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Evidence for the transmission of information through electric potentials in injured avocado trees

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ABSTRACT

Electrical excitability and signaling, frequently associated with rapid responses to environmental stimuli, have been documented in both animals and higher plants. The presence of electrical potentials (EPs), such as action potentials (APs) and variation potentials (VPs), in plant cells suggests that plants make use of ion channels to transmit information over long distances. The reason why plants have developed pathways for electrical signal transmission is most probably the necessity to respond rapidly, for example, to environmental stress factors.

We examined the nature and specific characteristics of the electrical response to wounding in the woody plant *Persea americana* (avocado). 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 was expressed in the form of variation potentials. For tipping and pruning, signal velocities of 8.7 and 20.9 cm/s, respectively, were calculated, based on data measured with Ag/AgCl microelectrodes inserted at different positions of the trunk. 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. Real time detection of remote EP signaling can provide an efficient tool for the early detection of insect attacks, strong wind damage or handling injury during fruit harvest.

Our results indicate that electrical signaling in avocado, resulting from microenvironment modifications, can be quantitatively related to the intensity and duration of the stimuli, as well as to the distance between the stimuli site and the location of EP detection. These results may be indicative of the existence of a specific kind of proto-nervous system in plants.

Introduction

Plant neurobiology is a newly developed discipline in the field of plant physiology, aimed at establishing the structure of information networks that exist within the plant, which are manifested as responses to environmental stimuli by means of electrochemical signals (Baluska et al., 2004; Brenner et al., 2006; Trewavas, 2005). These signals seem to complement other plant signals: hydraulic, mechanical and hormonal, already well documented in plant science (Fromm and Lautner, 2007; Gil et al., 2009). Conducted electrical events may serve for translation of environmental parameters and cues, obtained via sensory systems, into biological information and processes. In plants, most cells are electrically excitable and active, releasing and propagating action potentials (APs), which may affect such central physiological processes as photosynthesis and respiration (Masi et al., 2009). In the last decade, numerous papers have been published on the study of variation and action potentials in plants. However, only rarely have the researches focused on woody plants, although it is in such plants that the need for rapid and efficient signals other than chemicals (hormones) and hydraulic becomes more obvious (Fromm and Lautner, 2007; Gil et al., 2008; Gurovich and Hermosilla, 2009). These studies have associated the effect of water stress, irrigation, and light cycles with electrical signaling in fruit tree species including avocado, blueberry, lemon and olive. Changes in the electrical potential (EP) were detected between the base of the stem and leaf in response to drought, irrigation, and diurnal changes in light and dark. In avocado, the changes in EP between the base of the stem and leaf petiole observed in response to decreased soil water content have been associated with a decrease in stomatal conductance, indicating that stomatal closure might be associated with an electrical signal.

Abbreviations: ξ (cm), distance from injury site to electrode position in the tree; Ø ex, signal relative intensity; t (s), time of electric signal detection by each electrode; τ, recovery time of pre-injury signal intensity.

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Two types of electrical impulses have been reported in plant signaling: action potentials (APs) and variation potentials (VPs). An action potential is an electrical signal that spreads quickly among plant tissues and organs, traveling at a relative high speed and constant amplitude (Davies, 2004; Lautner et al., 2005; Trebacz et al., 2006; Fromm and Lautner, 2007), its duration is of the order of milliseconds and are generated by a stimulus that requires a specific threshold for its initiation (Volkov and Ranatunga, 2006, Brenner et al., 2006). An action potential is caused by the movement of ions across the plasma membrane, resulting from a change in its specific permeability to different ions, with transient variations of the cytosol and its external environmental and electrochemical potential (Gelli and Blumwald, 1997; Volkov, 2000; Volkov and Brown, 2006).

A variation potential consists of a transient change in membrane potential (depolarization and subsequent slow repolarization), where its high persistence over time represents its main difference from action potentials. A variation potential is characterized by a continuous reduction in its amplitude and velocity, which decreases with the distance from the site of occurrence of the stimulus. According to Dziubinska et al. (2003), action potentials occur with weak stimuli and variation potentials are due to strong stimuli.

An interesting report on the spatio-temporal dynamics of the electrical network activity in the root apex in maize has been published by Masi et al. (2009), elucidating the nature of EP in plants and defining the major differences between AP and VP measured in plants. In contrast to chemical signals such as hormones, electrical signals are able to transmit information quickly over long distances from one point to another within the plant (Fromm and Lautner, 2007; Gil et al., 2008, 2009; Oyarce and Gurovich, 2010). It is postulated that the action and variation potentials may be considered plant physiological properties, enabling information flow between plant tissues and organs, as an essential biological adaptation to generate specific reactions to modifications in the environment (Fromm and Fei, 1998; Volkov et al., 2008; Lautner et al., 2005; Gil et al., 2008; Gurovich and Hermosilla, 2009).

The existence of electric mechanisms for transmitting information between different organs of a fruit tree has been postulated (Datta and Palit, 2004; Volkov et al., 2009; Wang et al., 2009), allowing plants to express quick and accurate reactions to specific mechanical stimuli, such as a tipping or pruning. These reactions can be detected and monitored in real time and could serve as early indicators of conditions of biotic and abiotic stress.

The objective of this research was to characterize the extracellular electrical potential (EP) variations in avocado plants resulting from mechanical injury, such as tipping and pruning.

Materials and methods

Electrical potentials were monitored in 2-year-old avocado plants (*Persea Americana* Mills., cv. Hass) grafted onto Mexicola monoclonal rootstock. At the beginning the experiment, trees had a 7.0–9.0 cm diameter trunk and 3–5 branches, with 50–70 leaves; each tree was kept in a 25 L container filled with an inert sandy substrate.

Electrical potentials were monitored continuously with non-polarizable Ag/AgCl microelectrodes inserted into different positions along the trunk; microelectrode characteristics have been reported by Gurovich and Hermosilla (2009), Gil et al. (2009), Oyarce and Gurovich (2010), and consist on a 0.35 mm-diameter silver wire (99.99% Ag), chlorated in a solution of HCl 0.1 N 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 3 M solution; both needle ends are heat-sealed with polyethylene (Fig. 1).

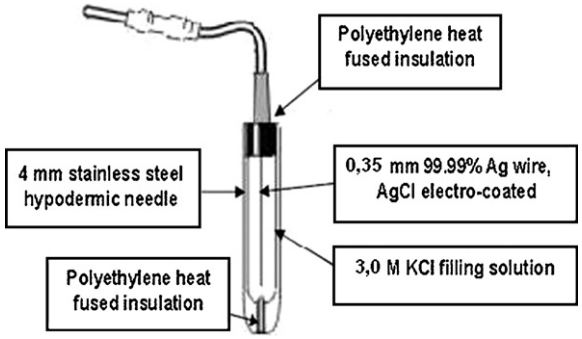

Fig. 1. Ag/AgCl microelectrode construction.

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.

EP real time measurements was implemented using a multivoltmeter (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 10^5 ms. Signals obtained were analyzed with the software ExceLINX-1, utility provided by Microsoft© Excel. EP measurements were made keeping the trees within a Faraday-type electromagnetic insulation cage, installed in the laboratory to control constant light and temperature conditions.

Treatment descriptions

For the tree tipping experiment, the distal apex of the tree (2 cm) was mechanically excised ($n = 5$ plants); 2 days before the topping, seven microelectrodes were inserted along the trunk, below the topping site (Fig. 2a).

For the tree pruning experiment, the branch closest to the soil was excised from the trunk by mechanical pruning ($n = 5$ plants); 2 days before the pruning three and four microelectrodes were inserted over and below the pruning site, respectively (Fig. 2b). Electrode positioning at each tree is detailed in Tables 1a and 1b, for the tipping and pruning experiments, respectively. After electrode insertion, EP was continuously monitored for a 4-day period, before the tipping or pruning events took place, in order to eliminate any

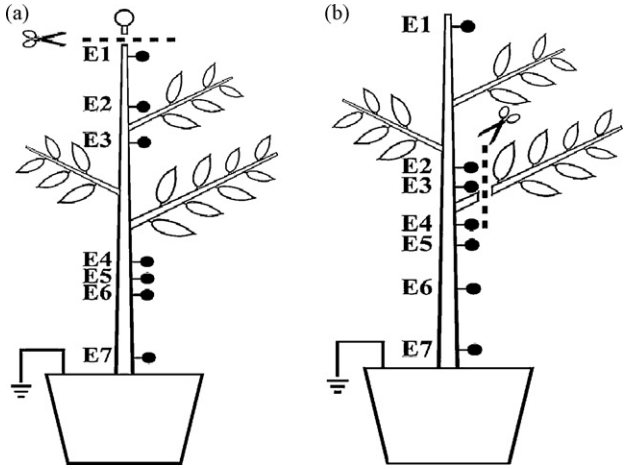

Fig. 2. (a) Electrode placement; tipping experiment. (b) Electrode placement; pruning experiment.

Table 1a
Microelectrode locations for the tipping experiment.

Distance between electrodes (cm)		Cumulative distance from tipping site (cm)	
Tipping–E1	2.0	Tipping–E1	2.0
E1–E2	32.2	Tipping–E2	34.2
E2–E3	2.1	Tipping–E3	36.2
E3–E4	44.0	Tipping–E4	80.2
E4–E5	2.0	Tipping–E5	82.2
E5–E6	2.0	Tipping–E6	84.2
E6–E7	31.6	Tipping–E7	115.8

Table 1b
Microelectrode locations for the pruning experiment.

Distance between electrodes (cm)		Cumulative distance from pruning site (cm)	
E1–E2	31.0	Pruning–E1	+35.2
E2–E3	2.1	Pruning–E2	+4.2
E3–Pruning	2.1	Pruning–E3	+2.1
Pruning–E4	2.1	Pruning–E4	−2.1
E4–E5	2.1	Pruning–E5	−4.2
E5–E6	44.0	Pruning–E6	−48.2
E6–E7	31.0	Pruning–E7	−79.2

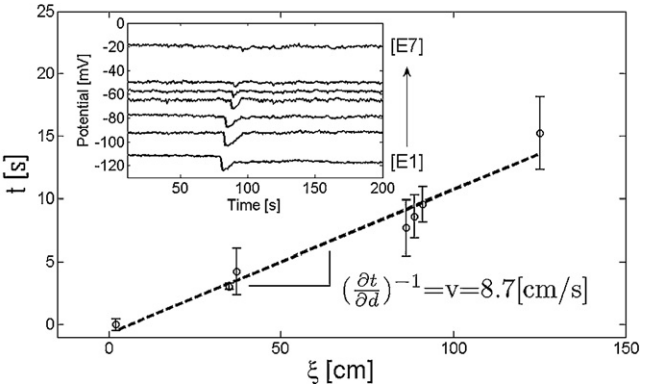

Fig. 3. Average EP speed of transmission along the trunk, as a result of tipping (n = 5 plants), t (s) = time at which the electrode detected the electric signal, ξ (cm) = distance of electrodes from the tipping point. Error bars represents +1 std. dev. (location of electrodes 1–7 is defined in Table 1a).

possible effect of electrode installation injuries on EP; these electrode insertion effects were detected only for an initial 60–70 min after the electrode insertion (data not shown).

Results

Tipping experiment

Tipping was performed 79 s after initiating the EP measurements, which were made at a constant 1 s interval, completing a total of 200 s (Fig. 3). EP signals detected correspond to a variation potential (VP), and transmission occurs from the stimulus point to the trunk base, and presumably even into the root, with an average linear velocity of 8.7 cm/s, so that there was a time lag in the reception of the signal along the trunk; the lag increased linearly as the distance from the electrode to the tipping point increased, indicating clearly that there was a physiological response of the plant resulting from a mechanical stimulus (Fig. 3). Variability in EP measurements between plant replicates accounted for less than ±3% of the mean values presented in Fig. 3. However, it is interesting to note that the variability in response time between different electrode locations was increased when the distance to the tipping point increased, possibly as a result of the differences in the amount of plant material at the vicinity of the respective electrode location (Table 2).

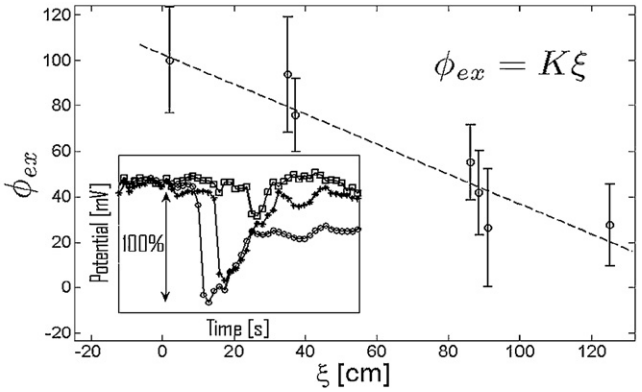

Fig. 4. Relative intensity of EP as a result of tipping (n = 5 plants). Ǿ ex = relative intensity of the signal (%), ξ (cm) = distance from the electrode to the tipping point. Error bars represents +1 std. dev.

EP intensity decreased with increasing distance between the tipping point and the electrode; the signal was virtually undetectable at 115.8 cm from the tipping point (Fig. 3). This linear intensity decrease (K = −0.68) can be visualized in Fig. 4, if data is restricted to 50 s and the signal intensity is expressed as a % of the maximal intensity measured in electrode 1 (the closest to the tipping point). Interestingly, the signal strength at electrode 7 was greater than that detected at electrode 6, possibly because its location corresponds to the rootstock (Mexicola) and not to the grafted cultivar (Hass). A similar observation was made for the pruning experiment (Fig. 7 below).

Recovery time to pre-tipping EP values was also affected by the distance and signal intensity from the tipping point to the specific electrode position (Fig. 5). Electrode 1 located 2 cm below the tipping point, failed to completely recover its pre-tipping EP after 200 s (Table 3), as a result of the high signal intensity at this point (11 mV), in comparison to the average EP signal intensity (5 and 7 mV) measured at electrodes E2–E7.

Tree tipping resulted in a decrease in EP, lasting just a few seconds, before a recovery period was initiated; this recovery time span was inversely proportional to the signal intensity detected at different locations along the trunk; after reaching a 100% recovery, EP increased slightly over the pre-tipping values.

Table 2
Tipping experiment. Signal detection time lag, minimum EP value and time span from detection until reaching the minimum EP value.

Electrode	Distance from tipping point (cm)	Signal detection after (s)	Minimum EP value (mV)	Time from EP signal detection to minimum value (s)
E1	2.0	0	11.00	5.0
E2	34.2	3.1	10.32	3.0
E3	36.2	3.3	7.64	3.0
E4	80.2	7.7	4.34	7.0
E5	82.2	8.5	3.70	2.0
E6	84.2	9.5	2.40	2.0
E7	115.8	15.2	1.25	1.0

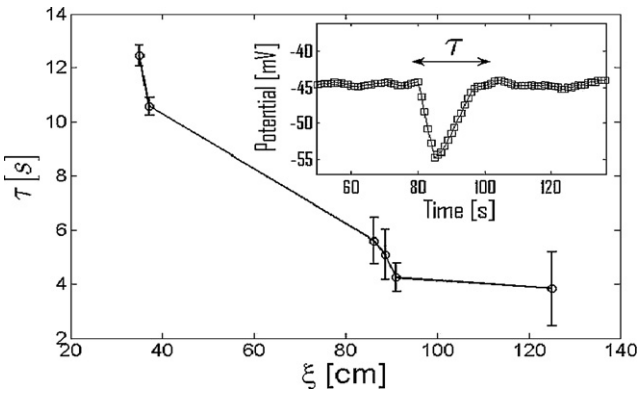

Fig. 5. Recovery time of the pre-tipping EP potential (n = 5 plants), τ = recovery time signal, ξ (cm) = distance from the electrode to the tipping point. Error bars represents +1 std. dev.

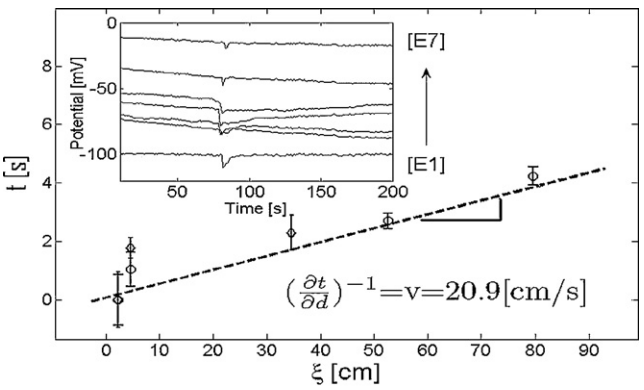

Fig. 6. Average EP speed of transmission along the trunk after pruning, measured above and below the pruned branch (n = 5 plants), t (s) = time at which the electrode detected the electric signal, ξ (cm) = distance of electrodes from the pruning point. Error bars represents +1 std. dev. (location of electrodes 1–7 is defined in Table 1b).

Pruning experiment

Pruning was performed 79 s after initiating the EP measurements, which were made at a constant 1 s interval, completing a total of 200 s (Fig. 6). The lowest tree branch was completely eliminated; this branch was the most developed, with the largest number of leaves.

EP signals corresponded to a variation potential (VP) and were transmitted along the tree trunk both above and below the pruned branch site (Fig. 6). Variability in EP measurements between plant replicates accounted for less than ±4% of the mean values presented in Fig. 6. Time response to the stimulus was detected sequentially, both upwards from electrode 3 to electrode 1 as well as downwards, from electrode 4 to electrode 7, with a linear average velocity of 20.9 cm/s; no differences in signal velocity transmission in both directions were detected (Table 4).

Signal reception time lag from one electrode to the next increased linearly, as the distance from the pruning point to the specific electrode increased, clearly indication that this was a physiological response of the plant, resulting from a mechanical stimulus. Also, it is interesting to note that the variability in response time between different electrode locations was increased when the distance to the pruning point increased, possibly as a result of the differences in the amount of plant material that was affected by the electric signal at the vicinity of the respective electrode location.

If data presented in Fig. 6 is restricted to 50 s and the signal intensity is expressed as a % of the maximal intensity measured in electrodes 3 and 4 (the closest above and below to the pruning site, respectively), it can be observed (Fig. 7) that the loss in signal intensity was related to the direction of transmission, with a lower transmission rate in the upward direction, possibly as a result of the differences in the amount of plant material at the vicinity of the respective electrode location. Interestingly, the signal strength at electrode 7 was greater than that detected at electrode 6, possibly because its location corresponded to the rootstock (Mexicola) and not to the grafted cultivar (Hass). A similar observation was made for the tipping experiment, as presented in Fig. 4. Recovery time to pre-pruning EP values was also affected both by the distance and by the signal intensity from the pruning point to the specific electrode position (Fig. 8).

Electrodes 4 and 5 (Fig. 2b and Table 3) showed a recovery time of 51 and 49 s, respectively; however, its maximal EP was only 70.2

Table 3
Percentage of recovery of EP as related to pre-tipping EP..

Cumulative distance from tipping point (cm)	Relative recovery (%) of EP signal after the tipping, related to pre-tipping EP													
	(s)													
	0	1	2	3	4	5	6	7	8	9	10	11	12	13
2.0	0.0	0.0	0.0	0.0	0.0	0.0	1.5	2.9	3.3	8.8	14.0	14.2	15.6	17.1
34.2	0.0	0.0	0.0	0.0	4.3	13.8	27.9	36.3	51.9	62.9	73.5	84.6	92.3	104.0
36.2	0.0	0.0	0.0	0.0	5.8	12.8	27.3	35.3	63.3	76.3	89.2	102.0		
80.2	0.0	0.0	0.0	19.8	41.1	61.5	83.9	103.0						
82.2	0.0	0.0	0.0	32.5	51.3	66.1	89.0	102.0						
115.8	0.0	0.0	0.0	50.0	87.5	100.0	104.0							
117.8	0.0	0.0	101.0											

Table 4
Pruning experiment. Signal detection time lag, minimum EP value and time span from detection until reaching the minimum EP value.

Electrode	Distance from tipping point (cm)	Signal detection after (s)	Minimum EP value (mV)	Time from EP signal detection to minimum value (s)
E1	+35.2	2.7	4.61	2.0
E2	+4.2	1.7	6.44	2.0
E3	+2.1	0	9.25	1.0
E4	−2.1	0	13.40	1.0
E5	−4.2	1.3	7.00	2.0
E6	−48.2	2.7	3.57	2.0
E7	−79.2	4.6	3.88	2.0

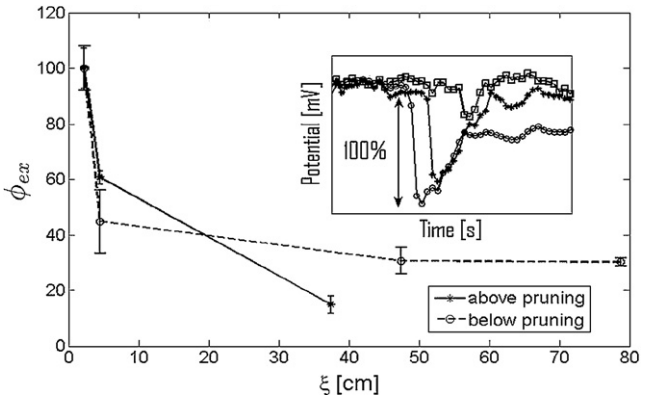

Fig. 7. Relative EP intensity as a result of pruning ($n = 5$ plants). Ø ex = relative intensity of the signal (%), ξ (cm) = distance from the electrode to the pruning site. Error bars represents +1 std. dev.

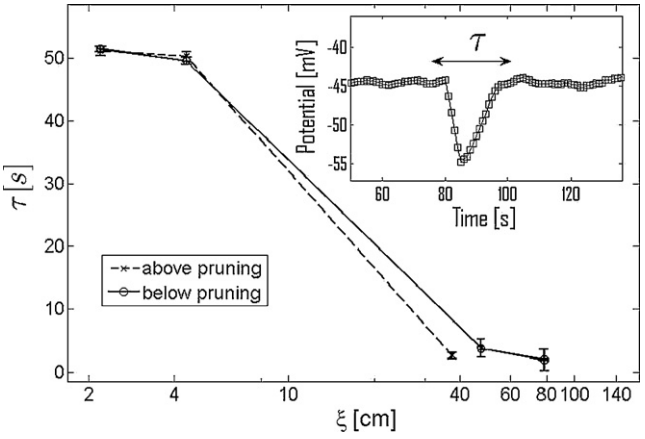

Fig. 8. Recovery time of the pre-pruning EP potential ($n = 5$ plants), τ = recovery time signal, ξ (cm) = distance from the electrode to the tipping point (log scale). Error bars represents +1 std. dev.

and 82.3% of the pre-pruning EP values, respectively. After 51 s, EP tended to decrease again, and this tendency was maintained throughout the rest of the experiment (200 s after pruning). Recovery time for electrodes 1 and 7, located at greater distances from the pruning site, where the EP signal detected was only 4.61 and 3.88 mV respectively, was reached after 5 s. During the experiment, EP measured by any electrode did not recovered its pre-pruning EP value, regardless of position or EP intensity reduction due to the pruning event (Table 5).

Discussion

A significant EP signal, corresponding to a variation potential, was generated as a response of tipping or pruning in avocado plants; the signal was transmitted along the tree trunk at a specific velocity, which is dependent on the distance to the mechanical injury. The EP signal intensity also decreases with distance between the mechanical injury site to the electrode position in the trunk. Several physiological explanations for this behavior have been proposed by Trewavas and Malhó (1997), Zimmermann et al. (1997), Stankovic et al. (1998), Volkov and 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.

Active proton–ATPase pumps (also called *primary active transport* mechanisms), have been proposed as not only the source of EP signals in plants (Bonza et al., 2001), but also channel opening (*passive transport*) (Martinoina et al., 2000; Morillon et al., 2001) and ion carriers (*secondary active transport*) (Maathius et al., 1997), both located in the plasmatic membrane, have been mentioned, considering that ion channel opening and closing enable an ion flux between the cytosol and the extracellular microenvironment, which creates EP differentials across the membrane (Gelli and Blumwald, 1997; Demidchik et al., 2006). Variations in Ca^{2+} concentrations in the cytosol modify the catalytic activity of the enzyme calmonduline (Vian et al., 1996; Leon et al., 2001) as well as the activity of different protein kinases (CDPKs) dependent on Ca^{2+} (White and Broadley, 2003; Ludwing et al., 2004; Medvedev, 2005).

According to several authors, EP signal transmission from the injury site is dependent not only on the stimuli intensity, but also on its specific characteristics. Malone et al. (1994) and Stankovic et al. (1998) reported signal transmission rates of 10 cm/s and 7–10 cm/s for heat-shock injury, respectively. Fromm and Bauer (1994) published data on EP signal transmission measurements for cold-shock injury in the range of 3–7 cm/s, while Stankovic et al. (1998) measured EP signals caused by direct flame injury to leaves, in the range of 40–50 cm/min. Stankovic et al. (1998) also experimented with sudden modifications of light/dark incidence in the canopy, reporting EP signal transmission rates of 8–14 and 30–40 cm/min, respectively. In our experiments, EP signal transmission rates in the tipping and pruning were 8.7 cm/s (Fig. 2) and 20.9 cm/s (Fig. 5), respectively.

Results presented in this paper support work reported by Mancuso (1999), who induced EP signals in *Vitis vinifera*, by burning small areas of the leaf, concluding that action and variation potentials differ both in their mechanism of propagation and electrogenic nature; action potentials are genuine self-propagating electrical signals traveling at a velocity of about 10 cm/s, with a metabolic nature involving active components (electrogenic pumps). On the

Table 5
Percentage of EP recovery as related to pre-pruning EP.

Cumulative distance from tipping point (cm)	Relative recovery (%) of EP signal after the pruning																
	After pruning (s)																
	0	1	2	3	4	5	6	7	8	45	46	47	48	49	50	51	52
35.2	0	0	0	50.1	78.0	98.6	97.7										
4.2	0	0	0	6.2	29.2	43.2	48.1	51.4	60.9	82.9	84.6	87.6	88.7	91.5	89.5		
2.1	0	0	4.1	5.6	7.3	10.3	12.5	15.6	22.5	60.4	62.9	63.2	64.4	67.0	68.7	70.2	67.9
−2.1	0	0	7.9	15.6	20.0	21.9	25.7	29.9	38.0	74.5	75.8	76.8	78.4	80.7	81.4	82.3	80.4
−4.2	0	0	0	5.3	20.1	35.4	43.1	51.4	60.0	78.5	83.6	87.4	89.9	92.6	89.8		
−48.2	0	0	0	57.0	69.3	92.4	96.4										
−79.2	0	0	0	84.5	91.3	97.3	95.7										

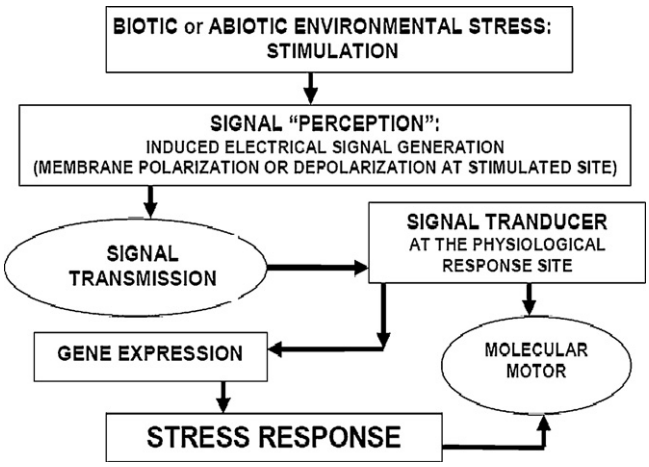

Fig. 9. Proposed mechanism of electric potential signals in plants (adapted from Volkov and Ranatunga, 2006 and Gibert et al., 2006).

other hand, variation potentials represent a local response to the passage of a hydraulic wave, support the hypothesis that both ion channels and pumps are involved in variation potential depolarization.

A preferential phloematic pathway for EP signal transmission has been postulated by Davies (2004) and Lautner et al. (2005), considering that the phloem tissue is characterized by a continuity of cell plasmatic membranes, through its relatively large sieve plate perforations, its lack of vacuoles and the reduced number in lateral plasmodesmata connecting accompanying cells and surrounding parenchyma (Volkov, 2000; Fromm and Lautner, 2007). EP signals are also transmitted to several plant organs, like roots, branches and shoots (Gurovich and Hermosilla, 2009), as well as to the leaf petiole (Gil et al., 2009) and leaf lamina (Dziubinska et al., 2001), but at a considerable slower rate and intensity, indicating further evidence for the phloematic role of signal transmission.

Our results indicate that electrical signaling in avocado, similar to observations for other woody plants, reported by Gurovich and Hermosilla (2009) and Gil et al. (2009), resulting from microenvironment modifications, can be quantitatively related to the intensity and duration of the stimuli, as well as to the distance between the stimuli site and the EP detection location; these results can be indicative of a specific kind of proto-nervous system in plants, similar to the conceptual model (Fig. 9) proposed by Volkov and Ranatunga (2006) and Gibert et al. (2006) to account for EP signal detection and transmission in plants.

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