BIOELECTRICITY
Volume 5, Number 1, 2023

DOI: 10.1089/bioe.2023.0011.editorial

Guest Editorial

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Bioelectricity in Plants: From So Simple a Beginning

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In the heady days of the Victorian era, a forward thinking British scientific community formulated, tested, and contested new scientific concepts with remarkable vitality. The ''Origin of the species'' and many other groundbreaking books had been recently published, primary scientific societies were increasingly opened to the public, and their proceedings reported in the popular press. Electricity had become a public and scientific fascination, and physicochemical discoveries were strongly linked to the dizzying pace of the industrial revolution. Overall, there was a generalized wonder at the power of science and what it could achieve.

In this climate, physiological botany emerged as a scientific pursuit with a primary emphasis on the possibility of mechanistic similarities between animals and plants. Although still somewhat zoocentric in nature, as a full appreciation of the scale of evolutionary history and the archaic origins of species required time to develop, the exploration of physiological commonalities was pursued by many of the notable biologists of the period. Darwin himself discussed the plant digestion, sensitivity, and other ''animal-like'' properties in his 1875 book *Insectivorous Plants*. J. Burdon-Sanderson, a contemporary of Darwin's son Francis and eventually a Regius professor at the University of Oxford, was intrigued by these observations. In the period from 1873 to 1880 Darwin and Burdon-Sanderson met frequently, exchanged materials through his son Francis and exchanged over 60 catalogued and curated[1] letters on the subject, right until Darwin's death in 1882.

Although in most of this correspondence the main theme was digestion, on August 13, 1873, Burdon-Sanderson drifted from the main subject and wrote, ''…It has occurred to me that it would be very interesting to show that when the Drosera leaf is excited the same electrical changes occur as in muscle & nerve. If you think so, it would not be difficult to plan an experiment. The fact if it can be demonstrated, would afford additional evidence of the identity of the processes.'' Two days after (August 15) Darwin responded: ''I should think that it would be extremely interesting to ascertain whether there is any electrical change in the leaves of Drosera when they are excited; but I should think Dionæa would be much better for the purpose'' (Fig. 1a). Sanderson worked quickly, and 3 months later communicated to the Royal Society his results on the Venus flytrap, including the observations:[2]

''(…) **Negative variation—a**. If, the leaf being so placed on the electrodes that the normal leaf-current is indicated by a deflection, a fly is allowed to creep into it, it is observed that the moment the fly reaches the interior (so as to touch the sensitive hairs on the upper surface of the lamina), the needle swings to the right, the leaf at the same time closing on the fly. **b**. The fly having been caught does not remain quiet in the leaf; each time it moves, the needle again swings to the right, always coming to rest in a position somewhat further to the left than before, and then slowly resuming its previous position. **c**. The same series of phenomena present themselves if the sensitive hairs of a still expanded leaf are touched with a camel-hair pencil.'' And so Burdon-Sanderson described the first plant bioelectric phenomenon in the form of what we would today call an action potential[3] when describing a bioelectric response that evolved in carnivorous plants to capture animal preys.

It is appropriate that on the 150th anniversary of this accomplishment, we revisit the state of the art of bioelectricity in plants. It is especially relevant that it comes in the form of a special issue within a journal that emerged from the necessity to provide a conceptual space for the discussions of the paradigms inherent to BioElectricity. These processes that intrigued and fascinated Darwin and Burdon-Sanderson, keep us busy today as they are among the most intriguing biological phenomena still requiring a full comprehension.

The Long and Winding Road to Contemporary Plant Bioelectricity

Warranting justice to Darwin's suggestion to examine *Dionaea* 150 years ago, many of the principles at stake in these early discussions are still being experimentally addressed using the Dionaea system due to its unique electrophysiological properties and adaptations. The genome has been described and experimentation with the system has

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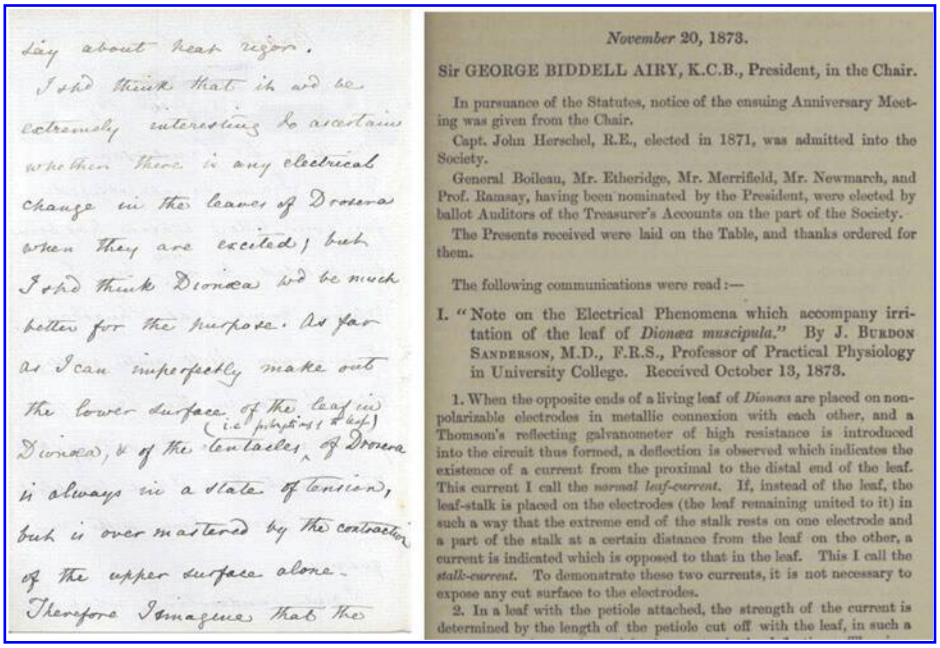

say about heat rigor.
I shd think that it wd be
extremely interesting to ascertain
whether there is any electrical
change in the leaves of Drosera
when they are excited; but
I shd think Dionaea wd be much
better for the purpose. As far
as I can imperfectly make out
the lower surface of the leaf in
(i.e. properties of the leaf)
Dionaea, & of the tentacles of Drosera
is always in a state of tension,
but is over mastered by the contraction
of the upper surface alone.
Therefore I imagine that the

November 20, 1873.

Sir GEORGE BIDDELL AIRY, K.C.B., President, in the Chair.

In pursuance of the Statutes, notice of the ensuing Anniversary Meeting was given from the Chair.

Capt. John Herschel, R.E., elected in 1871, was admitted into the Society.

General Boileau, Mr. Etheridge, Mr. Merrifield, Mr. Newmarch, and Prof. Ramsay, having been nominated by the President, were elected by ballot Auditors of the Treasurer's Accounts on the part of the Society.

The Presents received were laid on the Table, and thanks ordered for them.

The following communications were read:—

I. "Note on the Electrical Phenomena which accompany irritation of the leaf of *Dionæa muscipula*." By J. Burdon Sanderson, M.D., F.R.S., Professor of Practical Physiology in University College. Received October 13, 1873.

1. When the opposite ends of a living leaf of *Dionæa* are placed on non-polarizable electrodes in metallic connexion with each other, and a Thomson's reflecting galvanometer of high resistance is introduced into the circuit thus formed, a deflection is observed which indicates the existence of a current from the proximal to the distal end of the leaf. This current I call the *normal leaf-current*. If, instead of the leaf, the leaf-stalk is placed on the electrodes (the leaf remaining united to it) in such a way that the extreme end of the stalk rests on one electrode and a part of the stalk at a certain distance from the leaf on the other, a current is indicated which is opposed to that in the leaf. This I call the *stalk-current*. To demonstrate these two currents, it is not necessary to expose any cut surface to the electrodes.

2. In a leaf with the petiole attached, the strength of the current is determined by the length of the petiole cut off with the leaf, in such a

FIG. 1. Left: Facsimile of a letter from Darwin to Burdon-Sanderson, suggesting the usage of *Dionea* (venus flytrap) to test the hypothesis that plants could have an electrically stimulated mechanism of motion as animals do. Right: Facsimile of the 1873 publication of Burdon-Sanderson in the Proceedings of the Royal Society, reporting the first evidence of a bioelectric phenomenon in plants (Ref.[2]). Color images are available online.

revealed how action potentials are generated by different channels,[4,5] as well as how these mechanism interface with the digestive processes of digestion that so fascinated Darwin.[6]

But like in many other areas of biology, new experimental approaches required appropriate instrumentation. Crucial for Burden-Sanderson were the instruments invented by German pioneer Emil du Bois-Reymond, considered the father of electrophysiology. Among his inventions, the German scientist created neutral means of coupling instruments to tissue, invented the ''magneto-electrometer'' (AC generator), the ''rhecord'' (potentiometer) and the galvanometer, which was sensitive enough to record his results. With these devices, du Bois-Reymond was able to detect the first action currents in frog muscles in 1843.[7]

Following du Bois-Reymond footsteps, Jagadish Chandra Bose, a polymath credited for exceptional discoveries and insight in many areas (e.g., microwave, radio, and physics of materials) invented many instruments adapted for various plant physiology applications (Fig. 2). By the end of the 19th century, Bose had invented specialized tools to measure many features of plants (e.g., the ''crescograph'' to measure growth), and had explored multiple species that exhibited animal-like ''irritability'' (e.g., *Mimosa pudica*). Bose produced an unrivalled body of literature on plant bioelectricity (Fig. 2). His most outstanding contribution to the field of biophysics is considered to be the demonstration of the electrical nature of the conduction of various stimuli (e.g., wounds and chemical agents).

Umrath subsequently found the filamentous algae *Nitella* to be the best model organism for the first ever demonstration of an action potential by means of an intracellular electrode in 1930[8] (Fig. 3), two decades before a similar achievement was reported for animals.[9] The first measurements of resting membrane potentials in roots[10] would inaugurate an extremely proficuous decade for plant physiology, with many of the hydric and mineral relationships in plants being elucidated by means of electrophysiological experimentation.

The 1970s witnessed the rising of the new patch-clamp methods invented by Erwin Neher and Bert Sakmann in Germany, which ultimately led them to the Nobel prize. Up until today, this method is the single most relevant to the study of individual channels and membrane biology. Its application to plant cells was nevertheless delayed by the nature of plant cell walls. The requirement for direct attachment of the electrode to the plasma membrane implies the cell wall as a serious limitation to the application of patch-clamp in plants. This hurdle was finally circumvented by two teams in Germany and the United States, which almost simultaneously showed the feasibility of patch-clamping after enzymatically removing the cell wall to produce protoplasts (cell-wall naked plant cells).[11,12]

These demonstrations effectively paved the way to the utilization of many of the methods developed for neurobiology and have supported the development of new paradigms in plant bioelectricity field making this area vibrant and thriving. Interestingly, plants have much more negative membrane potentials, an enormous dependence on electric-based phenomena associated to the transport of ions from the soil, their translocation through the plant body and the regulation of gas traffic by stomata, raising unique conceptual questions. Vindicating Darwin and Burdon-Sanderson curiosity about the ''animal-like'' properties of plants, plants have been shown to propagate defensive signals through long-distance slow electric potential waves[13–15] (Fig. 4) many of which are dependent on ionotropic glutamate receptors, the very same hallmark of neurons and neural communication.[16]

In This Issue on Bioelectricity in Plants

This issue covers a wide range of topics and levels of organization, from electron transfer biology during photosynthesis, to organismic competition and mutualism during plant biotic interactions.

Man and colleagues explore oxygenic photosynthesis mechanisms, where light and chlorophyll interaction result in

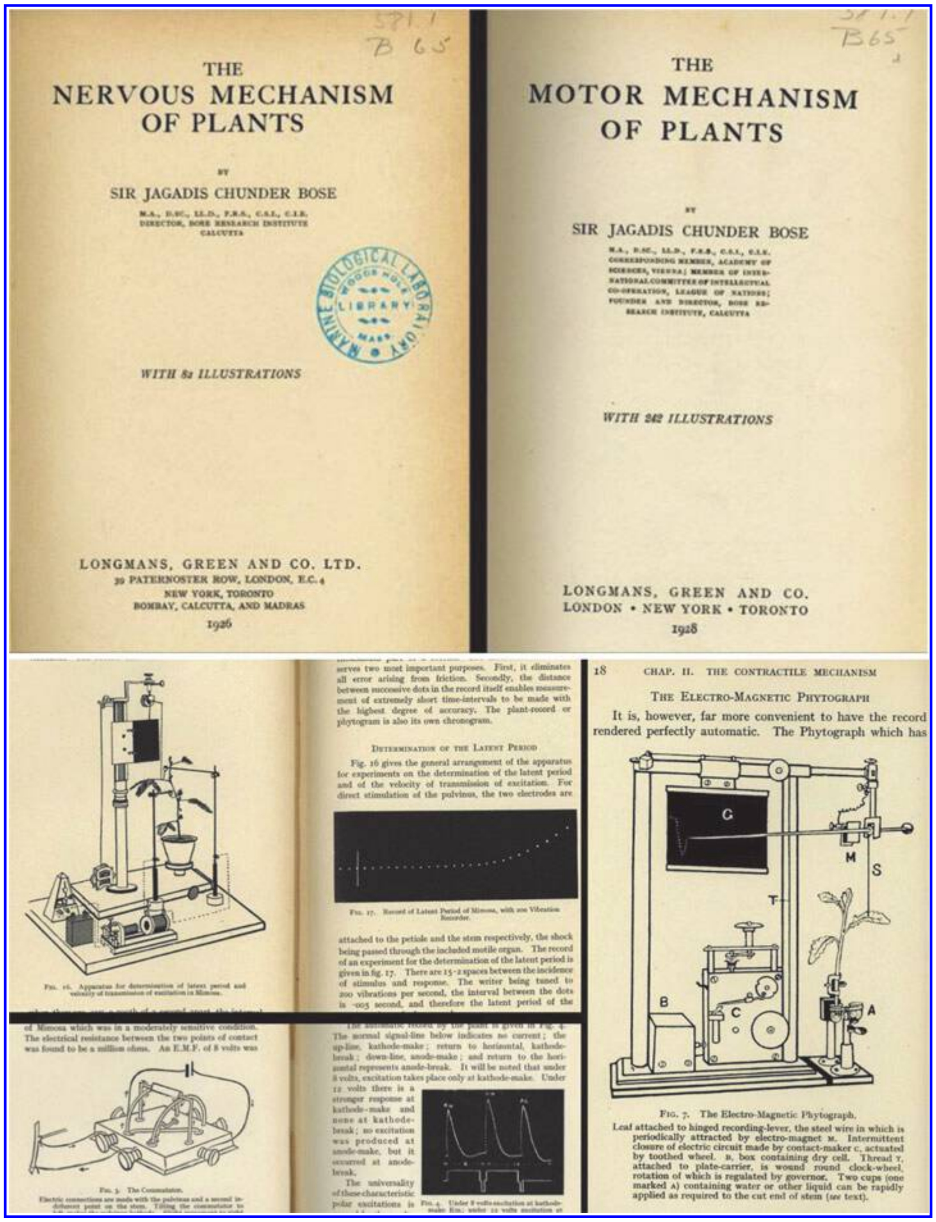

FIG. 2. Top: Facsimiles of two of the most prominent *magnum opuses* of Sir Jagadish Chandra Bose that revolutionized our knowledge of bioelectricity in plants and continue to inspire successive generations ever since. Bottom: Facsimiles of various devices that Bose invented and developed to record bioelectric or growth patterns in plants. Counterclockwise, apparatus for determination of latent period and velocity of transmission of excitation in *Mimosa*, and respective trace; device to record electric variations between the pulvinus and the second indifferent point on the stem of *Mimosa*, and respective record of the excitation patterns in the form of action potentials; the ''electro-magnetic phytograph'' that records temporal series of contractile responses of parts of a plant, namely leaves.

quantum phenomena not completely understood. The energy from these interactions leads to the breakdown of the water molecule, releasing the oxygen that feeds all respiratory phenomena of life in this planet, and two bioelectric, membrane-based, phenomena. On the one hand, electrons are released to energize a compact set of proteins and lipids, where electrons are transferred down ladders of redox potentials to produce Reduced Nicotinamide Adenine Dinucleotide Phosphate. On the other hand, protons are partitioned between two compartments into a Mitchell canonical chemosmotic system to generate Adenosine TriPhosphate (ATP).

These two molecules transfer the photonic energy to the production of carbon polymers that feed earth's ecosystems. The chapter by Nixon's group provides a textbook approach to these processes, systematically highlighting the unknown aspects and caveats of the current understanding of photosynthesis, as well as new approaches that might be employed to optimize productivity. These are hot topics, in times where completely synthetic methods of generating food from electricity generated by photovoltaic panels start to constitute alternative proof of principle for the ''green'' photosynthesis.[17]

Brownlee and Wheeler write an authoritative review of the field of Ca^{2+} signaling in plants and algae, with a focus on cell polarity and tip growth, and a wide coverage of all channels and mechanisms that may be involved in these processes. Brownlee was for decades the director of the prestigious *Marine Biology Association Laboratory of Plymouth* and a leader in experimentation with algal membrane biology and Ca^{2+} signaling. Among others he has studied algae from different groups namely *Fucus*, *Chlamydomonas*, and more recently Coccolithophores and diatoms. The diatoms would be the organism used to one of his latest major breakthroughs, the finding that these organisms possess functional equivalents to the Ca^{2+}/Na^{+} four-domain channel proteins that underpin many of the fast-gating properties behind the properties of the animal nervous system.[18]

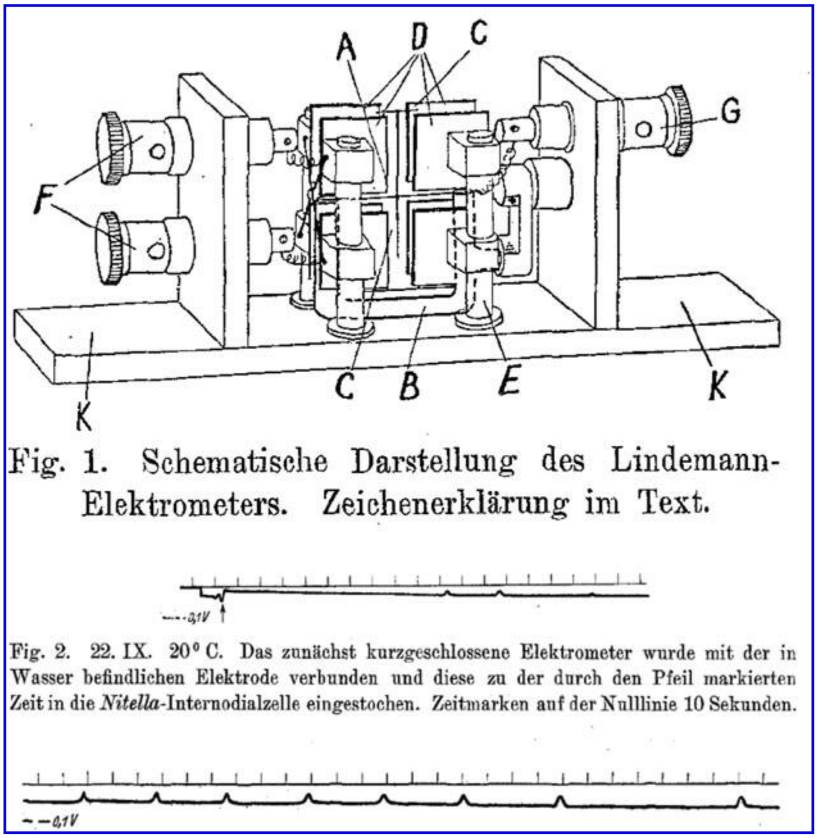

FIG. 3. Top: Diagram of the ''electrometer'' used by Umrath to impale filaments of the green algae *Nitella* and record the first intracellular action potentials of any cell, shown in the middle and bottom traces (adapted from Ref.[8]).

No land plant possesses an equivalent system, thus lacking the possibility of generating millisecond-like action potentials. These channels were thought to have evolved on the animal lineage alone, but Brownlee and his team showed that a one-domain channel with similar fast-gating properties evolved in diatoms, and is used for fast locomotion, relaunching the whole debate of when and why fast channels supporting millisecond action potentials may have initially evolved. These and many aspects related to the anatomy of ion transport and signaling, the inherent basis of bioelectric phenomena, are described by one of the more relevant names in the area for decades.

Next, Corti and colleagues extend the discussion of bioenergetic endo-symbiotic organelles to mitochondria, specifically addressing the elusive functional cross talk between mitochondria and chloroplasts. Team leader Ildiko Szabo has been long associated with the description and characterization of one of the most relevant ion channels for mitochondria function, the elusive mitochondrial calcium uniporter.[19] She has also been involved in the characterization of plant glutamate receptor phenotypes associated with Ca^{2+}.[20]

Now the team builds on these and other pieces of evidence to propose a coordinated action of Ca^{2+} and reactive oxygen species as a way of synchronizing the response of plant cells

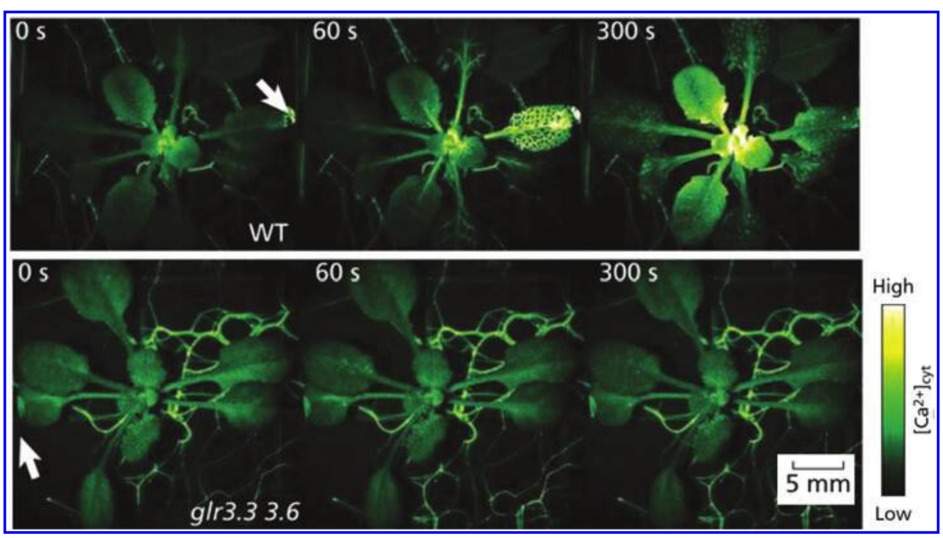

FIG. 4. Top: Temporal series of propagation along the whole plant, leaf by leaf, of a glutamate induced (arrow) wave of electric potential as reported by a Ca^{2+} sensor. Bottom: The same experiment but using plants mutated for the Arabidopsis glutamate receptors 3.3 and 3.6, showing no propagation of the signal (adapted from Ref.[15]).

to environmental signals. Both mitochondria and plastid have highly energized membrane systems, with membrane potentials compatible to their functions, and inherently these mechanisms should bear the existence of bioelectric patterns in the form of specific choreographies of membrane potential and ionic concentration that Corti and colleagues now propose to integrate in a new functional model.

Nunes and Feijó introduce readers to the pollen tube with a new perspective. Pollen tubes have long been known to generate the largest extracellular electric fields around any cell,[21,22] and in the past decades this group and others have systematically deconstructed the various ionic components that underlie this electric field, and their molecular mechanisms. Here the authors go a step forward, by revisiting a previous hypothesis that the polarized distribution of channels and pumps could generate a cytosolic standing electric field.[23] The detailed knowledge of localization of various transport proteins, activities, and phenotypes (e.g., the AHA-type H^+-ATPases[24]), and the quantification of the conspicuous apical gradients of various ions (Ca^{2+}, H^+, Cl^-, and possibly K^+) allow for better supported predictions of membrane voltage gradients and eventual cytosolic electric fields. If these hypotheses receive full experimental validation, they could have relevant impact in our current understanding of cell polarity and formation of intracellular domains.

In the only experimental article of this collection, Li and colleagues also explore the uniqueness of the pollen tube system to dissect the differential choreographies of cytosolic H^+ and Ca^{2+} variations, arguably the two most relevant ionic second messengers. For this purpose, they use a novel dual Ca^{2+}/pH probe (CapHensor) designed by leading author Kai Konrad.[25] The specificities of this probe, which expresses two probes on equimolar concentration and balanced fluorescence, enable high temporal and spatial sensitivity. Li and colleagues explored these properties to generate detailed maps and correlations between the activities of these two second messenger ions, and opens the door to new interpretations of macroscopic phenomena by synchronization of waves and oscillations associated to ion activity and electric potential.

Morato and Sena provide a discussion on the provocative field of bioelectric interaction and putative communication between plant roots and microbes and then move to insect–flower interactions. The authors make an extensive revision of diverse fields and provide a detailed account of various levels of organization and interactions where physiological electric fields may have a functional impact in plant biology. Among others, mycorrhization and nodulation in the root, as well as electric interactions during pollination are the focus of special attention.

The *pièce de résistance* of the present issue comes in the form of an autobiographic account by Dale Sanders. The format is the one that the journal has been establishing as a trademark closing article for special issues, ''My experiments in BioElectricity.'' Active for more than three decades, Sanders has been an international reference and leader in all-things ion transport and related physiological consequences. Picking up on all the excitement inherent to the knowledge about channels that patch-clamp brought, gearing much of the research in the 1980s, Sanders built a career from doctoral and postdoctoral training on some of the best laboratories, before landing at a position in the University of York.

There, he helped establishing what would be some of the highest standards in the fields of plant membrane biology and electrophysiology. His account on how some of these discoveries unfolded is well revealing of the finesse of his intellectual method. Many of his associates became leaders on his own. He edited and reviewed and became a driving force behind the series of tri-annual International Workshops in Plant Membrane Biology (this year in its 19th iteration in Taipei[26]), the most representative meeting for people involved in researching plant bioelectricity, directly or indirectly. Among many accolades, he became a fellow of the Royal Society, and his laboratory quickly became known both by the quality of the work and by an amazing productivity, during many years putting out a solid article every month on average.

Later in his life Dale became the director of the prestigious John Innes Research Center and, in difficult conditions, helped keeping the John Innes for years as the number one BioMedical Institution in the world in terms of research indicators. Although surely that implied a major constraint in terms of focus in practicing science, he continued to collaborate and leading many high-impact research projects, such as the elucidation of plant signaling after aphid attack,[27] or the discovery of the elusive Ca^{2+} channel that promotes the Ca^{2+} nuclear oscillations that trigger nodulation in the roots of legumes.[28]

Although this special issue does not have the ambition of a thorough coverage of everything happening in the field of plant BioElectricity, we feel confident that it makes for a good showcase for the many directions to where the field is evolving. In the year in which we commemorate the 150 years of the pioneering studies of Burdon-Sanderson, we hope that this collection may be inspiring and contribute to the visibility of a field that gave so much to science in general and in Plant Biology in particular.

Acknowledgments

Special thanks to Angus Murphy, Custodio Nunes, Colin Brownlee, and Marta Rufino for the careful and swift revision of the article that greatly improved its content and readability.

Author Disclosure Statement

No competing financial interests exist.

Funding Information

J.A.F. lab is supported by the National Institute of Health (R01-GM131043) and the National Science Foundation (MCB-1930165).

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