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# Electrical response of plants to environmental stimuli: A short review and perspectives for meteorological applications



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## ABSTRACT

Meteorological knowledge of a given locality is one of the necessary conditions to understand the climate evolution of a zone. It results in a better understanding and prediction of the environmental impact due to current climate change in the world. The sensors used to take these physical measurements are, for the most part, categorized as electronic or mechanical devices. Paradoxically, the new generations of sensors result in increased pollution because of the synthetic material used in their manufacturing process. In addition, the design of these measuring devices is complex and results in high costs. One of the solutions to the problem would be to replace these measurement sensors with biosensors that are more environmentally friendly, cheap and very simple to develop. Plants could play a role in these biosensors. Indeed, studies carried out on plants show that they have a great capacity to interact with their environment. They are living beings, capable of reacting to the meteorological conditions to which they are exposed. This reaction to the variation in the weather conditions of the surrounding environment is automatically translated into the appearance of a variable electrical signal created by the plant. The electrical phenomena produced by biological plants could be easily measured, and signals could be exploited as a characteristic of the meteorological state of the surrounding environment. Biological plants are therefore potential replacements for existing conventional sensors. The study presented in this work summarizes, in a single table, the research conducted to date into the various electrical and analytical models of the activity of a biological plant. All existing experiments in the laboratory and in situ are also reviewed. A SWOT analysis (strengths, weaknesses, opportunities, threats) of these experiments has been carried out to better perceive any future opportunities to use the electrophysiological phenomena of the biological plant in metrology (i.e., how to transform biological plants into biosensors).

## 1. Introduction

Meteorological knowledge of a given locality is one of the conditions that are necessary to understand the climate evolution of an area. It allows us to better understand and predict the environmental impact of

current global climate change. Meteorological stations are composed of sensors that record and provide values of meteorological parameters related to climate variations. Usually, data from these stations are known to be used in climate prediction or in studies of human comfort inside a building. These measurements are also indispensable in research, especially when it comes to studying renewable energy source production in

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Nomenclature	
$\phi$ (Wb)	Time variation of extracellular potentials and membrane
$\rho$ ( $\Omega.cm$ )	Resistivity
$\tau$ (s)	Constant time
$C_1$ ( $\mu F$ )	Capacitance of the Charged capacitor from the voltage source
$C_2$ ( $\mu F$ )	Capacitance of the plant tissue
$C_m, C$ ( $\mu F$ )	Membrane capacitance
$E_k$ (mV)	Equilibrium potential of $K^+$
$E_m$ (mV)	Membrane potential
$E_{Ca}$ (mV)	Equilibrium potential of $Ca^{2+}$
$E_{Cl}$ (mV)	Equilibrium potential of $Cl^-$
$E_{PCa}$ (mV)	Equilibrium potential of $Ca^{2+}$ - ATPases
$E_{PH}$ (mV)	Equilibrium potential of $H^+$
$E_{sy}$ (mV)	Equilibrium potential of $2H^+/Cl^-$ symporter
$g_k$ ( $S.m^{-1}$ )	Electrical conductivity of $K^+$
$g_l$ ( $S.m^{-1}$ )	Leak ion conductance
$g_{Ca}$ ( $S.m^{-1}$ )	Electrical conductivity of $Ca^{2+}$
$g_{Cl}$ ( $S.m^{-1}$ )	Electrical conductivity of $Cl^-$
$g_{PCa}$ ( $S.m^{-1}$ )	Electrical conductivity of $Ca^{2+}$ - ATPases
$g_{PH}$ ( $S.m^{-1}$ )	Electrical conductivity of $H^+$
$g_{sy}$ ( $S.m^{-1}$ )	Electrical conductivity of $2H^+/Cl^-$ symporter
$I_j$ (mA)	Ionique current
$I_{ext}$ (mA)	External stimulus current
$I_{ion}$ (mA)	Ionique current
$I_{stim}$ (mA)	External stimulus current
$R_s$ ( $\Omega$ )	Internal resistance of the power source
$U_1$ (V)	Electrical potentials at $C_1$ capacitors
$U_2$ (V)	Electrical potentials at $C_2$ capacitors
$U_c$ (V)	Capacitor voltage
$U_o$ (V)	Initial Capacitor voltage
$U_R$ (mV)	Resistor R voltage
$V_m$ (mV)	Membrane potential
$V_{in}$ (V)	Input voltage
A (-)	Polynomial containing common set of poles for both the system and noise model
B,F,C,D (-)	Polynomial represent the numerator and denominator of the system an noise model
E (mV)	Voltage between the trunk electrode and the ground electrode
e(t) (-)	Error (zero mean white Gaussian noise)
fit (%)	Percentage fit
g ( $S.m^{-1}$ )	Ion conductance
h (-)	Degree of inactivation of the ion channel
I (mA)	Memristor current
m (-)	Degree of activation of the ion channel
M(q) (-)	Memristor
q (C)	Electric charge
r ( $\mu m$ )	Distance from the cell
R ( $\Omega$ )	Resistance
U (V)	Capacitor voltage
u(t) (-)	Input signal
V (V)	Output voltage
y(t) (-)	Output signal
<b>Acronyms</b>	
AP	Action Potential.
DMM	Digital Multimeter.
ECG	Electrocardiogram.
ETP	Electrotonic Potential.
FCCP	Trifluo-romethoxyphenylhydrazone.
IBM	International Business Machines Corporation.
NLARX	Non-Linear Autoregressive with exogenous.
NLHW	Non-Linear Hammerstein-Weiner.
PCI	Peripheral Component Interconnection.
PCP	Pentachlorophenol.
SWOT	Strengths Weaknesses Opportunities Threats.
VP	Variation Potential.
VS	Variation peaks.
VT	Voltage Transients.

direct relation to the climatic conditions, for example. In these cases, the physical variables commonly measured are the ambient temperature, relative humidity, wind speed and direction, solar radiation, and the precipitation around the environmental system being studied (i.e., microclimate). The sensors used to take these physical measurements are mostly electronic or mechanical devices. Paradoxically, the new generations of sensors result in increasing pollution due to the synthetic material used in their manufacturing process. One of the solutions proposed by scientists has been to replace these measurement sensors with biosensors. A biosensor is composed of a biological part and an electronic part. The biological part detects information related to the variation of a biological element such as an enzyme, a plant or animal cell, a DNA fragment, or lipids. This information is then processed by the electronic part. Biosensors are categorized according to their type of transducer, which may be electrochemical, optical, piezoelectric or calorimetric [1–3]. The scope of the application of biosensors is considered broad. The first discoveries concerning biosensors were used in medical applications to check the blood sugar level of diabetic patients, and the levels of cholesterol, amino acids, urea, and alcohol in the human body. The amperometric biosensor is the most frequently used biosensor in this field. In the pharmaceutical industry biosensors are used, for example, to quantify and analyze drugs [4,5]. Biosensors are also used in various other fields, such as industry applications (agriculture, food) and the environment. In the agricultural industry, biosensors are used to detect traces of pesticides that are harmful to consumers [4,6–8]. In the food

industry, biosensors are used to quantify nutrient intake (carbohydrates, acids) and alcohol levels, and to detect bacteria, viruses, and microbes [9–11]. For example, biosensors are used in the detection of pathogenic organisms in meat and eggs. In the environmental sector, some biosensors designed for environmental monitoring can detect various pollutants in river water and the concentration of heavy ions in nature [12]. They are also used in the security, defense, and military sectors to alert bioterrorist attacks or genetic disorders and criminals [13,14]. However, the manufacturing process of a biosensor requires the extraction of plant or animal tissue, an expensive and complex process, compounded by the equally expensive and complex design of this measuring device. One of the solutions to this problem would be to replace them with more environmentally friendly biosensors that are cheap and very simple to develop. Plants could accomplish this role. Indeed, studies conducted on plants show that they have a great capacity to interact with their environment. Plants produce various types of intracellular and intercellular electrical signals in the form of electric potential in response to changes in the state of their environment [15–20]. The easily measured signals of plants could be exploited as a characteristic of the meteorological state of the surrounding environment. Plants are therefore potential replacements for existing conventional sensors. They, therefore, respond to abiotic stresses which are physical variations of the Earth such as climatic variations. For example, they can react to drought, temperature, radiation, as well as any other environmental stimuli encountered such as atmospheric pollutants. Electrical activities in plants are also caused by

**Table 1**  
Summary of existing models

Name	Model	Input variables	Output variables	Parameters	Ref.
Hodgkin-Huxley model	$I_{ext} = C_m \frac{dV_m}{dt} + I_{ion}$ with $I_{ion} = \bar{g}_{Na} m^3 h (V_m - E_{Na}) + \bar{g}_K n^4 (V_m - E_K) + \bar{g}_L (V_m - E_L)$	$I_{ion}$	$I_{ext}$	$C_m$ $V_m, t, m, h, g, g_L$	[34,47]
Modified dHodgkin-Huxley Model (Action Potential Generation Model)	$I_{ext} = C_m \frac{dV_m}{dt} + I_{ion}$ Modified equation with the $Cl^-$ and $Ca^{2+}$ $I_{Cl^-} = \bar{g}_{Cl^-} (V_m - E_{Cl^-})$	$I_{ion}$	$I_{ext}$	$C_m, V_m, t, m, h, g$	[33,40]
Zhao Model	$I_{stim} = C_m \frac{dV_m}{dt} + \sum I_j$ with $\phi \propto I_m \propto \frac{dV_m}{dt}$ and $\phi = \frac{\rho}{4\pi} \sum_n \frac{I_j(t - \tau_i)}{r_i}$	$I_j$	$I_{stim}$	$C_m, V_m, t, \phi, \rho, \tau, r$	[36]
Biologically Enclosed Electric	$U_c(t) = U_0 \exp - \frac{t}{\tau}$ with $\tau = RC$	$U_0$	$U_c$	$\tau, C, R$	[48,51]
Theoretical tree energy source model	$E \cdot \frac{R}{R_s + R} = U_R$	External Stimulus	E	$R, R_s, U_R$	[58]
Model of Leon Chua	$V(t) = M(q(t)) \cdot I(t)$ with $M(q) = \frac{d\phi}{dq}$ and $I = \frac{dq}{dt}$	External Stimulus	$M(q), V$	$q, \phi$	[64–66]
Model of activities of the Mimosa pudica leaves	Discharge of the capacitor $\log_{10} U(t) = \log_{10} U_0 - t/2.3\tau$ with $\tau = RC$ $C_1 \frac{dU_1}{dt} = -\frac{1}{R_1} (U_1 - U_2) \quad C_2 \frac{dU_2}{dt} = -\frac{1}{R_1} U_1 - \left( \frac{1}{R_1} + \frac{1}{R_2} \right) U_2$	$U_0$	$U(t)$	$U, U_0, t, \tau, C_1, C_2$	[49–51]
Model of propagation of the action potential along the Aloe Vera leaf	Differentiator $V(t) = RC \frac{d}{dt} (V_{in}(t) - V(t))$	$V_{in}$	V	$V, V_{in}, R, C$	[29]
Dynamic Chatterjee model	A linear system modeling using variants of LSE - Auto Regressive eXogenous (ARX) estimator $A(q^{-1})y(t) = B(q^{-1})u(t) + e(t)$ - Auto Regressive Moving Average eXogenous (ARMAX) estimator $A(q^{-1})y(t) = B(q^{-1})u(t) + C(q^{-1})e(t)$ - Box-Jenkins (BJ) estimator $Y(t) = \frac{B(q^{-1})}{F(q^{-1})} u(t) + \frac{C(q^{-1})}{D(q^{-1})} e(t)$ - Output-Error (OE) estimator $Y(t) = \frac{B(q^{-1})}{F(q^{-1})} u(t) + e(t)$ Estimation of non linear models - Nonlinear ARX (NLARX) estimator $y(t) + a_1 y(t-1) + a_2 y(t-2) + \dots + a_n y(t-n) = b_1 u(t) + b_2 u(t-1) + \dots + b_m u(t-m) + e(t)$ - Nonlinear Hammerstein-Wiener estimator $y_p(t) = h \left( \frac{B(q^{-1})}{F(q^{-1})} (f(u(t))) \right)$ and $fit = \left[ 1 - \frac{ y - \hat{y} }{y - \bar{y}} \right] \times 100\%$	$u(t)$	$y(t)$	$u(t), y(t), e(t), \{B, F, CD\}, \{A\}, fit$	[46]
Sukhov and Vodeniev model	$E_m = \frac{g_K E_K + g_{Cl} E_{Cl} + g_{Ca} E_{Ca} + g_{PH} E_{PH} + g_{PCa} E_{PCa} + g_{Sy} E_{Sy}}{g_K + g_{Cl} + g_{Ca} + g_{PH} + g_{PCa} + g_{Sy}}$	External Stimulus	$E_m$	$E_K, E_{Cl}, E_{Ca}, E_{PH}, E_{PCa}, E_{Sy}, g_K, g_{Cl}, g_{Ca}, g_{PH}, g_{PCa}, g_{Sy}$	[40–43]

biotic stress, which is induced by the effects of other living organisms. Indeed, many studies show that the plant has a complex defense mechanism in the form of signals about diseases, injuries caused by herbivores, and pathogenic microbes [21,22]. For example, leaf larvae that induce action potentials in potatoes (*Leptinortsa decemlineata* (Say); Coleoptera; Chrysomelidae) [23] and insect bites that cause a slow wave formation that displaces the leaves of an *Arabidopsis* [24]. In this review, it will be shown that plant signals could be exploited as a characteristic of the meteorological state of the surrounding environment. Plants are therefore potential replacements for existing conventional sensors.

## 2. Modeling: electrical signals in plants

Electrical signals in plants were recognized 200 years ago. Although the existence of these signals has been disputed, studies have been

published on electrochemical and electrical signals in plants. The study of these signals in plants was initiated by the medical physiologist Sir John Burdon-Sanderson in approximately 1873. He conducted experiments on the leaves of *Dionea muscipula Ellis*. This experimentation allowed him to discover the action potential, which is an electrical signal. The closing of the *Dionea muscipula Ellis* hatch inspired much research on the action potential of plants. An action potential is a low amplitude electrical impulse caused by stimulation that does not destroy the plant. These excitations can be electrical stimulation, temperature variation, light variation, and chemical agents. The action potential manifests itself at the level of a cell with a change in the membrane potential. It propagates automatically in the plant through the phloem with a given speed at a constant amplitude. Propagation is linked to the living tissues of the plant, particularly through calcium ion channels. Thus, it is considered a long-distance electrical signal [25,26].

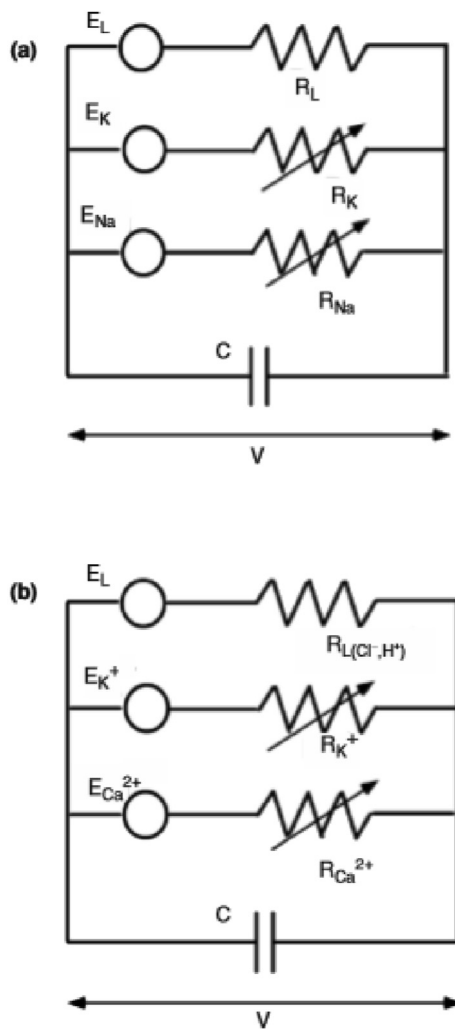


Fig. 1. The equivalent Hodgkin-Huxley (HH) circuit for an axon (a) and the modified HH circuit for phloem screening tubes (b) [47].

Following the discovery of the action potential, the term potential for variation was introduced by Houwinck in 1935. The variation potential is an electrical signal of an undetermined form. The shape of the signal depends on the nature of the stimulation and the plant. The variation potential is caused by injury or burning. It propagates at a low speed through the xylem with a variable amplitude of approximately 10 mV. Like the action potential, the variation potential is considered to be a long-distance signal [26]. The electrotonic potential is also an electric potential found in small neurons. It propagates over a short distance with an amplitude that is related to that of the stimulus, and decreases. This electrical potential is often noticed during electrostimulation experiments. These experiments have been carried out on several plant species, such as *Dionaea muscipula* Ellis, *Aloe Vera*, *Mimosa pudica*, and the fruit of an apple tree [27–30]. For example, electrotonic potentials are noticed during electrostimulation by a square pulse of the upper or lower leaves of the Venus flytrap. The speed and distance of propagation are described in Ref. [27].

Thus, mechanically sensitive biological plants that are considered to possess reflexes similar to those of an animal's nervous reflex have been the most studied. Insect trapping carnivorous plants and *Mimosa pudica* belong to this category. The results of studies conducted on these plants have made it possible to distinguish their different electrical activities, including their action potential (AP), variation potential (VP), voltage transients (VT) or voltage peaks (VS) and electrotonic potential (ETP) [19,20,26,27,31]. In this section, the analytical and electrical modeling

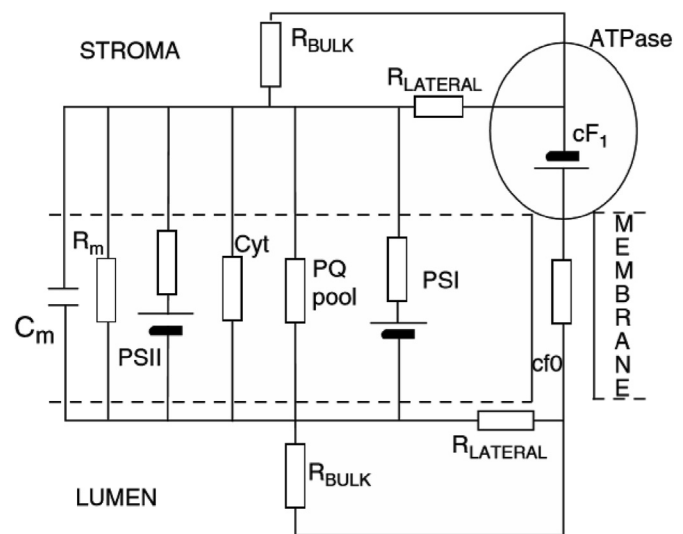


Fig. 2. Electronic circuit equivalent of PSII and PSI photosystems [47].

of the electrical activities of plants will be detailed. The analytical models are mainly concerned with the generation of electrical potentials at the cell level. However, the electrical models are concerned with both microscopic and macroscopic equivalent circuits.

### 2.1. Analytical modeling

Several modeling approaches have been adopted to develop models of the electrical responses in plants. The first mathematical model was proposed by Beilby and Coster. They adapted the Hodgkin-Huxley model of squid cells. They proved that the model can be used to simulate the electrical activity of a plant. The model has been applied to *Chara* algae experiments, but it does not take into account all the properties of the plants since the other parameters used in this model are specific to those of animals, such as the activity of the  $Na^+$  channel [32–35].

The activities of channels  $Ca^{2+}$  and  $Cl^-$  as well as a reducing form of the dynamics of the particles suspended in these channels included in the model for generating potential actions are described in Table 1.

Despite the limitations of Beilby and Coster's results, other researchers have used them to simulate the electrical signals of higher plants. Zhao developed an experimental model that described a multicellular system in which each plant cell represented a potential source of electric current [36].

Gradmann and his collaborators have also conducted several types of research on the electrical activities of plants. They began with a specific study on the green alga *Acetabularia* [15]. Then they continued their work on the study of electrical oscillations in higher plants by describing the incoming and outgoing channels  $Cl^-$ ,  $K^+$ ,  $H^+$  - ATPase, and  $2H^+/Cl^-$  symporter. Their work also describes the changes in ion concentrations in the cytoplasm and apoplast and their buffering capacity.

However, Gradmann's studies have limitations because they do not consider the simulation of electrical signals caused by stimuli and do not take into account certain plant-related systems [37–39].

The results of these studies were then taken up by other researchers such as Sukhov, Vodeniev and Sherstneva. They provided new elements in the modeling of the potential for variation [40–43]. These elements describe the regulation of  $H^+$  -ATPase and  $Cl^-$  channel activities by  $Ca^{2+}$ ,  $Ca^{2+}$  and  $Ca^{2+}$  -ATPase channels. They also characterize the anti-carrier  $K^+/H^+$ , which participates in the establishment of the stationary concentrations  $K^+$  and  $H^+$ .

In comparison, Hills' studies describes stoma activity (opening and closing) and the generation of intracellular signals [34,44]. Existing analytical methods are also exploited to test hypotheses about electrical



signals in plants. For example, a study on the classification of electrical signals was carried out by Chen and colleagues [45]. Chatterjee adopted the method with the nonlinear Hammerstein-Wiener estimator (NLHW) and nonlinear autoregressive exogenous models (NLARX) to describe light-induced electrical responses in plant leaves in 2014. The study aimed to predict plant responses to different light stimuli [46].

## 2.2. Electrical analogy

To date, all studies have shown that the electrical activity of biological plants is due to excitation at the cellular level. The action potential then propagates through their membranes. Researchers have therefore described this activity at the biological plant cell level using equivalent electrical circuits. A great deal of research has led to results that are relevant to the studied subject. In 1952, Hodgkin and Huxley modeled the squid membrane. The model was formulated in terms of the leakage channels of  $K^+$ ,  $Na^+$  ions, and ions in the giant axons of squid (1).

The resting potential of the membrane for each ion is considered to be a battery. The degree of opening of the ion channel is replaced by a variable resistance (Fig. 1 a). In 1993, Fromm and Spanswick deduced after experimentation that  $Ca^{2+}$ ,  $K^+$ , and  $Cl^-$  ions also played a role in the propagation of action potentials in phloem (Fig. 1,b and [47]).

Researchers have also discovered that photosynthesis induces electrical activities in biological plants. Variations in daylight create electrical potentials in a plant. Two photosystems come into play during photosynthesis [47]. These two photosystems are represented by the equivalent electrical schematic in Fig. 2).

Other circuits of the electrical behavior of plants have been developed according to their specificities. Models were developed through experiments in which plants were stimulated. As an example, we found the equivalent electrical circuits of the *Dionaea muscipula* trap (Venus flytrap) [48], circuits describing the activities of the *Mimosa pudica* leaves [49–51] and the circuit describing the propagation of the action potential along the Aloe Vera leaf [29].

In general, standard electrical circuits consist of a resistor, a capacitor, and an inductor. In the early 1980s, the concept of a fourth basic element of the electrical circuit was discovered by Leon Chua.

This fourth basic element is the memory resistor or memristor in plants. The memristor, or memory resistor, is a two-terminal nonlinear passive electrical element that connects magnetic flux and electrical charge [28,52,53]. Memorization faculties were noted in *Mimosa pudica*, Venus Flytraps, aloe vera, apple fruit, potato tubers, and pumpkin seeds [28,29,52–56]. There are several theories about memory in plants. Another aspect concerns the capacity of plants to store information. In the latter case, the response to the stimulus is delayed [53]. This storage memory capacity is found in the Venus Flytrap, which accumulates small charges below the threshold. When the threshold value is reached, the plant trap closes.

Many types of research confirm that a tree is the equivalent of an electrical network [57–63]. The model representing the macroscopic activity of a tree is equivalent to a voltage generator and a resistance in series [58].

Table 1 Summarizes the different patterns of electrical activity in plants.

## 3. Experimentation: methods for measuring and recording electrical potentials in a plant

There are two different methods for measuring the electrical potential of a plant: extracellular and intracellular recording [31]. The first technique used to measure the electrical signal in a plant involves the use of surface electrodes. This is an extracellular method of detecting the signal on the surface of the plant. This technique is often used to determine the electrical potential between the trunk of a tree and the soil where the electrodes are placed [67]. It is also possible to deduce the electrical potentials of cells with this method by having the injury potential as a

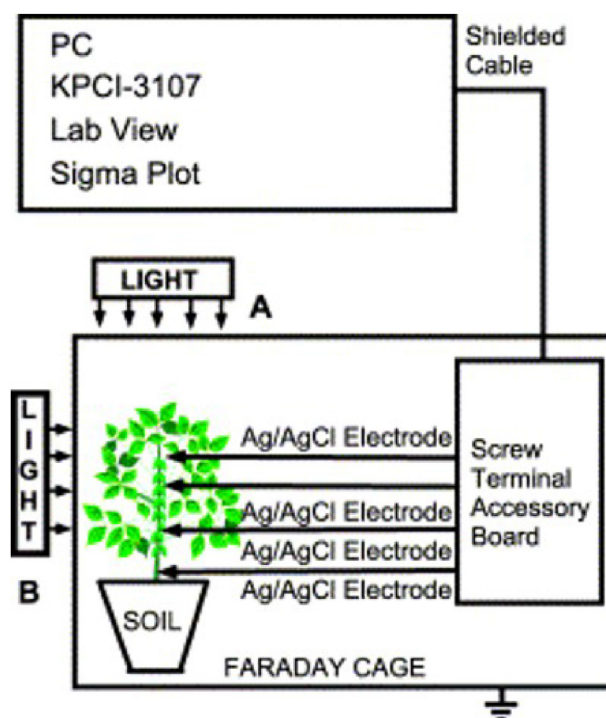


Fig. 3. Experimental setup for measuring electrical signals in green plants [68]. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

reference. In this case, the signal obtained is unreliable because it is exposed to interference that appears at the contact surface. With membrane theory and the discovery of microelectrodes, intracellular measurements can be implemented. Intracellular measurements are carried out using glass microelectrodes. With this method, the membrane potentials of the cells and the electrical signals can be specifically derived. A microelectrode is an electrode with a tip that is fine enough to be inserted into a cell. This technique was first used in the large cells of charophyte algae. However, inserting the tip of the microelectrode damaged other plants. Thus, with the evolution of technology and design improvements, the technique has become reliable [26]. The choice of an electrode type and location depends on the expected results. Electrodes can be placed in the root, stem, trunk, leaves, or soil depending on the parameters that are measured. The materials used for their design are also related to the intended purpose. For years, many experiments on plants have used the electrode method to study and analyze their electrical behavior [15,17,18,20,27–29,52,55,68–73]. These experiments can be carried out either in the laboratory or in situ. In this section, both types of experimentation will be detailed with examples. Laboratory experiments involve the artificial stimulation of small plants such as mimosa, soybeans, Aloe vera, and others. In situ tests are carried out on large plants such as poplars, oaks and fruit trees.

### 3.1. Artificial experiments

Since the discovery of electrical signals in plants, many experiments have been conducted on this subject. Using various measurement techniques, hypotheses about the source, cause, mode of propagation, characteristics, and roles of electrical signals have been established and tested. The rapid development of digital technology facilitates the analysis and processing of recorded signals. In general, the artificial experimental device consists of a plant, electrodes, and a data acquisition system. The plant is placed in a Faraday cage (metal enclosure) to be isolated from surrounding noise and electric fields. The experiment is carried out at a constant temperature. All the experimental devices are

placed on a table stabilized against vibration [27–29,52,55,68,69,72]. Initially, in order to obtain an initial state with a stable electrical potential, the plant is left to rest for a certain time before being stimulated. These stimulations can be electrical stimulation [29,69] or chemical stimulation [71], irradiation [68], charge injection [70,72], or periodic wave electrostimulation [28,52,55].

In 2004, soybean plants were irradiated with lights ranging from ultraviolet to infra-red in two directions, A and B (see Fig. 3). The stimulation aimed to perceive the effect of long-distance signal propagation. The experimental setup consisted of soybean seedlings approximately 3 weeks, Ag/AgCl electrodes, and an IBM microcomputer with a KPCI-3107 data acquisition card. The sampling capacity of the data acquisition system was 100 samples/s. After inserting the electrodes, a rest period of 1–2 h was required. The plants were irradiated in two directions A and B (see Fig. 3). The results showed that an action potential was generated at wavelengths  $450 \pm 50$ , 670 nm and 730 nm. This electrical potential depended on both the wavelength of the irradiation and its direction. The hypothesis that the location of the electrodes could affect the characteristics of the action potential was rejected. It was also noted that the speed of transfer of the electrical signal between the cells depended on many environmental factors and previous stresses to the plant. This signal could propagate from the root to the stem or in the opposite direction. Bioelectrochemical or electrophysiological signals were detected in areas that were distant from the stimulated part [68].

In 2007, based on the same principle of experimentation by artificial stimulation, the closure of the Venus flytrap plant trap was studied. The Venus flytrap could capture mechanical movements. The experiment was based on the charged capacitor method. The experimental device consisted of the plant *Dionaea muscipula* (Venus flytrap) and Ag/AgCl electrodes. The electrodes were connected to an NI-PCI-6115 data acquisition system. The data logging system operated in real-time. Stimulation was in the form of an electrical pulse with different voltage levels. The amplitude and duration of this pulse were controlled by two optically isolated electronic circuits. The experiments were repeated fifty times on different Venus flytrap plants. The results showed that the electrical stimulation of the Venus flytrap caused its trap to close. However, it did not allow it to open. Furthermore, it was noticed that the time for closing the trap was the same as with mechanical stimulation. The author demonstrated by this study that alternative method to mechanical stimulation existed for the analysis of rapid activities in plant cells [69]. The results of this experiment were confirmed by a similar study in 2008 [70]. Recently, another more in-depth study on the Venus flytrap has been conducted to better understand the functioning of the lobe. The hunting process of the Venus flytrap was highlighted as well as the very high sensitivity of the mechanoreceptors. Electrical activities occurred during the contact of prey with the mechanoreceptor. Thus, the agitation of the prey led to the appearance of a succession of action potentials [74].

Another study was conducted on the Venus flytrap in 2013. Electrical stimulation was performed using more modern devices. The electrical stimulation was produced by an FG300 function generator (Yokagawa, Japan). The data were recorded by Ag/AgCl electrodes. The whole setup was interfaced with an NI-PXI-1042Q microcomputer. This experiment gave a wider choice of the characteristics of the electrical signals injected into the plant. The electrical stimulation was divided into two parts. First, the plant was electrically stimulated at a low voltage. The lower and upper leaves of the Venus flytrap were electrostimulated separately. These actions made it possible to close the plant's Flytrap under different conditions. Additionally, by stimulating the plant with a square signal, electrotonic potentials were observed. Afterward, high voltage tests were carried out. Electrotonic potentials were also observed when the voltage exceeded a threshold value. In conclusion, the author suggested that environmental changes might be studied by this method [27]. Also, in a study focusing on how the plant feeds, it was found that most trap closures are caused by wind and rain and not always by a prey species [75].

In 2010, using the same method as the charged capacitor, the mechanical properties of *Mimosa pudica* were studied. Indeed, in response

to various stimuli, the mimosa performed thigmotactic or seismonastic movements. The determination of the source of this movement was complex. However, thanks to specific experiments, three hypotheses were proposed (see Ref. [72]). The electrostimulation experiment aimed to use the charged capacitor method to analyze the electrical properties of the plant. The value of the capacitor was 47  $\mu\text{F}$ . The use of two types of electrodes, Ag/AgCl and platinum, led to the same conclusion. Data recording was carried out using an NI-PXI-4071 digital multimeter (DMM) combined with a bus system based on the Peripheral Component Interconnection (PCI) bus. High-performance digital cameras and recorders were used to observe the movements of the *Mimosa pudica*. The purpose of the study was to create an electrical circuit equivalent to a capacitor discharge in a plant. This circuit simplified the understanding of electrical activities in the *Mimosa pudica*.

Other experiments were conducted following similar measurement protocols. In these trials, the measuring devices included Platinum and Ag/AgCl electrodes and a data acquisition system. The common objective was to demonstrate the existence of a memory resistor in the studied specimen. Plants were electrostimulated by sinusoidal or triangular waves. To prove the existence of a memory resistor, a hysteresis loop pinched in the voltage-current plane of the same frequency as the excitation signal should appear. In 2008, the study focused on Irish potato tubers (*Solanum tuberosum* L.). The trial was repeated 14 times [56]. Similarly, in 2016, the experiment was carried out on Golden Delicious and Arkansas Black apples (*Malus Domestica* Borkh.). This time, the experiment was repeated 20 times [28]. The results of these two experiments affirmed that there is a resistance of memory in plants because a phenomenon of hysteresis was observed. To test this hypothesis in seeds, pumpkin seeds were analyzed in the same way. The principle of experimentation remains the same i.e. by electrostimulation of the seed by a periodic signal. After repeating the experiment 20 times, it was noted that when the seeds are dry and dormant, the hysteresis phenomenon does not appear. However, after soaking the seeds in water, when the experiment was repeated the hysteresis phenomenon reappeared [52].

Most of the experiments revealed the existence of electrical potential. Knowing that the electric potential could disperse in a plant, its mode of propagation was analyzed in the case of Aloe vera. Ag/AgCl electrodes were placed along an Aloe Vera leaf. Both intracellular and intercellular electrodes were used in the tests. Additionally, for intercellular measurements, three types of electrodes were used: platinum electrodes inserted into the leaf; Ag/AgCl electrodes attached to the surface of the leaf; and ECG electrodes placed on the surface of an Aloe vera leaf. Both active (action potential) and passive (electrotonic potential) potentials were detected. It has been shown that the location of the electrodes affected the characteristics of the electrotonic potential. The results obtained could be used to advance studies on the electrical activities of plants [29].

Although mechanical and electrical stimulation has been identified as a source of electrical activity in a plant, plants also react to chemical stimulants. In a study of the plant's reaction to alamehthicin, a new form of electrical potential was observed. This electrical potential, called a "system potential", was a long-distance signal that moved systemically from leaf to leaf. The test was carried out on dicotyledonous lima beans (*Phaseolus lunatus* L.) and monocotyledonous barley (*Hordeum vulgare* L.). A new measurement protocol was adopted as microelectrodes were placed in the stomatal cavities. A decrease in the potential difference of 40 mV at 5 cm and 45 mV at 25 cm was detected on beans and barley leaves, respectively. The theoretical speed of the signal propagation was  $2.5 \text{ cm min}^{-1}$ . The objective of experimentally proving that alamehthicin induced electrical potentials had been achieved. However, the explanation of the mechanism of signal creation and transfer remains complex [71].

In the same context of chemical stimulation, the reaction of soybean plants to two different chemical solutions was tested. These chemical solutions were pentachlorophenol (PCP) [21] and carbonyl cyanide 4-trifluoromethoxyphenylhydrazone (FCCP) [76]. The experimental

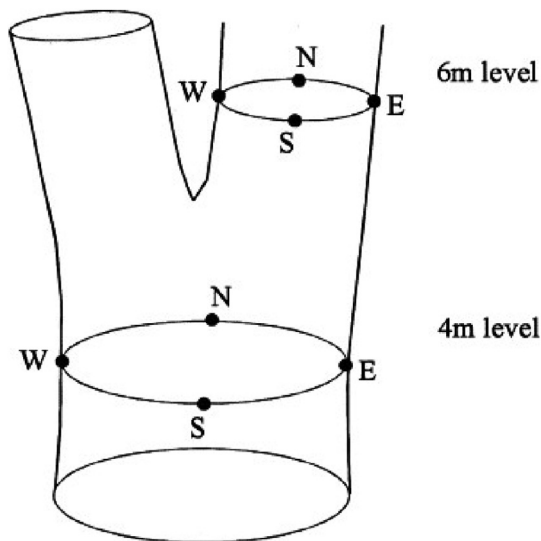


Fig. 4. In situ experimentation on an oak tree (*Quercus cerris*) [67].

device was based on Ag/AgCl electrodes and a data acquisition system with an IBM microcomputer with various characteristics (see Refs. [21, 76]). The test protocol consisted of pouring the solutions into the soil. In both trials, the results showed that both chemical stimulants induced ultrafast action potentials of  $30m.s^{-1}$  to  $40m.s^{-1}$ . Additionally, it was noted that the potential for variation decreased in the soybean plant. These experiments could be exploited to further study the signal propagation and the effect of environmental stimuli in the plant.

### 3.2. In situ experiments

Experiments requiring extracellular measurements are most often carried out on woody plants [59,61–63,67]. It is not possible to carry out laboratory tests on trees. Therefore, experiments are carried out in situ. On the one hand, intracellular measurements allow the electrical signal of the plant to be characterized. On the other hand, in situ experiments allow the identification of the environmental impact on the plant through the recorded signals.

In 2000, eight electrodes were implanted in the trunk of an oak tree (*Quercus cerris*). The objective of this experiment was to study the daily and annual variation of the electrical signal between each electrode and a reference on the ground. Of the eight electrodes, four were placed on the south, west, north and east sides at a height of 6 m. The other four were inserted in the same way at a height of 4 m (Fig. 4). The mean values of the voltages in 1 min were recorded with a sampling interval of 1 s. The values selected for analysis were those collected outside periods of rain and abnormal electric fields. This was because the signals were not detectable during environmental disturbances. The shape of the signals was then almost sinusoidal during the day, and the different electrode channels had different voltage values. During the year, two voltage peaks were recorded. Thus, these peak values were considered to be related to the flow of sap from the tree [67].

In 2006, an experiment in Brittany aimed to observe the spatial and temporal variation of the electrical signal of poplars (*Populus nigra*). The electrodes were inserted in the roots, on two circumferences and a vertical profile of the tree (Fig. 5). Electrical potential measurements were made with a sampling interval of 1 min. Simultaneously, the values of the wind speed and direction, atmospheric pressure, temperature, humidity, and precipitation in the vicinity of the tree were recorded every 15 min. Additionally, the internal temperature and humidity of the tree were measured to identify any sensitivity of the electronic devices to environmental conditions. The tests were carried out without taking into account the temperature present on the electrodes. By applying the heat

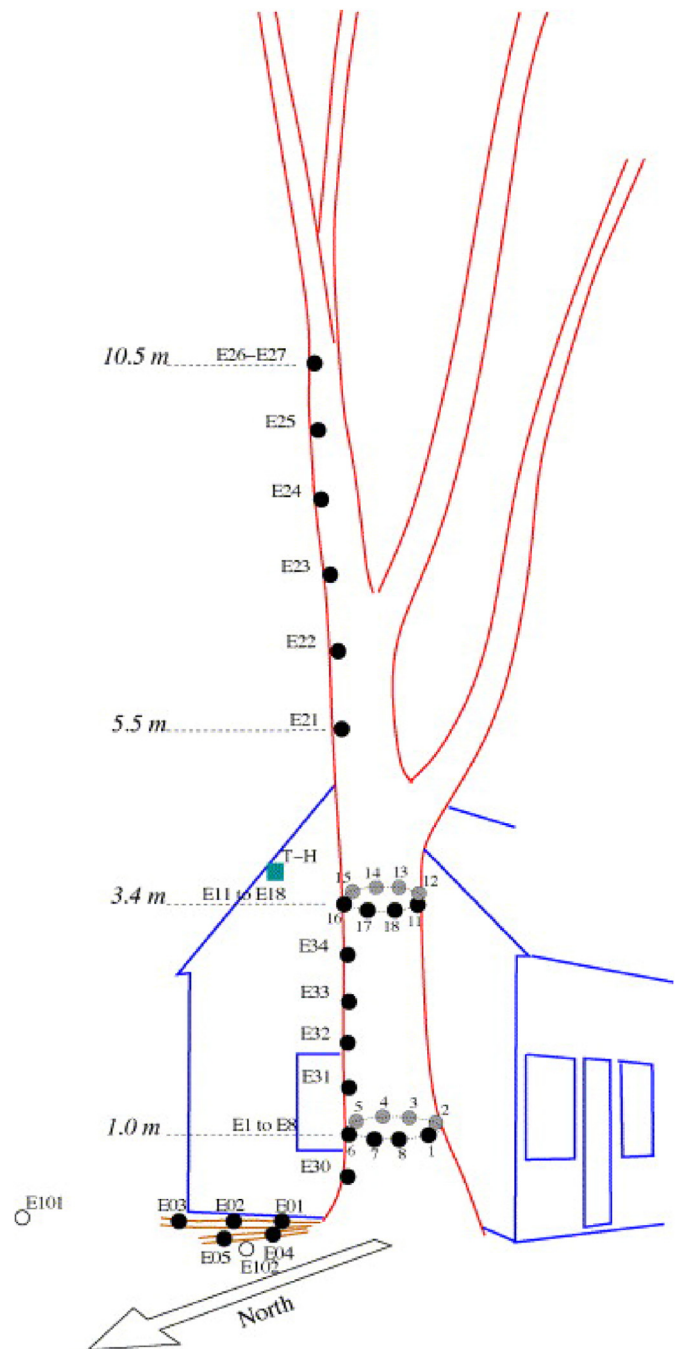


Fig. 5. In situ experiment on a poplar tree (*Populus nigra*) [59].

flow method, the results obtained confirmed the relationship of sap flow with the variation in the measured electrical signal, similar to the study in Ref. [67]. However, the author noted that the variation in the signal depended not only on this parameter but also on variables affecting the tree such as the xylem. He suggested that increasing the number of distributed electrodes would be another step toward obtaining other results [59].

Mouël and his collaborators continued the previous studies performed by Murten in 1984, Koppin in 2000, and Gibert in 2006 on poplar tree (*Populus nigra*). They used the same measurement protocols by placing the electrode at different heights. Within a few minutes, 120 signals of the same shape were recorded on the electrodes. Oscillations with the same characteristics as the signals from the electrodes were also observed for 10 min. Their amplitudes increased as a function of the



electrode height. The maximum value observed was 50 mV, corresponding to a current on the order of milliamperes. These results added another explanation to the origin of the electric potential variations along the tree trunk. The author concluded that this variation was due to the electric field in the atmosphere during thunderstorms [63].

Electrode measurements between the trunk of a tree and the ground prove that an electrical signal exist. Several previous experiments have highlighted the variation in this signal on a daily and annual basis. Based on the hypothesis that the electrical phenomenon in the tree can be exploited as a source of electrical energy, some parameters related to this source have been studied in detail.

The internal resistance of plants was one of the most important parameters. In in situ experiments from April 2014 to April 2015, the feeding model was used to study the internal resistance of a poplar tree in China. Two electrodes were used to measure the voltage between the trunk of the poplar tree and the ground. The objective of the study was to establish a reference for the applied research. A load resistor of 10 kΩ was connected between the two electrodes (one electrode placed on the trunk and another one inserted on the ground). An acquisition device allowed measurement with or without a load. The data were automatically read every hour with an accuracy of 5 s. The value of the internal resistance obtained varied between 1 kΩ and 5 kΩ. This value varied according to the season. It was high in winter and decreased in other seasons when it was warmer. Determining the value and the variation of the internal resistance of the tree would allow the use of a possible alternative source to be optimized [58] (see Table 1).

At the same time, from November 2014 to June 2017, experiments on seven different types of trees were carried out. The species and diameter of each tree were different. The objective of this study was to identify the effects of electrode characteristics on the measured signal. The size of the electrode could affect the voltage coming from the power source. Six electrodes were placed on each tree. A logarithmic relationship between the surface of the ground electrode and the electrical potential was noted. In conclusion, a 10 cm × 10 cm × 0.3 cm electrode was considered optimal for a tree-based power source [62].

## 4. Meteorological biosensor perspectives

### 4.1. Mechanical stimulation

The mechanosensation of plants was the first phenomenon that led to the study of electrical signals. Plants have mechanically sensitive channels. Two types of mechanosensitive channels have been distinguished in plants by the patch-clamp technique [77]. If a mechanical force is applied to a cell membrane, these channels translate this phenomenon into electrical or biochemical signals. These channels ensure the plant's survival by regulating its development and monitoring its environmental impacts. Mechanosensation can be present in all plants, but it is most evident in plants such as the Venus flytrap (*Dionaea muscipula*) and Mimosa pudica [27,51,69,70,72,78–81]. The Venus flytrap is a carnivorous plant. Several studies have been conducted on the closure of the trap of this plant. Volkov demonstrated in an experiment that the closing time of the Venus trap by the electrical stimulation of motor cells was equal to that induced by mechanical stimulation. This hypothesis was verified during electrostimulation between a median rib and a lobe that activated its motor cells. The results of the experiment showed that the closing time of the Venus flytrap door was 0.3 s and the action potential lasted approximately 1.5 ms [69]. After experimenting with the injection of electric charges on the same plant, Markin confirmed these results [70]. In the case of Mimosa pudica, its leaves close under mechanical pressure, and its petioles hang down in response to wind. It is a plant that is sensitive to vibration, electrical stimulation, and touch. It uses this ability as a defense mechanism to protect itself from animals and insects [80]. Apart from studies on electrical signaling, the elastic properties of Mimosa Pudica Main Pulvinus are studied by designing tactile sensors [51,81].

### 4.2. Daylight stimulation

Sensitivity to light is observed in plants [26,68,82]. Volkov suggests that the interpretation of electrical signals generated during photosynthesis can contribute to the improvement of agriculture [83]. Plants react to natural light using specific photoreceptors: phototropin, cryptochromes, and phytochromes [84–86]. Phototropin is a flavoprotein photoreceptor. It reacts to blue light (360–500 nm), which induces phototropism. Phototropism represents the plant's ability to bend toward light. The plant's phototropic response goes through several stages. Once stimulated, the phloem, which is the distribution beam of the elaborated sap, also propagates electrical impulses. Thus, a constant voltage action potential affects the membranes at rest. The cryptochromes of flavoprotein photoreceptors are responsible for the phenomena that modify the shape and color of plants induced by light. They also perceive blue light and ultraviolet light (315–400 nm). The phytochrome is a photoreceptor that regulates the development of the plant. It can react to red light (650–730 nm). In 2004, an experiment was carried out to observe the electrophysiological responses induced by blue and red light-sensitive systems in soybean plants. The wavelengths of 400–500 nm and 650–730 nm induce action potentials that last approximately 0.3 ms. The plant does not react to irradiation at wavelengths between 500 nm and 630 nm [68]. Another study showed the impact of light spectra on plant physiology. In this experiment involving greenhouse production, it was shown that changing the intensity and wavelength of light had an impact on the metabolism of a plant. Different types of artificial light were tested, and the responses of the plants were recorded [87]. In the development of a predictive model on *Laurus nobilis*, the characteristics of the stimulating light could be determined through the electrical responses of plants [46]. All these experiments using light stimulation allow us to affirm that electrical activities are perceived at different wavelengths at approximately 300 nm–750 nm. As a result, we can deduce that it is possible to find a relationship between the electrical signal of a plant and the daylight levels'.

### 4.3. Stimulation related to air pollution

Plants have sensory receptors to detect environmental stimuli. These can be electrochemical, optical, and mechanical transducers. Studies have shown that plants react to ions in the atmosphere [34,88,89]. They can detect air pollutants such as ozone [63]. Ozone ( $O_3$ ) is considered to be one of the most important air pollutants. In this context, several studies have alluded to the ability of plants to detect this type of pollutant [90–96]. In 1995, Karlsson and their colleagues stated that clover could be used as an ozone indicator [97]. In 2007, leaf lesions were observed on the Paluma de Guajava plant. These lesions were induced by the exposure of the plant to ozone. Since then, Paluma de Guajava has been considered a potential bioindicator of phytotoxic  $O_3$  levels in the tropics [91]. Similarly, the results of experiments on black cherry (*Prunus serotina*) [92], plants native to Switzerland [93], Egyptian plants (*M. sativa*) [94] and plants native to the northeastern United States and southern Spain [95] corroborate this hypothesis. In 2015, a wireless device network was designed to detect ground-level ozone. This device used electrical signals from plants to monitor environmental conditions. The objective was to analyze the air quality using an algorithm that took into account the wind speed and direction, temperature, humidity, precipitation, and solar radiation. The device was designed to detect ozone in the atmosphere [73]. In 2019, a study was carried out in India on four types of plants in two tropical forests. The objective of the study was to determine the ability of the plants to survive in environmental conditions highly polluted with heavy metals. The results made it possible to distinguish the impact of air pollutants on the plant organism. Moreover, it was noticed that some plants have a high tolerance to pollutants and could be exploited in the reduction of pollution [98]. In Poland, a study based on the same principle demonstrated the effects of air pollution on plants. The plants were placed in a park, near a road and a factory [99].

4.4. Thermal stimulation

There are few specific studies concerning the electrical responses of plants to temperature. Nevertheless, most experiments carried out on plants take temperature into account. Therefore, it can be concluded that temperature affects electrical signaling in a plant. In 2005, an experiment on poplar shoots (*Populustrichocarpa*, *Populus tremula* 3P. *tremuloides*) using thermal stimulation was carried out by Lautner and their colleagues. Several parts of the plant were stimulated by the flame of a lighter for 3 s. These areas were then cooled with 4°C ice water. Responses to the stimuli are noted by the depolarization and hyperpolarization of the membrane potential [100]. This study proves that plants respond to rapid temperature changes. In 2017, further work showed that plants also react to slow temperature changes. By measuring the internal resistance of a poplar for one year, it was noted that its value is high in winter and lower during other seasons when it is hot [58].

5. SWOT (strengths, weaknesses, opportunities, threats) analysis

In this section, we will perform a SWOT analysis on some of the experiments cited in this article. These experiments are chosen because they summarize in situ and artificial plant stimulation trials. SWOT analysis is a tool for internal and external diagnosis. This tool assists in the evaluation of a given activity or system. Intensive strengths and weaknesses as well as external opportunities and threats are evaluated to set objectives or make a choice.

6. Conclusion

So far, it has been proven that plants produce electrical signals. These signals are due to variations in their environment. Hypotheses have been developed and tested on the origin and mode of the propagation of these signals. Most of the models found that the electrical signals of the plant show that they are created at the cell level. The very first studies on the subject focused on mechanically sensitive plants such as *Mimosa pudica* and the carnivorous Venus flytrap plant. Analytical models and equivalent electrical circuits have been proposed to facilitate the understanding of the plant's electrical activities. Some research has led to the conclusion that the electrical signal in plants is due to sap flow. In situ experiments confirm this hypothesis by demonstrating that the signal varies according to the sap flow of the biological plant. However, other authors have found that this is not the only factor involved. With the same objective, researchers have conducted artificial experiments to determine the relationship between the signal emitted by the plant and various stimuli. These experiments were conducted in laboratories under specific conditions. The plants were placed on an antivibration table surrounded by a Faraday cage where the temperature was often kept constant. During these artificial tests, mechanical, electrical, chemical, and thermal stimulation were applied. The results of these experiments made it possible to determine the existence of electrical potentials. They were observed in the stem, root, and leaves depending on the stimulation and measurement methods. Additionally, different types of electrical signals, such as action potential, variation potential, system potential, and electrotonic potential, could be identified. These electrical signals were recorded and analyzed. There are several measurement methods, but they are always based on the use of electrodes. The electrodes can either be inserted into the cells (microelectrodes), placed on the surface (ECG electrodes), or inserted directly into the plant. Several experiments have been conducted on different types of plants, such as soybeans, *Mimosa Pudica*, poplar, oak, algae, and fruit trees. The interpretation of the obtained data shows that the electrical signals from plants can translate useful information related to climate variation. Similarly, studies show that the plant reacts to touch, mechanical pressure, various chemical agents, temperature, and irradiation. The use of the plant's sensory capacities to make measurements of climatic variables is certainly of interest. However, many parameters must be taken into account. By carrying out a SWOT analysis,

Table 2

Summarizes the different experiences cited in this article as well as their respective SWOT analyses.

Table 2: Summary of the experiments and SWOT analysis	
The experimental environment: In situ [67]	
Plant:	<i>Quercus cerris</i>
Stimulation:	environment
Objectives:	Identification of the annual variation in the amplitude of the daily electrical variation of a tree
Observation:	Annual variation in the amplitude of the electrical signal
STRENGTH	The use of the convolution filter technique allows useable average values to be obtained The measurement results are consistent The use of eight electrodes allows for more precise measurements compared to other experiments with two measuring electrodes
WEAKNESSES	Inserting the electrodes into the trunk of the tree requires the removal of bark from the area in question. The results are not directly useable (additional studies are required)
OPPORTUNITIES	The combination of the multielectrode technique and a specific data selection method will provide new information related to the behavior of plants concerning the environment
THREATS	Measured data are distorted during environmental disturbances (Amplitude change of the internal and external signal of the plant in function of her characteristics.) The trunk is nonhomogenous Environmental microvariation is present on the trunk
The experimental environment: In situ [59,63]	
Plant	<i>Populus nigra</i>
Stimulation	Environment
Objectives	Study of the spatial and temporal variations in the electrical potential distribution of a tree
Observation	Diurnal variation of the electrical potential during different seasons
STRENGTHS	The use of 26 electrodes and a long period results in for accurate and reliable measurements. The contact between the electrodes and the tree is protected against weather. The data acquisition system used is capable of recording in real-time The environmental constraints affecting the measuring device are initially and rigorously checked
WEAKNESSES	The weather conditions around the tree are measured by a weather station
OPPORTUNITIES	The experiment is performed on a single tree Possibility of assessing the effects of climate change by estimating the sap flow through the interpretation of the behavior of the tree's electrical signal
THREATS	The flow of sap determines factors in the tree's physiology. However, its study is complex because it depends on numerous parameters The electrode array may be influenced by temperature. The grounding electrodes may be unstable. There are transient signals whose amplitude increases with the height of the electrodes, and it is interesting to study the source of these signals
The experimental environment: In situ [58]	
Plant	<i>Populus nigra</i>
Stimulation	Environment
Objectives	Study of the characteristics of the internal electronic resistance of a tree and establishment of a reference
Observation	Internal resistance
STRENGTHS	Experimentation is long term

(continued on next page)

Table 2 (continued)

Table 2: Summary of the experiments and SWOT analysis	
WEAKNESSES	The designed measuring device allows several parameters to be recorded simultaneously (voltages, temperature, and humidity) The measurement of the internal resistance of the tree is indirect. It is calculated according to the value of two variable voltages. This variation can lead to calculation errors
OPPORTUNITIES	The consideration of the value of the internal resistance of a tree will result in a higher supply voltage
THREATS	The resistance of a tree has several components, and its value varies according to the environment
The experimental environment: Artificial [68]	
Plant	Soybean
Stimulation	Irradiation
Objectives	Description of long-distance plant communication
Observation	Electrical potential
STRENGTHS	The data acquisition system is a high performance system
WEAKNESSES	It is necessary to wait 1 h to 2 h to stabilize the electrical potential of the plant due to the insertion of the electrodes
OPPORTUNITIES	Bioelectrochemical measurement methods are exploitable in the study of signal propagation in the plant The use of the plant as a biosensor of red and blue light is possible
THREATS	The signal transfer mechanism at the cellular level remains complex
The experimentation environment: Artificial [69]	
Plant	<i>Dionaea muscipula</i> Ellis (Venus flytrap)
Stimulation	Electrostimulation
Objectives	Study of electrical activities in the fly trap of the carnivorous plant Venus
Observation	Electrical potential, mechanical response
STRENGTHS	A high-performance, real-time data acquisition system has been developed, and the results are validated with a second, equally high-performance device. The aliasing effect is eliminated due to high-speed recording The electronic control system for stimulation is equipped with optical isolation
WEAKNESSES	It is necessary to wait to stabilize the electrical potential of the plant due to the insertion of the electrodes. The share of the action of electrical stimulation has not been identified (triggering or participation in triggering the closure of the plant trapdoor)
OPPORTUNITIES	The plant allows fast signal transmission (high-precision biosensors)
THREATS	The tissues of higher plants are complex
The experimental environment: Artificial [70]	
Plant	<i>Dionaea muscipula</i> Ellis (Venus flytrap)
Stimulation	Charge injection
Objectives	Study of the closing mechanism of the flytrap of the carnivorous plant Venus
Observation	Electrical potential and mechanical response
STRENGTHS	Implementation of a new hydroelastic model of the closing mechanism The elastic property of plants is considered in the study
WEAKNESSES	It is necessary to wait to stabilize the electrical potential of the plant due to the insertion of the electrodes
OPPORTUNITIES	The new model will advance our understanding of the relationship between the stimuli and induced responses
THREATS	The tissues of higher plants are complex
The experimental environment: Artificial [72]	
Plant	<i>Mimosa pudica</i> pulvini
Stimulation	Charge injection

Table 2 (continued)

Table 2: Summary of the experiments and SWOT analysis	
Objectives	Study on the mechanism of movement of <i>Mimosa pudica</i> leaves
Observation	Electrical potential and mechanical response
STRENGTHS	Several types of electrical signals are found in the mimosa (action potentials, variation potentials, slow-wave potentials, and flux potentials)
WEAKNESSES	Three hypotheses are included in the mechanical response of the <i>Mimosa pudica</i> , but studies do not link them together It is necessary to wait 3 h–25 h to stabilize the electrical potential of the plant after insertion of the electrodes
OPPORTUNITIES	The proposed equivalent electrical circuitry is a reference for further studies on plant susceptibility The plant's sensitivity to wind, touch or vibration can be used as a climate biosensor The tissues of higher plants are complex
THREATS	The experimental environment: Artificial [27]
Plant	<i>Dionaea muscipula</i> Ellis (Venus flytrap)
Stimulation	Periodic wave electrostimulation
Objectives	Studies on the propagation of the electrotonic potential and its interaction with the action potential
Observation	Propagation of electric potential along the rod
STRENGTHS	A high-performance data acquisition system is used
WEAKNESSES	The study of electrical potentials at the level of a single cell is impossible in the plant
OPPORTUNITIES	The results can be used to clarify electrical communication at the plant cell level. The observation of electrical signals in plants could be an effective method for monitoring the state of environmental change The tissues of higher plants are complex
THREATS	The experimental environment: Artificial [55]
Plant	Red tubers of an Irish potato
Stimulation	Periodic wave electrostimulation
Objectives	Study of memory resistance in potato tubers
Observation	Memoristor
STRENGTHS	A high-performance data acquisition system is used The experiments were repeated 14 times
WEAKNESSES	The addition of chemicals to the soil results in a 48- to 90-h waiting period between stimulations
OPPORTUNITIES	The results can be references for future studies on the memory and daily behavior of plants The tissues of higher plants are complex
THREATS	The experimental environment: Artificial [28]
Plant	Golden Delicious and Arkansas Black apples ( <i>Malus domestica</i> Borkh.)
Stimulation	Periodic wave electrostimulation
Objectives	Study of the memory resistor and differential circuits in fruits
Observation	Memoristor
STRENGTHS	A high-performance data acquisition system is used The experiments were repeated 20 times
WEAKNESSES	The representation of the memory of the plant is in the form of complex electrical circuits composed of several basic electrical elements
OPPORTUNITIES	The results can be references for future studies on the electrochemical and electrophysiological properties of electrical activities in fruit The tissues of higher plants are complex
THREATS	The experimental environment: Artificial [52]
Plant	Pumpkin seed <i>Cucurbita pepo</i> L., cv. Cinderella, <i>Cucurbita maxima</i> L. cv Warty Goblin, and <i>Cucurbita maxima</i> L., cv. Jarrahdale
Stimulation	Periodic wave electrostimulation
Objectives	Study of the memory resistance in pumpkin seed
Observation	Memoristor
STRENGTHS	A high-performance data acquisition system is used

(continued on next page)

Table 2 (continued)

Table 2: Summary of the experiments and SWOT analysis	
WEAKNESSES	The experiments were repeated 20 times The representation of the memory of the plant is in the form of complex electrical circuits composed of several basic electrical elements
OPPORTUNITIES	The results will allow a better understanding of memory activities in seeds
THREATS	The tissues of higher plants are complex
The experimental environment: Artificial [29]	
Plant	Aloe Vera
Stimulation	Electrostimulation
Objectives	Study of the characteristics of the propagation of electrical potentials in Aloe Vera
Observation	Propagation of electrical potentials along a leaf
STRENGTHS	A high-performance data acquisition system is used The tests were performed with several types of electrodes
WEAKNESSES	The transport of the electrotonic potential is unknown (xylem or phloem)
OPPORTUNITIES	The proposed equivalent electrical circuit is a reference for other studies on the electrical activities of plants and the direct relationship with stimuli
THREATS	The tissues of higher plants are complex

the advantages related to this subject of study outweigh the disadvantages. The majority of the studies carried out on the subject conclude that the plant organism is complex but the opportunities are numerous and relevant. Studies conducted on the electrical activities of plants tend towards the same conclusion that applications such as environmental monitoring (detection of pollutants, pesticides, climate change) are possible. In this case, future research can be directed towards the use of plants as an environmental biosensors for meteorology prediction in a microclimate environment. Meteorological models adapted to the biological plant must therefore be developed in order to transform the biological plant into a biosensor. Table 2 summarizes the obstacles and therefore the future perspectives in the domain that could be the subject of further research.

#### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### References

- [1] T. Bhardwaj, Review on biosensor technologies, *Int. J. Adv. Res. Eng. Technol.* 6 (2) (2015) 27.
- [2] S. Bobade, D. Kalorey, S. Warke, Biosensor Devices: a review on their biological applications, 10.21786/bbrc/19.1/20, *Biosci. Biotechnol. Res. Commun.* 9 (1) (2016) 132–137. URL, [http://bbrc.in/bbrc/papers/pdf%20files/Volume%209%20-%20No%201%20-%20Apr%202016/BBRC6\\_020.pdf](http://bbrc.in/bbrc/papers/pdf%20files/Volume%209%20-%20No%201%20-%20Apr%202016/BBRC6_020.pdf).
- [3] N. Bhalla, P. Jolly, N. Formisano, P. Estrela, Introduction to biosensors, 10.1042/EBC20150001, *Essays Biochem.* 60 (1) (2016) 1–8. URL, <https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4986445/>.
- [4] A.A. Ciucu, C. Negulescu, R.P. Baldwin, Detection of pesticides using an amperometric biosensor based on ferophthalocyanine chemically modified carbon paste electrode and immobilized bienzymatic system, 10.1016/S0956-5663(02)00173-2, *Biosens. Bioelectron.* 18 (2) (2003) 303–310. URL, <http://www.sciencedirect.com/science/article/pii/S0956566302001732>.
- [5] O.V. Soldatkina, O.O. Soldatkin, T.P. Velychko, V.O. Prilipko, M.A. Kuibida, S.V. Dzyadevych, Conductometric biosensor for arginine determination in pharmaceuticals, 10.1016/j.bioelechem.2018.07.002, *Bioelectrochemistry* 124 (2018) 40–46. URL, <http://www.sciencedirect.com/science/article/pii/S1567539418301117>.
- [6] A. Amine, H. Mohammadi, I. Bourais, G. Palleschi, Enzyme inhibition-based biosensors for food safety and environmental monitoring, 10.1016/j.bios.2005.07.012, *Biosens. Bioelectron.* 21 (8) (2006) 1405–1423. URL, <http://www.sciencedirect.com/science/article/pii/S0956566305002198>.
- [7] P. Zhang, T. Sun, S. Rong, D. Zeng, H. Yu, Z. Zhang, D. Chang, H. Pan, A sensitive amperometric AChE-biosensor for organophosphate pesticides detection based on

- conjugated polymer and Ag-rGO-NH<sub>2</sub> nanocomposite, 10.1016/j.bioelechem.2019.02.003, *Bioelectrochemistry* 127 (2019) 163–170. URL, <http://www.sciencedirect.com/science/article/pii/S1567539418304134>.
- [8] F. Arduini, S. Cinti, V. Caratelli, L. Amendola, G. Palleschi, D. Moscone, Origami multiple paper-based electrochemical biosensors for pesticide detection, *Biosens. Bioelectron.* 126 (2019) 346–354, <https://doi.org/10.1016/j.bios.2018.10.014>. URL, <http://www.sciencedirect.com/science/article/pii/S0956566318308248>.
  - [9] X. Zhang, D. Wu, X. Zhou, Y. Yu, J. Liu, N. Hu, H. Wang, G. Li, Y. Wu, Recent progress in the construction of nanozyme-based biosensors and their applications to food safety assay, 10.1016/j.trac.2019.115668, *Trac. Trends Anal. Chem.* 121 (2019) 115668. URL, <http://www.sciencedirect.com/science/article/pii/S0165993619303474>.
  - [10] C. Griesche, A.J. Baeumner, Biosensors to support sustainable agriculture and food safety, 10.1016/j.trac.2020.115906, *Trac. Trends Anal. Chem.* 128 (2020) 115906. URL, <http://www.sciencedirect.com/science/article/pii/S0165993620301357>.
  - [11] J. Riu, B. Giussani, Electrochemical biosensors for the detection of pathogenic bacteria in food, 10.1016/j.trac.2020.115863, *Trac. Trends Anal. Chem.* 126 (2020) 115863. URL, <http://www.sciencedirect.com/science/article/pii/S0165993620300923>.
  - [12] B.M. Paddle, Biosensors for chemical and biological agents of defence interest, 10.1016/0956-5663(96)82333-5, *Biosens. Bioelectron.* 11 (11) (1996) 1079–1113. URL, <http://www.sciencedirect.com/science/article/pii/0956566396823335>.
  - [13] A.G. Volkov, M.I. Volkova, V.S. Markin, Phytosensors, Phytoactuators, 10.1149/05012.0003ecst, *ECS Trans.* 50 (12) (2013) 3–11. URL, <https://iopscience.iop.org/article/10.1149/05012.0003ecst>.
  - [14] R. Liu, Z. Li, Z. Huang, K. Li, Y. Lv, Biosensors for explosives: state of art and future trends, 10.1016/j.trac.2019.05.034, *Trac. Trends Anal. Chem.* 118 (2019) 123–137. URL, <http://www.sciencedirect.com/science/article/pii/S0165993619301025>.
  - [15] H. Mummert, D. Gradmann, Action potentials in *Acetabularia*: measurement and simulation of voltage-gated fluxes, 10.1007/BF01994359, *J. Membr. Biol.* 124 (3) (1991) 265–273, <https://doi.org/10.1007/BF01994359>. URL.
  - [16] E. Davies, Electrical signals in plants: facts and hypotheses, in: A.G. Volkov (Ed.), *Plant Electrophysiology: Theory and Methods*, Springer, Berlin, Heidelberg, 2006, pp. 407–422, [https://doi.org/10.1007/978-3-540-37843-3\\_17](https://doi.org/10.1007/978-3-540-37843-3_17). URL.
  - [17] A.G. Volkov, D.R.A. Ranatunga, Plants as environmental biosensors, *Plant Signal. Behav.* 1 (3) (2006) 105–115, <https://doi.org/10.4161/psb.1.3.3000>. URL.
  - [18] A.G. Volkov, M.I. Volkova-Gugeshashvili, A.J. Osei, Plants as environmental biosensors: non-invasive monitoring techniques, in: E.K. Yanful (Ed.), *Selected Technologies for Environmental Protection in the Developing World: Abstract Papers from ERTEP 2007, July 17–19 2007, Ghana, Africa*, Springer Netherlands, Dordrecht, 2009, pp. 349–356, [https://doi.org/10.1007/978-1-4020-9139-1\\_34](https://doi.org/10.1007/978-1-4020-9139-1_34). URL.
  - [19] V. Sukhov, E. Sukhova, V. Vodeneev, Long-distance electrical signals as a link between the local action of stressors and the systemic physiological responses in higher plants, *Prog. Biophys. Mol. Biol.* 146 (2019) 63–84, <https://doi.org/10.1016/j.pbiomolbio.2018.11.009>. URL, <http://www.sciencedirect.com/science/article/pii/S0079610718302153>.
  - [20] A.G. Volkov, S. Toole, M. WaMaina, Electrical signal transmission in the plant-wide web, *Bioelectrochemistry* 129 (2019) 70–78, <https://doi.org/10.1016/j.bioelechem.2019.05.003>. URL, <http://www.sciencedirect.com/science/article/pii/S1567539419301914>.
  - [21] A.G. Volkov, D.J. Collins, J. Mwesigwa, Plant electrophysiology: pentachlorophenol induces fast action potentials in soybean, *Plant Sci.* 153 (2) (2000) 185–190, [https://doi.org/10.1016/S0168-9452\(99\)00271-X](https://doi.org/10.1016/S0168-9452(99)00271-X). URL, <http://www.sciencedirect.com/science/article/pii/S016894529900271X>.
  - [22] X. Yan, Z. Wang, L. Huang, C. Wang, R. Hou, Z. Xu, X. Qiao, Research progress on electrical signals in higher plants, *Prog. Nat. Sci.* 19 (5) (2009) 531–541, <https://doi.org/10.1016/j.pnsc.2008.08.009>. URL, <http://www.sciencedirect.com/science/article/pii/S1002007109000161>.
  - [23] A.G. Volkov, R.A. Haack, Insect-induced bioelectrochemical signals in potato plants, publisher: Elsevier, *Bioelectrochem. Bioenerg.* 37 (1) (1995) 55–60, [https://doi.org/10.1016/0302-4598\(94\)01759-T](https://doi.org/10.1016/0302-4598(94)01759-T). URL, <https://www.sciencedirect.com/science/article/abs/pii/030245989401759T>.
  - [24] A. Kurenda, C.T. Nguyen, A. Chételat, S. Stolz, E.E. Farmer, Insect-damaged *Arabidopsis* moves like wounded *Mimosa pudica*, publisher: National Academy of Sciences Section: Biological Sciences, *Proc. Natl. Acad. Sci. Unit. States Am.* 116 (51) (2019) 26066–26071, <https://doi.org/10.1073/pnas.1912386116>. URL, <http://www.pnas.org/content/116/51/26066>.
  - [25] V. Sukhov, V. Nerush, L. Orlova, V. Vodeneev, Simulation of action potential propagation in plants, *J. Theor. Biol.* 291 (2011) 47–55, <https://doi.org/10.1016/j.jtbi.2011.09.019>. URL, <http://www.sciencedirect.com/science/article/pii/S0022519311004759>.
  - [26] A.G. Volkov, *Plant Electrophysiology: Signaling and Responses*, Springer Science & Business Media, 2012 google-Books-ID: OjlfVX665EC.
  - [27] A.G. Volkov, C.L. Vilfranc, V.A. Murphy, C.M. Mitchell, M.I. Volkova, L. Oâ€™Neal, V.S. Markin, Electrotonic and action potentials in the Venus flytrap, *J. Plant Physiol.* 170 (9) (2013) 838–846, <https://doi.org/10.1016/j.jplph.2013.01.009>. URL, <http://www.sciencedirect.com/science/article/pii/S0176161713000382>.
  - [28] A.G. Volkov, E.K. Nyasani, C. Tuckett, A.L. Blockmon, J. Reedus, M.I. Volkova, Cyclic voltammetry of apple fruits: memristors in vivo, *Bioelectrochemistry* 112 (2016) 9–15, <https://doi.org/10.1016/j.bioelechem.2016.07.001>. URL, <http://www.sciencedirect.com/science/article/pii/S1567539416300858>.



- [29] A.G. Volkov, E.K. Nyasani, C. Tuckett, J.M. Scott, M.M.Z. Jackson, E.A. Greeman, A.S. Greenidge, D.O. Cohen, M.I. Volkova, Y.B. Shtessel, Electrotonic potentials in *Aloe vera* L.: effects of intercellular and external electrodes arrangement, *Bioelectrochemistry* 113 (2017) 60–68, <https://doi.org/10.1016/j.bioelechem.2016.10.004>. URL, <http://www.sciencedirect.com/science/article/pii/S1567539416301438>.
- [30] A.G. Volkov, Y.B. Shtessel, Electrical signal propagation within and between tomato plants, *Bioelectrochemistry* 124 (2018) 195–205, <https://doi.org/10.1016/j.bioelechem.2018.08.001>. URL, <http://www.sciencedirect.com/science/article/pii/S1567539418300501>.
- [31] E. Król, H. Dziubińska, K. TrĄbacz, What Do Plants Need Action Potentials for? *Nova Science Publishers*, 2010, p. 26.
- [32] M.J. Beilby, H.G.L. Coster, The action potential in *Chara corallina* III.\* the Hodgkin-Huxley parameters for the plasmalemma, publisher: CSIRO PUBLISHING, *Funct. Plant Biol.* 6 (3) (1979) 337–353, <https://doi.org/10.1071/pp9790337>. URL, <https://www.publish.csiro.au/fp/pp9790337>.
- [33] M.J. Beilby, R.D. Keynes, N.A. Walker, R.D. Keynes, J.C. Ellory, Cl<sup>-</sup> channels in *Chara*, publisher: Royal Society. doi:10.1098/rstb.1982.0142, *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 299 (1097) 435–445. URL, <https://royalsocietypublishing.org/doi/abs/10.1098/rstb.1982.0142>.
- [34] E. Sukhova, E. Akinchits, V. Sukhov, Mathematical models of electrical activity in plants, 10.1007/s00232-017-9969-7, *J. Membr. Biol.* 250 (5) (2017) 407–423. URL, <http://link.springer.com/10.1007/s00232-017-9969-7>.
- [35] M.J. Beilby, *Chara braunii* genome: a new resource for plant electrophysiology, 10.1007/s12551-019-00512-7, *Biophys. Res. Commun.* 11 (2) (2019) 235–239, <https://doi.org/10.1007/s12551-019-00512-7>. URL.
- [36] D.-J. Zhao, Z.-Y. Wang, J. Li, X. Wen, A. Liu, L. Huang, X.-D. Wang, R.-F. Hou, C.-W. Recording extracellular signals in plants: a modeling and experimental study, 10.1016/j.mcm.2011.10.065, *Math. Comput. Model.* 58 (3) (2013) 556–563. URL, <http://www.sciencedirect.com/science/article/pii/S0895717711006704>.
- [37] D. Gradmann, J. Hoffstadt, Electrocoupling of ion transporters in plants: interaction with internal ion concentrations, 10.1007/s002329900446, *J. Membr. Biol.* 166 (1) (1998) 51–59, <https://doi.org/10.1007/s002329900446>. URL.
- [38] D. Gradmann, Impact of apoplast volume on ionic relations in plant cells, 10.1007/s00232-001-0074-5, *J. Membr. Biol.* 184 (1) (2001) 61–69, <https://doi.org/10.1007/s00232-001-0074-5>. URL.
- [39] D. Gradmann, Models for oscillations in plants, publisher: CSIRO PUBLISHING. doi:10.1071/pp01017, *Funct. Plant Biol.* 28 (7) (2001) 577–590. URL, <https://www.publish.csiro.au/fp/pp01017>.
- [40] V. Sukhov, V. Vodenev, A mathematical model of action potential in cells of vascular plants, 10.1007/s00232-009-9218-9, *J. Membr. Biol.* 232 (1–3) (2009) 59–67. URL, <http://link.springer.com/10.1007/s00232-009-9218-9>.
- [41] V. Sukhov, E. Akinchits, L. Katicheva, V. Vodenev, Simulation of variation potential in higher plant cells, 10.1007/s00232-013-9529-8, *J. Membr. Biol.* 246 (4) (2013) 287–296, <https://doi.org/10.1007/s00232-013-9529-8>. URL.
- [42] V. Sukhov, L. Surova, E. Morozova, O. Sherstneva, V. Vodenev, Changes in H<sup>+</sup>-ATP synthase activity, proton electrochemical gradient, and pH in pea chloroplast can be connected with variation potential, publisher: Frontiers. doi:10.3389/fpls.2016.01092, *Front. Plant Sci.* 7 (2016). URL, <https://www.frontiersin.org/articles/10.3389/fpls.2016.01092/full>.
- [43] L. Surova, O. Sherstneva, V. Vodenev, V. Sukhov, Variation potential propagation decreases heat-related damage of pea photosystem I by 2 different pathways, publisher: Taylor & Francis \_eprint, doi:10.1080/15592324.2016.1145334, *Plant Signal. Behav.* 11 (3) (2016), e1145334, <https://doi.org/10.1080/15592324.2016.1145334>. URL.
- [44] A. Hills, Z.-H. Chen, A. Amtmann, M.R. Blatt, V.L. Lew, OnGuard, a computational platform for quantitative kinetic modeling of guard cell physiology, publisher: American Society of Plant Biologists Section: CELL BIOLOGY AND SIGNAL TRANSDUCTION. doi:10.1104/pp.112.197244, *Plant Physiol.* 159 (3) (2012) 1026–1042. URL, <http://www.plantphysiol.org/content/159/3/1026>.
- [45] Y. Chen, D.-J. Zhao, Z.-Y. Wang, Z.-Y. Wang, G. Tang, L. Huang, Plant electrical signal classification based on waveform similarity, number: 4 Publisher: Multidisciplinary Digital Publishing Institute. doi:10.3390/a9040070, *Algorithms* 9 (4) (2016) 70. URL, <https://www.mdpi.com/1999-4893/9/4/70>.
- [46] S.K. Chatterjee, S. Ghosh, S. Das, V. Manzella, A. Vitaletti, E. Masi, L. Santopolo, S. Mancuso, K. Maharatra, Forward and inverse modelling approaches for prediction of light stimulus from electrophysiological response in plants, *Measurement* 53 (2014) 101–116. URL, <http://www.sciencedirect.com/science/article/pii/S0263224114001444>.
- [47] A.G. Volkov, C.L. Brown, *Electrochemistry of plant life*, in: A.G. Volkov (Ed.), *Plant Electrophysiology: Theory and Methods*, Springer, Berlin, Heidelberg, 2006, pp. 437–459, [https://doi.org/10.1007/978-3-540-37843-3\\_19](https://doi.org/10.1007/978-3-540-37843-3_19). URL.
- [48] A.G. Volkov, H. Carrell, V.S. Markin, Biologically closed electrical circuits in *Venus flytrap*, publisher: American Society of Plant Biologists Section: CELL BIOLOGY AND SIGNAL TRANSDUCTION, *Plant Physiol.* 149 (4) (2009) 1661–1667. URL, <http://www.plantphysiol.org/content/149/4/1661>.
- [49] A.G. Volkov, J.C. Foster, V.S. Markin, Signal transduction in *Mimosa pudica*: biologically closed electrical circuits, *Plant Cell Environ.* 33 (5) (2010) 816–827, eprint, <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1365-3040.2009.02108.x>. URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-3040.2009.02108.x>.
- [50] A.G. Volkov, J. Reedus, C.M. Mitchell, C. Tuckett, M.I. Volkova, V.S. Markin, L. Chua, Memory elements in the electrical network of *Mimosa pudica* L., e982029, publisher: Taylor & Francis \_eprint, *Plant Signal. Behav.* 9 (10) (2014), <https://doi.org/10.4161/15592324.2014.982029>.
- [51] B. Su, S. Gong, Z. Ma, L.W. Yap, W. Cheng, *Mimosa*-inspired design of a flexible pressure sensor with touch sensitivity, *Small* 11 (16) (2015) 1886–1891. URL, <https://onlinelibrary.wiley.com/doi/abs/10.1002/sml.201403036>.
- [52] A.G. Volkov, E.K. Nyasani, C. Tuckett, E.A. Greeman, V.S. Markin, Electrophysiology of pumpkin seeds: memristors in vivo, *Plant Signal. Behav.* 11 (4) (2016), e1151600, <https://doi.org/10.1080/15592324.2016.1151600> publisher: Taylor & Francis \_eprint.
- [53] V. Norris, C. Ripoll, M. Thellier, The theater management model of plant memory, *Plant Signal. Behav.* 10 (1) (2015), <https://doi.org/10.4161/15592324.2014.976157> e976157, publisher: Taylor & Francis \_eprint.
- [54] V.S. Markin, A.G. Volkov, L. Chua, An analytical model of memristors in plants, *Plant Signal. Behav.* 9 (10) (2014), <https://doi.org/10.4161/15592316.2014.972887> e972887, publisher: Taylor & Francis \_eprint.
- [55] A.G. Volkov, E.K. Nyasani, A.L. Blockmon, M.I. Volkova, Memristors: memory elements in potato tubers, *Plant Signal. Behav.* 10 (10) (2015), e1071750, <https://doi.org/10.1080/15592324.2015.1071750>.
- [56] A.G. Volkov, H. Carrell, T. Adesina, V.S. Markin, E. Jovanov, Plant electrical memory, *Plant Signal. Behav.* 3 (7) (2008) 490–492, <https://doi.org/10.4161/psb.3.7.5684>, publisher: Taylor & Francis \_eprint.
- [57] L.A. Gurovich, P. Hermosilla, Electric signalling in fruit trees in response to water applications and light–darkness conditions, *J. Plant Physiol.* 166 (3) (2009) 290–300. <http://www.sciencedirect.com/science/article/pii/S0176161708001727>.
- [58] Z. Hao, W. Li, J. Kan, J. Zhang, G. Wang, Internal resistance of a tree-based power source, *J. Renew. Sustain. Energy* 9 (6) (2017), 063104 publisher: American Institute of Physics, <https://aip.scitation.org/doi/10.1063/1.5011644>.
- [59] D. Gibert, J.-L. Le Mouél, L. Lambs, F. Nicollin, F. Perrier, Sap flow and daily electric potential variations in a tree trunk, *Plant Sci.* 171 (5) (2006) 572–584. URL, <https://linkinghub.elsevier.com/retrieve/pii/S0168945206001762>.
- [60] C.J. Love, S. Zhang, A. Mershin, Source of sustained voltage difference between the xylem of a potted *Ficus benjamina* tree and its soil, publisher: Public Library of Science, *PloS One* 3 (8) (2008), e2963. URL, <https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0002963>.
- [61] C. Himes, Using plants for directly powering nanoelectronic circuits, *Nanotechnol. Perceptions* 6 (1) (2010) 29–40. URL, <http://www.colbas.org/ntp/abstracts/N01H10A-abs.pdf>.
- [62] Z. Hao, K. Liu, W. Li, J. Zhang, J. Kan, X. Hao, Effects of electrode size on the voltage of a tree-based energy generator, *J. Renew. Sustain. Energy* 10 (4) (2018), 043101. URL, <http://aip.scitation.org/doi/10.1063/1.5032190>.
- [63] J.-L. Le Mouél, D. Gibert, J.-P. Poirier, On transient electric potential variations in a standing tree and atmospheric electricity, *Compt. Rendus Geosci.* 342 (2) (2010) 95–99. URL, <http://www.sciencedirect.com/science/article/pii/S1631071309002892>.
- [64] L. Chua, Memristor-The missing circuit element, *IEEE Trans. Circ. Theor.* 18 (5) (1971) 507–519, <https://doi.org/10.1109/TCT.1971.1083337>, conference Name: IEEE Transactions on Circuit Theory.
- [65] L. Chua, S.M. Kang, Memristive devices and systems, *Proc. IEEE* 64 (2) (1976) 209–223, <https://doi.org/10.1109/PROC.1976.10092>, conference Name: Proceedings of the IEEE.
- [66] L. Chua, Resistance switching memories are memristors, *Appl. Phys. A* 102 (4) (2011) 765–783, <https://doi.org/10.1007/s00339-011-6264-9>. URL.
- [67] A. Koppán, L. Szarka, V. Westergom, Annual fluctuation in amplitudes of daily variations of electrical signals measured in the trunk of a standing tree, *Compt. Rendus Acad. Sci. III Sci. Vie.* 323 (6) (2000) 559–563. URL, <http://www.sciencedirect.com/science/article/pii/S076444900001797>.
- [68] A.G. Volkov, T.C. Dunkley, S.A. Morgan, D. Ruff, Y.L. Boyce, A.J. Labady, Bioelectrochemical signaling in green plants induced by photosensory systems, *Bioelectrochemistry* 63 (1) (2004) 91–94. URL, <http://www.sciencedirect.com/science/article/pii/S1567539404000179>.
- [69] A.G. Volkov, T. Adesina, E. Jovanov, Closing of *Venus flytrap* by electrical stimulation of motor cells, *Plant Signal. Behav.* 2 (3) (2007) 139–145, <https://doi.org/10.4161/psb.2.3.4217>, publisher: Taylor & Francis \_eprint.
- [70] V.S. Markin, A.G. Volkov, E. Jovanov, Active movements in plants, *Plant Signal. Behav.* 3 (10) (2008) 778–783, <https://doi.org/10.4161/psb.3.10.6041>, publisher: Taylor & Francis \_eprint.
- [71] H. Maischak, M.R. Zimmermann, H.H. Felle, W. Boland, A. Mithöfer, Alamethicin-induced electrical long distance signaling in plants, *Plant Signal. Behav.* 5 (8) (2010) 988–990, <https://doi.org/10.4161/psb.5.8.12223>, publisher: Taylor & Francis \_eprint.
- [72] A.G. Volkov, J.C. Foster, K.D. Baker, V.S. Markin, Mechanical and electrical anisotropy in *Mimosa pudica* pulvini, *Plant Signal. Behav.* 5 (10) (2010) 1211–1221, <https://doi.org/10.4161/psb.5.10.12658>, publisher: Taylor & Francis \_eprint.
- [73] S. Morosi, M. Dolfi, E. Del Re, E. Masi, I. Colzi, S. Mancuso, F. Francini, R. Magliacani, A. Valgimigli, L. Masini, A WSN for ground-level ozone monitoring based on plant electrical activity analysis, in: 2015 International Wireless Communications and Mobile Computing Conference, IWCMC, 2015, pp. 715–720, <https://doi.org/10.1109/IWCMC.2015.7289171>, iSSN: 2376-6506.
- [74] R. Hedrich, E. Neher, *Venus flytrap*: how an excitable, carnivorous plant works, *Trends Plant Sci.* 23 (3) (2018) 220–234, <https://doi.org/10.1016/j.tplants.2017.12.004>. URL.
- [75] S. Lehtinen, Understanding the *Venus flytrap* through mathematical modelling, *J. Theor. Biol.* 444 (2018) 1–10, <https://doi.org/10.1016/j.jtbi.2018.02.003>. URL.



- [76] T. Shvetsova, J. Mwesigwa, A.G. Volkov, Plant electrophysiology: FCCP induces action potentials and excitation waves in soybean, *Plant Sci.* 161 (5) (2001) 901–909. URL, <http://www.sciencedirect.com/science/article/pii/S0168945201004848>.
- [77] A.Q. Ansari, D.J.F. Bowling, Measurement of the trans-root electrical potential of plants grown in soil, *New Phytol.* 71 (1) (1972) 111–117, <https://doi.org/10.1111/j.1469-8137.1972.tb04817.x>.
- [78] J. Fromm, S. Lautner, Electrical signals and their physiological significance in plants: electrical signals in plants, *Plant Cell Environ.* 30 (3) (2007) 249–257, <https://doi.org/10.1111/j.1365-3040.2006.01614.x>.
- [79] A.G. Volkov, H. Carrell, V.S. Markin, Molecular electronics of the *Dionaea muscipula* trap, *Plant Signal. Behav.* 4 (4) (2009) 353–354, <https://doi.org/10.4161/psb.4.4.8219>, publisher: Taylor & Francis\_eprint.
- [80] A.G. Volkov, J.C. Foster, T.A. Ashby, R.K. Walker, J.A. Johnson, V.S. Markin, *Mimosa pudica*: electrical and mechanical stimulation of plant movements, *Plant Cell Environ.* 33 (2) (2010) 163–173, eprint, <https://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1365-3040.2009.02066.x>.
- [81] S.N. Basir, H. Yusoff, N.I. Zahari, Simulation analysis of *mimosa pudica* Main Pulvinus towards biological tactile sensing modelling, *Procedia Comput. Sci.* 76 (2015) 425–429. URL, <https://linkinghub.elsevier.com/retrieve/pii/S1877050915037837>.
- [82] D. Loconsole, G. Cocetta, P. Santoro, A. Ferrante, Optimization of LED lighting and quality evaluation of romaine lettuce grown in an innovative indoor cultivation system, *Sustainability* 11 (3) (2019) 841, number: 3 Publisher: Multidisciplinary Digital Publishing Institute, <https://www.mdpi.com/2071-1050/11/3/841>.
- [83] A.G. Volkov, M.I. Volkova-Gugeshashvili, C.L. Brown-McGauley, A.J. Osei, Nanodevices in nature: electrochemical aspects, *Electrochim. Acta* 52 (8) (2007) 2905–2912, <https://doi.org/10.1016/j.electacta.2006.08.062>. URL, <http://www.sciencedirect.com/science/article/pii/S0013468606009431>.
- [84] J.J. Casal, Phytochromes, cryptochromes, phototropin: photoreceptor interactions in plants, *Photochem. Photobiol.* 71 (1) (2000) 1–11, eprint, <https://onlinelibrary.wiley.com/doi/pdf/10.1562/0031-8655%282000%290710001PCPPII2.0.CO2>.
- [85] S. Frechilla, L.D. Talbot, R.A. Bogomolni, E. Zeiger, Reversal of blue light-stimulated stomatal opening by green light, *Plant Cell Physiol.* 41 (2) (2000) 171–176, publisher: Oxford Academic, <https://academic.oup.com/pcp/article/41/2/171/1853516>.
- [86] T.E. Swartz, S.B. Corchnoy, J.M. Christie, J.W. Lewis, I. Szundi, W.R. Briggs, R.A. Bogomolni, The photocycle of a flavin-binding domain of the blue light photoreceptor phototropin, *J. Biol. Chem.* 276 (39) (2001) 36493–36500, publisher: American Society for Biochemistry and Molecular Biology, <http://www.jbc.org/content/276/39/36493>.
- [87] T. Ouzounis, E. Rosenqvist, C.-O. Ottosen, Spectral effects of artificial light on plant physiology and secondary metabolism: a review, *Hortscience* 50 (8) (2015) 1128–1135. URL, <https://journals.ashs.org/view/journals/hortsci/50/8/article-p1128.xml>.
- [88] T. Shvetsova, J. Mwesigwa, A. Labady, S. Kelly, D. Thomas, K. Lewis, A.G. Volkov, Soybean electrophysiology: effects of acid rain, *Plant Sci.* 162 (5) (2002) 723–731. URL, <http://www.sciencedirect.com/science/article/pii/S0168945202000134>.
- [89] D. Goyal, A. Yadav, T. Vats, Air pollution and its role in stress physiology, in: P. Saxena, A. Srivastava (Eds.), *Air Pollution and Environmental Health, Environmental Chemistry for a Sustainable World*, Springer, Singapore, 2020, pp. 115–140, [https://doi.org/10.1007/978-981-15-3481-2\\_6](https://doi.org/10.1007/978-981-15-3481-2_6). URL.
- [90] R.M. Moraes, A. Klumpp, C.M. Furlan, G. Klumpp, M. Domingos, M.C.S. Rinaldi, I.F. Modesto, Tropical fruit trees as bioindicators of industrial air pollution in southeast Brazil, 10.1016/S0160-4120(02)00060-0, *Environ. Int.* 28 (5) (2002) 367–374. URL, <http://www.sciencedirect.com/science/article/pii/S0160412002000600>.
- [91] C.M. Furlan, R.M. Moraes, P. Bulbovas, M. Domingos, A. Salatino, M.J. Sanz, *Psidium guajava* ‘Paluma’ (the guava plant) as a new bio-indicator of ozone in the tropics, 10.1016/j.envpol.2006.09.014, *Environ. Pollut.* 147 (3) (2007) 691–695. URL, <http://www.sciencedirect.com/science/article/pii/S0269749106005549>.
- [92] A. Chappelka, J. Renfro, G. Somers, B. Nash, Evaluation of ozone injury on foliage of black cherry (*Prunus serotina*) and tall milkweed (*Asclepias exaltata*) in Great Smoky Mountains National Park, 10.1016/S0269-7491(96)00120-0, *Environ. Pollut.* 95 (1) (1997) 13–18. URL, <http://www.sciencedirect.com/science/article/pii/S0269749196001200>.
- [93] J. Zhang, J.A. Ferdinand, D.J. Vanderheyden, J.M. Skelly, J.L. Innes, Variation of gas exchange within native plant species of Switzerland and relationships with ozone injury: an open-top experiment, 10.1016/S0269-7491(00)00175-5, *Environ. Pollut.* 113 (2) (2001) 177–185. URL <http://www.sciencedirect.com/science/article/pii/S0269749100001755>.
- [94] A.A. El-Khatib, The response of some common Egyptian plants to ozone and their use as biomonitors, 10.1016/S0269-7491(03)00045-9, *Environ. Pollut.* 124 (3) (2003) 419–428. URL, <http://www.sciencedirect.com/science/article/pii/S0269749103000459>.
- [95] T. Orendovici, J.M. Skelly, J.A. Ferdinand, J.E. Savage, M.J. Sanz, G.C. Smith, Response of native plants of northeastern United States and southern Spain to ozone exposures; determining exposure/response relationships, 10.1016/S0269-7491(03)00089-7, *Environ. Pollut.* 125 (1) (2003) 31–40. URL, <http://www.sciencedirect.com/science/article/pii/S0269749103000897>.
- [96] J. Peng, Y. Xu, B. Shang, L. Qu, Z. Feng, Impact of ozone pollution on nitrogen fertilization management during maize (*Zea mays* L.) production, 10.1016/j.envpol.2020.115158, *Environ. Pollut.* 266 (2020) 115158. URL, <http://www.sciencedirect.com/science/article/pii/S0269749120333339>.
- [97] G.P. Karlsson, G. Sellden, L. Skärby, H. Pleijel, Clover as an indicator plant for phytotoxic ozone concentrations: visible injury in relation to species, leaf age and exposure dynamics, *New Phytol.* 129 (2) (1995) 355–365, eprint, <https://nph.onlinelibrary.wiley.com/doi/pdf/10.1111/j.1469-8137.1995.tb04306.x>.
- [98] D. Karmakar, P.K. Padhy, Air pollution tolerance, anticipated performance, and metal accumulation indices of plant species for greenbelt development in urban industrial area, 10.1016/j.chemosphere.2019.124522. URL, *Chemosphere* 237 (2019) 124522, <http://www.sciencedirect.com/science/article/pii/S0045653519317461>.
- [99] I. Skrynetska, J. Karcz, G. Barczyk, M. Kandziora-Ciupa, R. Ciepał, A. Nadgórska-Socha, Using *Plantago major* and *Plantago lanceolata* in environmental pollution research in an urban area of Southern Poland, 10.1007/s11356-019-05535-x, *Environ. Sci. Pollut. Control Ser.* 26 (23) (2019) 23359–23371, <https://doi.org/10.1007/s11356-019-05535-x>. URL.
- [100] S. Lautner, T.E.E. Grams, R. Matussek, J. Fromm, Characteristics of electrical signals in poplar and responses in photosynthesis, 10.1104/pp.105.064196. URL, *Plant Physiol.* 138 (4) (2005) 2200–2209, <http://www.plantphysiol.org/lookup/doi/10.1104/pp.105.064196>.