



Action and variation potential electrical signals in higher plants

Ndung'u Ruth Wairimu¹, Kamweru Paul Kuria^{2*}, Kirwa Abraham Tuwei³

¹Physical Sciences Department, Chuka University, Chuka, Kenya. E-mail: ruthwairimu237@gmail.com

²Physical Sciences Department, Chuka University, Chuka, Kenya. E-mail: pkkamweru@chuka.ac.ke

³Basic Sciences, Tharaka University College, Kenya (Posthumous). E-mail: abraham.tuwei@tharaka.ac.ke

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Abstract

This review evaluates the types of electrical signals (ESs) in plants, generation and propagation of various ESs, their ways of transmission within the plant body and their corresponding physiological significance. It also outlines abiotic factors, e.g., light, temperature, water content as stimuli on the electrical potential (EP) of the plants. The paper also summarizes a review of the effects of ESs on photosynthesis, the mechanisms of the effects, and its physiological role in plants. Local irritations of plants induce various photosynthetic responses including fast and long-term inactivation of photosynthesis and its activation. The paper also reviews the concept of plant energy harvesting. The measurement techniques used for ESs in plants including extracellular measurement and intracellular measurement are also reviewed. A brief summary of the applications of these methods for investigating ES in plants is also given.

Keywords: *Electrical signals (ESs), Electrical potential, Plant energy harvesting*

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1. Introduction

Electrical signal (ES) is the most important physical signal in the organisms and is capable of transmitting signals more quickly over long distances when compared with chemical signals (Yan et al., 2009). Studies show that ESs are important for many physiological activities, such as photosynthesis, and are induced by external stimuli, e.g., temperature (Rhodes et al., 1996; Pyatygin et al., 2008 and Volkov et al., 2007), light (Datta and Palit, 2004; and Gurovich and Hermosilla, 2009), osmotic pressure (Zawadzki et al., 1991), Salinity (Gil et al., 2014), water content (Gil et al., 2007; 2008a and b and 2009) hormones (Brault et al., 2004) or wounding (Schaller and Oecking, 1999). ESs are useful in some carnivorous plants (Hedrich and Neher, 2018) via mechanosensitive activation (Awan et al., 2019) that acts through prey-induced action potentials (APs) (Böhm et al., 2016). These different environmental stimuli evoke specific responses in living cells that are capable of transmitting an ES to the responding region.

For example, a study (Koryzma-Zepp et al., 2014) to test the effects of salinity stress on electrical potentials (EP) in tangor citrus trees and to determine EP responses to salinity showed that there are detectable EP changes in response to salinity stress that are highly correlated with stem water potential. Another study to determine effects of short- and long-term drought on root to leaf electrical signaling in avocado confirmed that

* Corresponding author: Kamweru Paul Kuria, Physical Sciences Department, Chuka University, Chuka, Kenya.
E-mail: pkkamweru@chuka.ac.ke

in both situations significant changes in EP differences can be detected an extra-cellular ES and appears to be involved in root to leaf communication initiating stomatal closure (Gil *et al.*, 2009). Data obtained in other studies (Gil *et al.*, 2007; 2008a; 2011 and 2014; Fromm and Eschrich., 1993; Fromm and Fei., 1998; Fromm, 2016; Lautner *et al.*, 2005; Malone, 1996, and Oyarce and Gurovich, 2010) confirm the existence of specific daily variation of the EP in tree trunks as well as a rapid modification of EP when light intensity or soil water availability are modified. In avocado, the changes in EP between the base of the stem and leaf petiole observed in response to decreased soil water have been associated with a decrease in stomatal conductance indicating that stomatal closure might be associated with an ES (Gil *et al.*, 2007). Studies done on *Helianthus annuus* showed that osmotic stress suddenly applied on roots generated EP differences between roots and leaves, which were accompanied by decrease in stomatal conductance (Zawadzki *et al.*, 1991). More studies (Fromm and Lautner, 2007; Oyarce and Gurovich, 2010 and Gurovich and Hermosilla, 2009) have associated the effect of water stress, irrigation and light cycles with electrical signaling in plants.

All these studies and many more proves that real time plant electrical response measurements can anticipate actions, and this could be used to prevent the plant reaching actual stress conditions, optimizing stomata gas exchange and photosynthetic rates. This would be much useful in automation of agriculture, for example in scheduling irrigation (Ríos-Rojas *et al.*, 2015 and Zimmermann *et al.*, 2013).

For several decades, much about electric signals in plants has been investigated. There is a plethora of uncoordinated information in literature. The aim of this review paper is to communicate comprehensively the current knowledge of EP in plants, how these EP relates with photosynthesis and the EP measurements methods available and utilized. To begin with the paper has evaluated the types of ESs in plants, generation and propagation of various ESs, their ways of transmission within the plant body and their corresponding physiological significance. It also describes the impact on environmental factors (e.g. light, temperature, water content) on the EP of the plants. It summarizes works concerning the effects of ESs on photosynthesis, the mechanisms of the effects, and its physiological role in plants. Local irritations of plants induce various photosynthetic responses including fast and long-term inactivation of photosynthesis and its activation. It also reviews the concept of plant energy harvesting in several ways. The measurement techniques used for ESs in plants including extracellular measurement and intracellular measurement are also reviewed. A brief summary of the applications of these methods for investigating ES in plants is also given.

2. EP Signals in Plants

ESs in plants cells have been studied in various plants (see Table 1), and can be categorized as Action Potential (AP) and variation potential (VP). The two potentials has some relationships but also distinguishing characteristics as many studies have shown (Dziubinska *et al.*, 2001; Dziubinska *et al.*, 2003; and Stanković *et al.*, 1996 and 1998). The two types of ESs have been reported in plants as transient propagating depolarization using vascular bundles to cover within-plant distances (Gil *et al.*, 2014). APs are rapid propagating electrical pulses travelling through phloem cell membranes at a constant velocity and maintaining constant amplitude (Davies, 2006; and Fromm, 2007). Intriguingly, studies have shown recently that ESs between plants (interplants in comparison to intra-plant) exist either above ground or above ground. For example, studies have shown that there exists an ultrafast underground ES transmission between neighboring plants between roots through the soil (Volkov and Shtessel, 2016; Volkov and Shtessel, 2017; Volkov and Shtessel, 2018 and Volkov *et al.*, 2019). The focus of this article would be in ES within a plant.

AP in plants is a short-term electrical reaction (decrease of an electric potential difference) and repolarization (recovery of the potential difference) of plasma membrane (Davies and Stankovic, 2006; Trebacz *et al.*, 2006 and Beilby, 2007). AP generation has all non-or-none character, i.e., stimuli weaker than a certain threshold stimuli trigger the signal with constant amplitude (Trebacz *et al.*, 2006); in particular it is induced by electric currents (Krol *et al.*, 2006; Bulychev and Krupenina 2010 and Sevriukova *et al.*, 2014), cooling (Fromm and Bauer, 1994; Opritov *et al.*, 2004 and Krol *et al.*, 2006), touch (Sibaoka, 1991; Shepherd *et al.*, 2008; Degli Agosti, 2014) some chemical agents (Felle and Zimmermann, 2007) and changes in light regime (Trebacz and Sievers, 1998 and Pikulenko and Bulychev, 2005). AP is connected with changes in ion concentrations (Wacke *et al.*, 2003; Trebacz *et al.*, 2006; Felle and Zimmermann, 2007 and Sukhov and Vodeneev, 2009) including increased H⁺ and Ca²⁺ concentrations in the cytoplasm and their decreased concentrations in apoplasts. AP is a self-propagating ES (Trebacz *et al.*, 2006; Krol *et al.*, 2010 and Sukhov *et al.*, 2011). In algae and mosses, AP propagates through homogeneous symplast of body cells (Trebacz *et al.*, 2006); in higher plants, the process is connected with symplast of sieve elements (Fromm and Lautner, 2007; Zhao *et al.*, 2015) and on symplast of parenchyma cells (Opritov *et al.*, 1991 and Sukhov *et al.*, 2011) in vascular bundles.

VPs are long- range pulses (Davies, 2004 and Stahlberg, 2006) that vary with the intensity of the stimulus, with amplitude and speed decreasing as distance from the generation site increases (Davies, 2004, 2006; and Stahlberg, 2006). VP is a unique ES in higher plants (Stahlberg, 2006 and Vodeneev et al., 2015), in that it is a long-term (minutes to tens of minutes) electrical reaction with an irregular shape that includes long-term depolarization (long-term decrease in the electric potential difference on plasma membrane) and, in many cases, 'AP-like' spikes (Vodeneev et al., 2015). VP is induced by local damages (Stahlberg, 2006 and Vodeneev et al., 2015), including local burning, crushing and picking. VP is able to pass through inactive or dead tissues.

Currently VP is considered a local electrical response that is induced by propagation of a hydraulic signal (Stankovic et al., 1997; Mancuso, 1999; Pyatygin et al., 1999; Vodeneev et al., 2012; Stahlberg, 2006), chemical signal (Vodeneev et al., 2015), or a combined signal (Malone, 1994; and Vodeneev et al., 2012).

Table 1: Categorization of electric signals. Action and variation potentials as measured under different stimuli in different plants

Type	Plant measured	Stimuli	Physiological response	Findings	Reference
AP	<i>Dionaea muscipula</i> (Venus flytrap)	Mechanical	Trap closure	Use APs with specialized leaf traps to trap insects in order to secure nitrogen supply	Williams and Pickard 1972 Hedrich et al., 2016
	<i>Mimosa</i> (Sensitive Plant)	Chilling	Regulation of leaf movement	Regulation of leaf movement by electrical signals	Fromm and Eschrich 1988 Sibaoka 1966, 1969
	<i>Hibiscus</i> (Rose-mallow)	Pollination	Transient increase in ovarian respiration rate	Self-pollination as well as cross pollination induce a series of APs causing transient increase in the ovarian respiration rate	Fromm et al., 1995 Fromm et al., 2007
	<i>Zea Mays L.</i> (maize)	Chilling	Reduction in phloem transport Increase in gas exchange	APs triggered by cold shock of leaf tips cause reduction in phloem transport	Fromm and Bauer, 1994 Fromm et al., 2007
	<i>Zea Mays L.</i> (Maize)	Re-watering	Decrease of elongation growth of the stem	APs generated by re-watering plants in drying soil cause increases in the CO ₂ and H ₂ O gas exchange of the leaves	Fromm et al., 2018
	<i>Luffa aegyptiaca</i> (Vegetable sponge gourd)	Electrical/ cooling	Increase in response	Elongation growth of the stem decreases after the generation of a single AP	Shiina and Tazawa, 1986 Fromm et al., 2007
	<i>Conocephalum conicum</i> (Common Mushroom)	Electrical	Trap closure	Rate of respiration rise in relation to the AP depends on the character of excitation and the area of the thallus covered by it.	Dziubinska et al., 1989, Fromm et al., 2007
	<i>Drosera</i> (sundew)	Mechanical	Release of digestive enzymes	Tentacle movement of wrap around the insect by use of AP	Williams and Pickard., 1972

Table 1 (Cont.)					
Type	Plant measured	Stimuli	Physiological response	Findings	Reference
					Fromm et al., 2007
	<i>Salix Viminalis</i> L.(Willow)	Chilling	Effect on gas exchange	Effect on gas exchange. Rapidly evoked and propagated electrical signals are the route whereby stimulations are transmitted.	Fromm and Eschrich et al., 1993 Fromm et al., 2006
	<i>Cucurbita Pepo</i> (Pumpkin)	Chilling	Decrease in elongation growth of the stem	Decrease in elongation growth of the stem	Retivin et al., 1997 Cheng et al., 2009
	<i>Persea Americana Mill</i> (Avocado)	Water stress	Stomatal conductance changes	Stomatal closure associated with electrical signal that travels through the phloem correlated to soil moisture content	Gil et al., 2008b
	<i>Glycine max (L.) Merrill</i> (Soybean)	Heating	Induction of fast action potential	Plants transmit solitary waves and that the speed of AP in green plants is similar to speed of AP in mammalian.	Lang et al., 2008
	<i>Terminalia citrina</i> (Haleela Zard)	Enzyme activation	Extract exhibit significant genotoxicity and cytotoxicity	<i>Terminalia citrina</i> fruits are not safe in human	Akhtar et al., 2016
	<i>V. faba</i> and <i>H. vulgare</i> <i>S. littoralis</i>	Herbivory	Extracellular depolarization (or intracellular hyperpolarization) events were systematically detected	Herbivore feeding provokes various types of eIRs	Zimmermann et al., 2016
	<i>Helianthus annuus</i> Common sunflower	Osmotic and salt stress	Osmotically active solutions and salts affect membrane transport	Ions are important components of the cytoplasm and vacuole of living cells; therefore their content in environment as well as sensing and acquisition essential for their survival	Stolarz and Dziubinska, 2017b
	Mutant micro-tomato – cultivar Micro-Tom (MT) wild-type (MTwt),	Re-irrigation	Relationship between hydraulic, chemical and electrical signals	Action potentials is related to the degree of plasma membrane depolarization during water deficit Post re-irrigation stimulation induces the propagation of action	da Silva et al., 2020

Table 1 (Cont.)					
Type	Plant measured	Stimuli	Physiological response	Findings	Reference
	– isogenic mutant MTnotabilis (MTnot) and – transgenic MTsp12::NCED (MTNCED)			potentials in MTwt plants and ABA MTnot and MTNCED mutants. Action potentials promote increases in photosynthetic rate, stomatal conductance and transpiratory rate. The action potentials may also induce photosynthesis inactivation by adjusting stromal pH	
VP	<i>Lycopersicon esculentum</i> Mill (Tomato)	Electrical	Induction of <i>pin 2</i> gene expression	Propagated electrical signal generated electrical stimulus is effective in elevating <i>pin2</i> mRNA levels in distant tissues	Stankoviæ and Davies, E.(1996) Fromm et al., 2007
	<i>Lycopersicon esculentum</i> Mill (Tomato)	Wounding	Induction of <i>pin 2</i> gene expression	Regulation of the proteinase inhibitor gene (<i>pin 2</i>) expression which responds to wounding by induction of proteinase inhibitor activity in distant parts of the plant	Wildon et al., 1992) Davies and Stankovic 2006
		Electrical stimulus	SAPs propagate through the stem, including petioles and roots	APs generated by electrical stimulation propagate acropetally and basipetally along the stem, including petioles	Stankovic et al., 1997 Macedo et al., 2015
	<i>Pisum sativa</i> (garden pea)	Wounding	Inhibition of protein synthesis formation of polymes	Inhibition of protein synthesis, formation of polysomes (wounding)	Filek and Koscielniak 1997
	<i>Vicia faba</i> L. (horse bean)	Heating	Increase in respiration	Increase in respiration concomitant with the transmission of electrical signals	Koziolok et al., 2004
	Mimosa, populus	Heating	Transient reduction of photosynthesis	Flaming of a leaf pinna evokes a VP that travels rapidly into neighboring pinna to eliminate the net CO ₂ uptake rate and reduce the quantum yield of electron transport through photosystem	Fromm and Lautner, 2007
	<i>Helianthus annuus</i> L. (Sunflower)	Heating	Decrease in elongation growth of the stem	Heating evokes a typical VP that causes decrease the elongation growth of the stem	Stankovic et al., 1998 Fromm et al., 2007
		Osmotic and salt stresses	Affect membrane transport and thus evoke propagated electrical signals	Ions are important components of the cytoplasm and vacuole of living cells; therefore their content in environment as well as sensing and acquisition by plants is essential for survival	Stolarz and Dziubinska, 2017a

Table 1 (Cont.)					
Type	Plant measured	Stimuli	Physiological response	Findings	Reference
	<i>Helianthus annuus L.</i> (Sunflower)	Different light conditions	More SAPs transmitted basipetally than acropetally	Action Potentials play a role in plant adaptation to light conditions There is an ultradian rhythm of SAPs beside ultradian circumnutation rhythm.	Stolarz and Dziubinska, 2017b
	<i>Mimosa Pudica</i> (Aloe Vera)	Heating	Transient reduction in photosynthesis	Electrical signaling preceded the photosynthetic changes.Heating caused transient reduction in photosynthesis.	Koziolek et al., 2004
	<i>Vitis Vinifera</i> (Grapevines)	Irrigation and water content	Reduced ion transport	Multivariate statistical procedures such as principal component analysis (PCA) and partial least squares (PLS) with the orthogonal signal correction have the potential for quantifying soil moisture content indirectly from EP and EP measurements in stems of woody perennial fruit crops	Gil et al., 2014
	<i>Nicotiana tabacum L.</i> (Tobacco)	Local burning	Stomata closure, reduction in the rate of transpiration and CO ₂ assimilation	Fast electrical signal propagating through the tobacco plant after local burning induces short-term systemic photosynthetic responses	Hlavácková et al., 2006
	Pea leaves	Heating	Increase in ATP content in leaves	VP-induced inactivation of photosynthesis and activation of respiration increases ATP content in leaves	Surova et al., 2016
	<i>Nitelloopsis obtusa</i> (N.A.Desvaux)	Electrophysiological methods and complex multiparametrical	Multiple electrical signals of plant cells as biomarkers of the effects of chemical compounds	Plenty of chemicals and physical parameters can influence all ion transport systems involved in electrical signaling in plants	Kisnieriene et al., 2018
	Tomato	Electro stimulation	Amplitude of electrical responses increases with decreasing distance between Pt-electrodes in soil	Additional signaling pathway of electronic potentials propagation between roots of neighboring plants through soil	Volkov et al., 2018
	Aloe Vera	Electro stimulation	Electotonic potentials induced	Extracellular and intercellular communication in the form of electrical signals within plants and for direct interactions with actuators in plants	Volkov et al., 2017
	<i>Pisum sativum L.</i> (Pea seedlings)	Burning	Stimulation of non-photochemical loss of energy in photosystem II	Variation potential gradually increased the flow of light energy absorbed, trapped and dissipated by photosystem II	Sukhov et al., 2017

It has been postulated that AP and VP each serve as communication pathways between roots and leaves in response to certain biotic stresses such as water deficits, light intensity, osmotic pressure, temperature mechanical stimulation and salinity (Fromm and Fei, 1998 and Fromm and Lautner, 2007). In response to changes in these environmental variables, ESs are often generated at the site of stimulation and can travel rather quickly to adjacent cells (Volkov, 2000 and Volkov et al., 2004). These EP differences are often followed by changes in stomatal behavior, photosynthesis and/or respiration (Fromm and Eschrich, 1993; Mishra et al., 2001). For example, osmotic stress suddenly applied to *Helianthus annuus* roots generated EP differences between roots and leaves, which were accompanied decrease in stomatal conductance (Zawadzki et al., 1991). AP may serve as general stress signals, but provide little information about the type of stress that caused them (Zimmermann et al., 2009) while VP are likely generated as result of xylem pressure changes due to different external stimuli such as changes in plant water uptake (Stankovic et al., 1998) and transmit information about local stimuli to distant cells, promoting physiological responses (Brenner et al., 2006). VP changes in Avocado (*Persea Americana*) trees were associated with plant water deficits and subsequent stomatal closure due to withholding irrigation water from the plotting medium (Gil et al., 2008a, 2008b)

ES is transmitted via plasmodesmata to all other symplasmic cells after it has been generated (van Bel and Ehlers, 2018). Evidence of electrical coupling of cells was demonstrated by Spanswick and Conterton in 1967. If the information has to be transmitted to distant parts of the plant, electrical signaling via phloem appears to be used. The phloem can be considered as 'green cable' that allows transmission of APs induced by stimuli such as wounding and cold (Hedrich et al., 2016). The phloem extends continuously throughout the entire plant, and sieve elements may be considered low resistance pathways for AP transmission (Fromm and Lautner, 2007).

The lower degree of electrical coupling in lateral direction caused by only few plasmodesmata at the interface between companion cells (CC) and phloem parenchyma cells (PAs) also facilitates long-distance signaling (Kempers et al., 1998 and van Bell and Ehlers, 2018). However, the plasmodesmata may open up and following stimulation may make way for APs to propagate laterally from neighboring cells into the SEs/CCs. The transmission of ES along sieve tubes is achieved by ion channels in their plasma membranes and some channels have been identified, mainly K⁺ channels (Ache et al., 2001 and Fromm and Eschrich, 1988).

The large propagating depolarization of VPs is generated by a rapid loss of tension in the Xylem vessels after wounding. This hydraulic wave is transduced into local changes in ion flux through mechanosensory channels in the adjacent living cells (Stankovic et al., 1998 and Davies and Stankovic, 2006). The VP after being generated can move laterally, via plasmodesmata, into sieve elements where it can be transmitted over long distances. Some wounding substances, alternatively, can also be transported in the xylem via hydraulic shift and can evoke a VP via ligand-activated channel (Fromm and Lautner, 2007).

In summary, the transmission of ESs within the plant depends on the electrical conductance of plasmodesmata in lateral direction and on the high degree of electrical coupling via the sieve pores in longitudinal direction.

3. Electrical Potential and Photosynthesis

ESs, including AP, VP, and system potential, probably causes the photosynthetic responses in intact leaves via pathways that still requires more investigation. A possibility of such pathways might be associated with ES-connected acidification of chloroplast stroma inducing ferredoxin-NADP⁺ reductase accumulation at the thylakoids in Tic62 and TROL complexes (Sukhov, 2016).

Photosynthesis is the transformation of light energy into chemical energy, and it is the basis of the life of green plants. Regulation of photosynthesis under different environmental conditions is a fundamental activity for plants (Sukhov, 2016). Regulation of photosynthesis is especially important under stress conditions e.g. very intense light, high and low temperatures and drought (Zhang and Sharkey, 2009).

Stress- induced photosynthetic changes may participate in defense responses on a whole-cell level (Pfannschmidt et al., 2001). The local action of stressors (e.g., high temperature, mechanical wounding, shifts in water regime and electric current) can change photosynthetic processes in intact parts of the plant (Herde et al., 1995, 1999). Inactivation of photosynthesis and its activation have been observed after local irritations in

different combinations of photosynthetic responses (Fromm and Fei, 1998 and Grams et al., 2007). Various local irritations induce different photosynthetic responses in intact parts of plants which are revealed by changes in CO₂ assimilation rate under light conditions, photochemical quantum yields of photosystem 1 (PS1) and photosystem 2 (PS11), non-photochemical quenching (NPQ), etc.

A series of recent studies have focused on local and systemic effects of ESs on light and dark reactions in higher plants (Herde et al., 1999; Koziolok et al., 2004; Lautner et al., 2005; Hlavácková et al., 2006; Kaiser and Grams, 2006 and Grams et al., 2007). In particular, heat ESs caused a strong local as well as systemic reduction in net CO₂ uptake and quantum yield of electron transport as photosystem II (PS II) and hydro passive responses in stomatal aperture (Koziolok et al., 2004 and Kaiser and Grams, 2006). In *Zea mays*, it is confirmed that heat induced ES spread via the veins through the leaf lamina which gives the evidence that the photosynthetic response is caused the ES (Grams et al., 2009).

Sequences of different types of photosynthetic responses can also be observed (Sukhov et al., 2014). Moreover, the sequence can depend on the type of irrigation. Fast inactivation of photosynthesis is the most extensively investigated photosynthetic response. It includes a fast decrease of the CO₂ assimilation rate under light conditions, lowering of photochemical quantum yields of PS1 and PS11, reduction of linear electron flow through photosystems, increased NPQ and changes in the cyclic electron flow around PS1 (Grams et al., 2009 and Sukhov et al., 2012, 2015).

Inactivation of photosynthesis has been shown in Chara algae after current stimulation (Bulychev et al., 2004) and in different higher plants after burning, mechanical wounding and current stimulation (Herde et al., 1995 and Sukhov et al., 2012, 2014, 2015). The influences of ESs on photosynthesis over short time range (minutes) have different expressions and can be absent; however, AP- and VP- induced photosynthetic responses are similar. Fromm and Fei (1998) and Grams et al. (2007) showed that re-irrigation induces AP and increases the CO₂ assimilation rate under light conditions in maize leaves, which starts about 10 min after stimulation and reaches a maximum at 20-30 min.

ESs propagated over long distances as well as short distances are capable of modifying photosynthesis in trees (Lautner et al., 2005). Other studies had reported on the capacity of many plant species to generate and transmit APs as well as VPs (Pickard, 1973 and Davies, 1987). Both AP and VP can induce fast inactivation of photosynthesis. There are various studies of developing ES-induced inactivation of photosynthesis as has been investigated in a number of studies (Sukhov, 2016). The potential mechanisms of fast and long-term inactivation of photosynthesis have been summarized in figure below.

Herde et al. (1999) showed that long-term inactivation develops after a VP-inducing stimulus (heat treatment) and after a classical AP-inducing stimulus (electrical current application). Changes in ion concentrations accompanied with ESs are the probable mechanism of fast inactivation of photosynthesis (Pyatygin et al., 2008). There are two potential mechanisms of induction of inactivation in plants. First, Ca₂₊ concentration increases in the cytoplasm and later, in the chloroplast stroma, are initiators of inactivation of photosynthesis (Krupenina and Bulychev, 2007; Bulychev and Komarova, 2014). Long-term inactivation is connected to production of abscisic and jasmonic acids, and inactivation of H⁺ symporters. Further photosynthetic inactivation is mainly connected with the inactivation of the photosynthetic dark reactions which changes the light reactions; however, other pathways of ESs influence on the photosynthetic light reactions are also probable (Sukhov, 2016).

Recent experiments on signal transmission in *Mimosa Pudica* demonstrated that a link exists between a flame induced ESs and photosynthetic responses, as inferred from two-dimensional imaging analysis of chlorophyll fluorescence in combination with gas exchange assessment (Kaiser and Grams, 2006 and Koziolok et al., 2004). The experiments shows that increase in stomatal conductance is due to hydro passive stomatal movement caused by sudden loss of epidermal turgor the reduction of net CO₂ uptake is at least partially due to disturbance of light reactions. The study on poplar confirms the latter findings for trees. The results demonstrate that the different stimulation types and positions incite characteristic ESs, each with a specific

influence on photosynthesis (Lautner et al., 2005). The study provides evidence that rapidly evoked and phloem-transmitted signals can affect photosynthesis over long distances in trees.

4. Prospects of energy harvesting from higher plants

Weak electricity can be harvested from living plants (Chong et al., 2019). It has been discovered that there exists EP difference between the phloem of a living tree and the surrounding and it can be harvested (Ying et al., 2015). It has also been found that, the electricity generated from plants increases remarkably under sunlight and therefore photosynthesis increases the electricity activity in plants (Liu et al., 2019). Mechanism used to harvest energy from plants affect amount of energy collected. Mostly it is done by embedding pairs of electrodes into plants, where electrical energy is harvested by completing the connection with conditioning circuit (Chong, 2014 and Choo et al., 2013).

Research has been conducted on different types of plants covering non-succulent and succulent trees (Choo et al., 2013). These trees were *Alstonia scholaris* (Pulai tree), *Musa acuminata* (banana tree) for non-succulent and *Aloe Vera* for succulent. It was verified that the succulent plants much higher voltage compared to non-succulent which can potentially be useful to power up ultra-low power consumption devices (Choo et al., 2013, Choo and Dayou, 2014). In another experiment electrical energy was harvested from a bigleaf maple tree (*Acer macrophyllum*) which was fed to two specialized nano-electronic ICs which consisted of a boost converter and a low frequency time (Himes et al., 2010). Electrical energy harvested from pachira tree (*Pachira aquatic*) was used to power a wireless plant health monitoring system (Tanaka et al., 2012). Another research also shows that electrical energy has been harvested in poplar tree (Hao et al., 2013).

5. Methods of measuring EP

Two different methods are used to measure EP in plants i.e. intracellular and extracellular (Fromm and Lautner, 2007 and Volkov et al., 2017) as shown in table 2. Intracellular recording was first adopted for giant cells from charophytic algae later on complemented with precise electronic amplifies and voltage clamp circuits monitoring the activity of ion channels by direct measurements of ion currents instead of voltages (Higinbotham, 1973). Andras et al. (2000) gave evidence of the annual fluctuation of the amplitude of the daily electrical variation observed on a standing tree. Two improvements on the measurement of EP were made. First instead of unique channels, multi-electrodes system was used and a common ground, allowing the local effects measured at individual channels to be eliminated. The second improvement was the selection criterion for time intervals which allowed clear establishment of annual variation of the daily amplitude.

Extracellular potential measurements on the surface of higher plants have been widely performed in the past, and offer the advantage of being able to detect electric potential differences over long periods of time (Fromm and Lautner, 2007). Measurement using inserted electrodes has been made with various tree species. At different positions within the plant, from roots to fruits, electrodes are connected by insulated cables to a high-input impedance multi-channel electrometer. In addition, a reference electrode is inserted in the soil. When all channels are electrically stabilized, the following treatments can be evaluated: light-darkness sequences, drought-irrigation cycles, mechanical wounding, etc. The insertion of electrodes inevitably causes wound reactions while surface recordings are non-invasive. Various microelectrodes have been used for electrophysiological studies in plants. In most of the publications EPs are monitored continuously using non-polarizable Ag/AgCl microelectrodes have reported by Gurovich and Hermosilla (2009) Gil et al. (2009) Oyarce and Gurovich (2011).

ESs can propagate along the plasma membrane on long distances in vascular bundles and on short distances in vascular bundles and on short distances in plasmodesmata and protoxylem (Volkov, 2017). A recently study done on *Aloe Vera* induces electrotonic propagating along their leaves. In this study it was discovered that there is a difference in duration and amplitude of EPs measured by intercellular electrodes inserted in a leaf and extracellular Ag/AgCl electrodes attached to a leaf's surface.

Table 2: Methods and electrodes for measuring electric potentials				
Measurement method	Plant measured	Electro used	Findings	Reference
Extracellular Recording	<i>Salix Viminalis L.</i> (Willow)	Silver chloride	Different stimuli cause characteristic signals with specific influences on photosynthesis and transpiration.	Fromm and Spanswick, 1993
	<i>Vicia faba L.</i> (Horse bean)	Glass microelectrodes	Extracellular measurements results were spatiotemporal activities of multi-cells in plants	Dong and Cheng, 2013
	<i>Dionaea muscipula</i> (Venus flytrap)	Silver chloride	Action potentials in the petiole and amplitude and duration of signals obtained by extracellular or external electrodes can be different	Volkov et al., 2013
	<i>Lycopersicon</i> (Tomato)	Silver chloride	Both hydraulically induced APs are capable of evoking <i>pin 2 gene</i> expression	Stankovic and Davis, 1996
	<i>Persea Americana Mill</i> (Avocado)	Cotton thread	EP difference between avocado roots and shoots that can be readily measured and is correlated with soil moisture	Gil et al., 2007
	<i>Vitis Vinifera</i> (Grape Vine)	Stainless steel	Multivariate statistical procedures such as PCA and PLS with orthogonal signal correction have potential for quantifying soil moisture indirectly	Gil et al., 2014
	<i>Glycine max (L.) Merrill</i> (Soybean)	Silver	A single application of heat induces fast AP in soybean	Volkov, 2008
Intracellular	<i>Zea Mays L.</i> (Maize)	Silver chloride	Re-irrigation increases gas exchange	Vuralhan-Eckert et al., 2018
	<i>Pisum Sativa</i> (Garden pea)	Gold probes	Local heating- induced in photosynthesis	Sukhov et al., 2017
	<i>Rosa floribunda</i> (Garden rose)	Silver probes	Field-induced electrochomic gradients suggesting higher hole conductivity in isolated compartments but higher ionic conductivity across the whole leaf was observed	Stavrinidou et al., 2015
	<i>Chara Corallina</i> (Chara)	Agar	Sharp spike was generated by decreasing the turgor pressure	Shimmen et al., 2015

Measurement method	Plant Measured	Electro used	Findings	Reference
	Poplar	Silver chloride	Cooling the lower part of the shoot with ice water evoked a rapidly moving AP transmitted acropetally within the phloem	Lautner et al., 2005
Comparing Extracellular and intercellular	<i>Aloe Vera</i>	Silver chloride and platinum	There is a difference in duration and amplitude of electrical potentials measured by intercellular electrodes inserted in a leaf and extracellular attached to the leaf	Volkov et al., 2007

6. Conclusion

There exist great amounts of information concerning the electric potential in plants, how they are transmitted, effects in plants, and their physiological and electrochemical mechanisms. Despite all this information, there is much to be studied. The transmission of ESs is very important in how plants respond to their environment, however several questions remain open on how plants perceive simultaneous external stimuli and if they are capable to integrate different simultaneous stimuli in order to generate a complex response. On energy harvesting, there are several factors that affect the energy generation of plants, including temperature, moisture, soil PH, electrodes types and environment properties. Variables such as PH, temperature and moisture still need to be researched to make sure the harvesting operation is controlled. Further investigation on electric potentials in plants could also provide information on the outlook of possible uses of these phenomena for improvement of agricultural technologies. These reasons provide significant basis to the importance of further profound investigations of electrical phenomena in plants.

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