Adapted from Gurovich & Hermosilla 2009).

According to Gurovich & Hermosilla (2009) effects of sunset, daybreak and water application are clearly reflected as fast changes in the EP between the base and leaf area electrode locations on the trunk or stem (Figure 12). Electrical potential fluctuations during light and dark periods may be due to differential sap flow velocity at different times of the day as a result of stomata closure during the night. Electrical potential values were reduced during the initial hours after daybreak, and started to increase after midday, as a result of transient water stress conditions; the first dark hours after sunset resulted in rapid increases of voltages and after midnight these increases tended to slow down. Also, a small but consistent increase in voltage was detected about 1–2 hours before daybreak. Explanations for this behavior may also be related to circadian rhythms detected in plants, but need further study to be fully understood (Dodd et al, 2005; Horta et al., 2007).

The effects of irrigation and day – night cycles on the electric behavior of avocado trees has been reported also by Oyarce & Gurovich (2010) under controlled conditions (Figure 13) EP vary in daily cycles throughout the measurement period: during the morning (2:00 to 7:59 AM), the mean 4-day EP average is in the range $-89.991 \pm 0,46$ mV at 25 cm and -121.53 ± 0.5 mV at 85 cm above the ground, respectively. During the afternoon (14:00 at 19:59 PM), EP values rise, reaching mean values of -79.71 ± 2.16 mV at 25 cm and -104.05 ± 1.21 mV at 85 cm above the ground, respectively, and maximum values of -76.16 ± 20 mV at 17:10 PM (25 cm) and -101.35 ± 5.05 mV at 18:30 PM (85 cm). These values indicate the existence of significant differences in EP between the periods compared (see Oyarce & Gurovich, 2010, Table 2). The effect of irrigation applied every day at 11:00 AM is clearly expressed by a significant decrease in EP, of the order of 7.10 ± 1.56 mV and 7.53 ± 1.39 mV, for micro electrodes inserted in the tree trunk at 25 and 85 cm above the soil surface respectively, representing specific characteristics of an action potential (AP). The recovery of EP values measured before irrigation requires an average period of 16 minutes. On the fourth day, irrigation applied at 15:35 PM did not induce changes in the electrical potential probably due to a low atmospheric demand at that time.

Oyarce & Gurovich (2011) examined the nature and specific characteristics of the electrical response to wounding in the woody plant *Persea americana* (avocado) cv. Hass. Under field conditions, wounds can be the result of insect activity, strong winds or handling injury during fruit harvest. Evidence for extracellular EP signaling in avocado trees after mechanical injury is expressed in the form of variation potentials. For tipping and pruning, signal velocities of 8.7 and 20.9 cm/s⁻¹, respectively, are calculated, based on data measured with Ag/AgCl microelectrodes inserted at different positions of the trunk (Figure 14 a to d). EP signal intensity decreased with increasing distance between the tipping and pruning point and the electrode. Recovery time to pre-tipping or pre-pruning EP values was also affected by the distance and signal intensity from the tipping or pruning point to the specific electrode position.

A significant EP signal, corresponding to a variation potential, is generated as a response of tipping or pruning avocado plants (Figure 14 a to d); the signal was transmitted along the tree trunk at a specific velocity, which is dependent on the distance to the mechanical injury. Mancuso (1999) reported a propagation velocity of the front of the main negative-going signal (VP) of 2.7 mm s⁻¹, while an AP propagated along the shoot with a velocity of about 100 mm s⁻¹. The EP signal intensity also decreases with distance between the mechanical injury sites to the electrode position in the trunk. Several physiological explanations for this

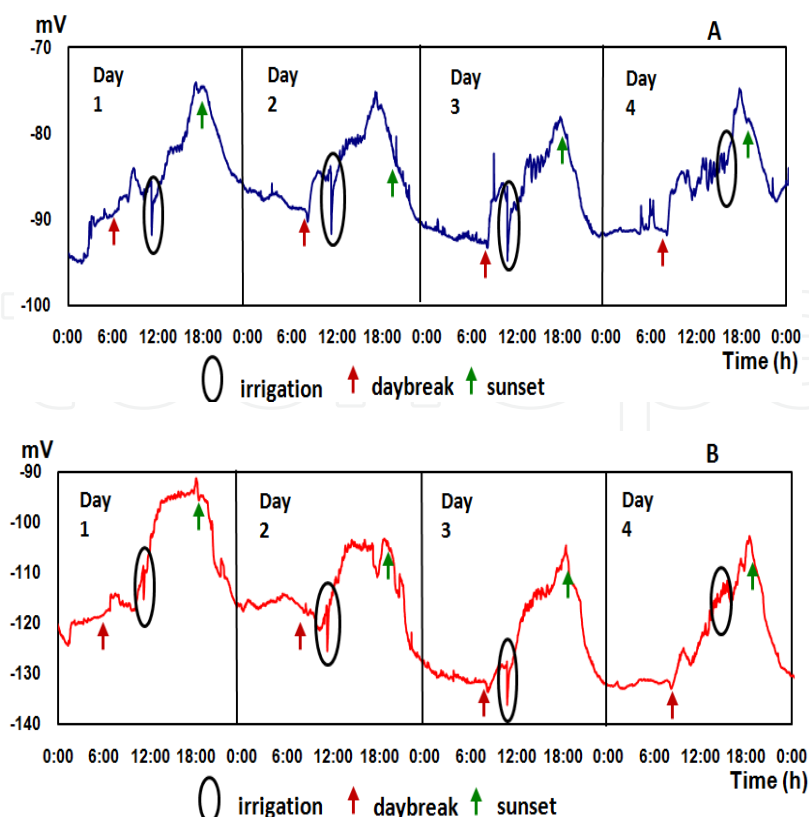


Fig. 13. Electric potentials (EP) in avocado trees during 4 irrigated days. (Average values for 7 trees). Micro electrodes inserted at 25 (A) and 85 (B) cm above the soil surface. (*Adapted from Oyarce & Gurovich, 2010*).

behavior have been proposed by Trewavas & Malho (1997), Zimmermann et al. (1997), Stankovic et al. (1998), Volkov & Brown (2006), Volkov et al. (2008), Baluska et al. (2004); Brenner et al. (2006). All these authors agree with the idea that a certain stimuli receptor must be present at the cell membrane, and that a transient polarization, induced by specific ion fluxes through this membrane, is the ultimate agent of the EP signal generation.

Results presented in these papers indicate a clear and rapid mechanism of electrical signal generation and transmission in woody plants, positively correlated to the intensity and duration of stimuli, such as light intensity, water availability and mechanical injury. The electrical signal is generated in a specific organ or tissue and is transmitted rapidly in the form of AP or VP to other tissues or organs of the plant. The measurement of electrical potentials can be used as a tool for real-time measurement of plant physiological responses, opening the possibility of using this technology as a tool for early detection of stress and for the operation of automatic high frequency irrigation systems.

7. Electrophysiology of some plant tropisms

Sedimenting amyloplasts act as statoliths in root and shoot cells specialized for gravisensing; also different auxins are involved in the gravi - stimulated differential growth known as *gravitropism*. However, no comprehensive explanation is available related to gravity signal perception and its transduction pathways in plants from the sedimenting statoliths to the motoric response of organ bending (Baluska et al., 2006).

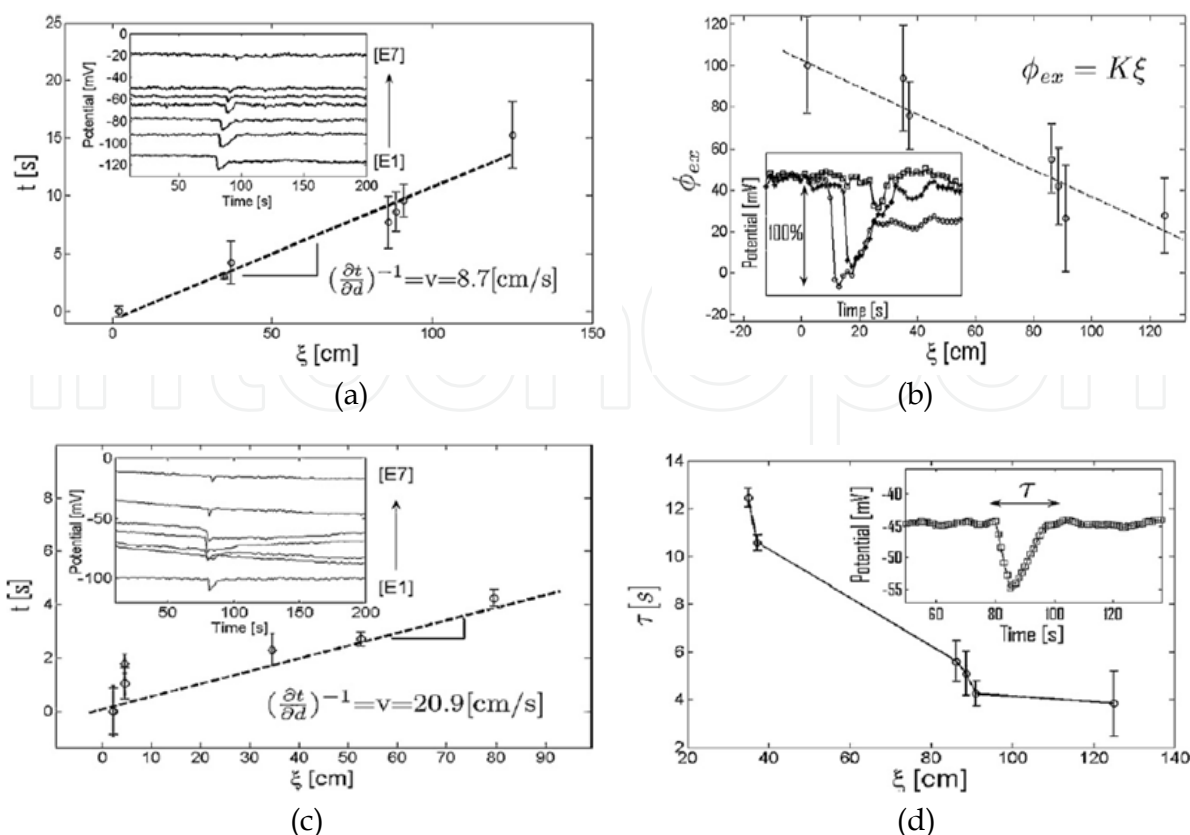


Fig. 14. *a*) Average EP speed of transmission along the trunk, as a result of tipping ($n = 5$ plants), t (s) = time at which the electrode detected the electric signal, ξ (cm) = distance of electrodes from the tipping point. Error bars represents ± 1 std. dev. *b*) Relative intensity of EP as a result of tipping ($n = 5$ plants). ϕ_{ex} = relative intensity of the signal (%), ξ (cm) = distance from the electrode to the tipping point. Error bars represents ± 1 std. dev. *c*) Average EP speed of transmission along the trunk after pruning, measured above and below the pruned branch ($n = 5$ plants), t (s) = time at which the electrode detected the electric signal, ξ (cm) = distance of electrodes from the pruning point. Error bars represents ± 1 std. dev. *d*) Recovery time of the pre-tipping EP potential ($n = 5$ plants), τ = recovery time signal, ξ (cm) = distance from the electrode to the tipping point. Error bars represents ± 1 std. dev (after Oyarce & Gurovich, 2011).

Bioelectrochemical signaling in green plants induced by photosensory systems have been reported by Volkov et al., (2004). The generation of electrophysiological responses induced by blue and red photosensory systems was observed in soybean plants. A phototropic response is a sequence of the following four processes: reception of a directional light signal, signal transduction, transformation of the signal into a physiological response, and the production of a directional growth response. It was found that the irradiation of soybean plants at 450 ± 50 , 670, and 730 nm induces APs with duration times and amplitudes of approximately 0.3 ms and 60 mV. Plants respond to light ranging from ultraviolet to far-red using specific photoreceptors and natural radiation simultaneously activates more than one photoreceptor in higher plants; these receptors initiate distinct signaling pathways leading to wavelength-specific light responses. Three types of plant photoreceptors that have been identified at the molecular level are phototropins, cryptochromes, and phytochromes respectively.

8. Plant electrophysiology modulated by neurotransmitters, neuroregulators and neurotoxins

Plants produce a wide range of phytochemicals that mediate cell functions and translate environmental cues for survival; many of these molecules are also found as neuro-regulatory molecules in animals, including humans. For example, the human neurotransmitter melatonin (N-acetyl-5-methoxytryptamine) is a common molecule associated with timing of circadian rhythms in many organisms, including higher plants. Its major concentrations are located within the phloem conducting vessels and it has been suggested that its action is centered in the electrochemical processes involved in plasmodesmata synaptic – like contacts. Plant synapse has been proposed, since actin cytoskeleton-based adhesive contacts between plant cells resemble the neuronal and immune synapses found in animals (Baluska et al., 2005). A comprehensive review of neurotransmitters in plants is provided by V. V. Roschina in the book *“Neurotransmitters in plant life”* (2001).

Whereas glutamate and glycine were shown to gate Ca^{+2} -permeable channels in plants, glutamate was reported to rapidly depolarize the plant cell plasma membrane in a process mediated by glutamate receptors (Baluška, 2010; Felle & Zimmermann, 2007); plant glutamate receptors have all the features of animal neuronal glutamate receptors, inducing plant APs (Stolarz et al., 2010). These publications strongly suggest that glutamate serves as a neurotransmitter-like in cell-to-cell communication in plants too. Whereas glutamate might represent a plant excitatory transmitter, gamma-aminobutyric acid (GABA) seems to act as an inhibitory transmitter in plants, as it does similarly in animal neurons. For instance, it is well documented that GABA is rapidly produced under diverse stress situations and also that GABA can be transported from cell-to-cell across plant tissues (Bouche et al., 2003).

Many fascinating questions in future research will define the role of neurotransmitters, neuroregulators and neurotoxins in the growth and development of plants. As newer technologies emerge, it will become possible to understand more about the role of neurological compounds in the inner workings of plant metabolism, plant environment interactions and plant electrophysiology. However, signaling molecules, by their nature, are short lived, unstable, difficult to detect and quantify, because they are highly reactive, and present in small concentrations within plant tissues.

9. Electrophysiological control of cyclical oscillations in plants.

Sanchez et al. (2011) reviewed the interaction between the circadian clock of higher plants to that of metabolic and physiological processes that coordinate growth and performance under a predictable, albeit changing environment. The circadian clock of plants and abiotic-stress tolerance appear to be firmly interconnected processes, by means of electrophysiological signaling (Volkov et al., 2011). Time oscillations (circadian clocks) in plant membrane transport, including model predictions, experimental validation, and physiological implications has been reported by Mancuso & Shabala (2006) and Shabala et al., (2008).

10. Conclusions

Plants have evolved sophisticated systems to sense environmental abiotic and biotic stimuli for adaptation and to produce signals to other cells for coordinated actions, synchronizing

their normal biological functions and their responses to the environment. The synchronization of internal functions based on external events is linked with the phenomenon of excitability in plant cells. The generation of electric gradients is a fundamental aspect of long-distance signal transduction, which is a major process to account for tree physiology. Outstanding similarities exist between AP in plants and animals and the knowledge about AP and VP/SWP mechanisms in plants, its physiological consequences and its technological applications is accumulating, but there is still a broad margin for questions and speculations to further elucidate the concepts described in this review; thus, an interesting challenge to understand the complex regulatory network of electric signaling and responses is still an open question. Future improvements in research methods and instruments will reveal more aspects of the signal complexity, and its physiological responses in plants.

Our future knowledge on the subject will help us considering electrical signals in plants as normal phenomena, to be used as a real – time communication mechanism between the plant physiologist and the plant, for example, for the early detection of plant stress, to enable proper and automatic modulation of the tree microenvironment, in order to optimize the agronomic performance of fruit bearing or wood producing trees. Also, highly modulated external electric impulses, to be applied on trees at specific intensities, durations and phenology timings, to modify water use efficiency or photosynthetic efficiency, could be developed from this knowledge.

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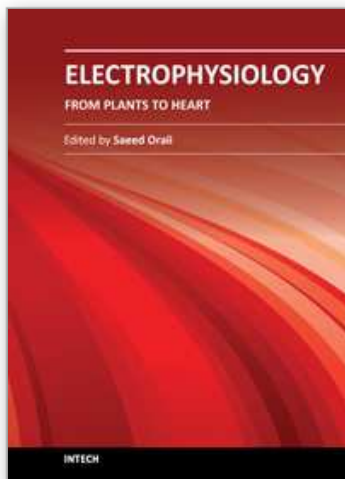
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The outstanding evolution of recording techniques paved the way for better understanding of electrophysiological phenomena within the human organs, including the cardiovascular, ophthalmologic and neural systems. In the field of cardiac electrophysiology, the development of more and more sophisticated recording and mapping techniques made it possible to elucidate the mechanism of various cardiac arrhythmias. This has even led to the evolution of techniques to ablate and cure most complex cardiac arrhythmias. Nevertheless, there is still a long way ahead and this book can be considered a valuable addition to the current knowledge in subjects related to bioelectricity from plants to the human heart.

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University Campus STeP Ri
Slavka Krautzeka 83/A
51000 Rijeka, Croatia
Phone: +385 (51) 770 447
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Unit 405, Office Block, Hotel Equatorial Shanghai
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中国上海市延安西路65号上海国际贵都大饭店办公楼405单元
Phone: +86-21-62489820
Fax: +86-21-62489821

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