Bioelectricity and the rhythms of sensitive plants – The biophysical research of Jagadis Chandra Bose

V. A. Shepherd

Nearly a hundred years ago, J. C. Bose began biophysical experiments on plants and came to some far-reaching conclusions. He was the first to recognize the ubiquitous importance of electrical signalling between plant cells in co-ordinating responses to the environment. He may have been the first to discover electrical 'pulsations' or oscillations in electric potentials and he proved that these were coupled with rhythmic movements in the telegraph plant Desmodium. Bose theorized that regular wave-like 'pulsations' in cell electric potential and turgor pressure were an endogenous form of cell signalling. He put forth a radical theory for the mechanism of the ascent of sap, based on electromechanical activities of living cells. Bose's place in history has now been re-evaluated, and he is credited with the invention of the first wireless detection device and the discovery of millimetre length electromagnetic waves. This paper is a re-appraisal of some of his neglected research into plants.

The cells of most, perhaps all, plants are excitable. Stimuli such as chilling, heating, cutting, touching, electric stimulus or changes in external osmolarity result in action potentials, transient depolarizations of cell membrane which are electrotonically transmitted at rates of 10–40 mm/sec and which resemble primitive nerve action potentials[1]. Until recently, the hegemony of plant biologists has been reluctant to view action potentials as of primary significance in plant responses. The principal reason for this was the discovery of the ubiquitous chemical signal auxin, but socio-political factors, such as institutional nationalism, racism and sexism, and the use of plants in parapsychology, have contributed[1]. Some prominent plant electrophysiologists have long argued that multi-functional electric signals (action potentials) are primarily responsible for co-ordinating plant responses to the environment[1–4]. Pickard[2] and Davies[3,4] proposed that a 'protease inhibitor inducing factor', a wound signal, could be electrical rather than chemical. This view has been confirmed by Wildon *et al.*[5], who showed that initiation of pin (proteinase inhibitor) genes in response to wounding in tomato leaves is not brought about by a chemical signal, but electrically, by transmitted action potentials. This has brought about a shift in attitude from that espousing the predominance of chemical signalling in plants to one emphasizing electrical signalling[6] – the very principle J. C. Bose sought to establish seventy years before.

The great Indian scientist Jagadis Chandra Bose (1858–1937) was one of the first biophysicists. His earliest research concerned generating and detecting electromagnetic radiation. Bose invented a device for generating 5 mm waves, and the 'self-recovering coherer' (a semi-conducting diode) for receiving microwaves[7–9]. Recently, it has been proved that a slightly modified version of this device was used by Marconi to receive the first transatlantic wireless signal in 1901, without acknowledgement of the real inventor[10]. In 1901, Bose turned his attention to experimenting with bioelectric potentials and movements in plants, believing that the meeting point between the physical, inorganic world and the world of the living was to be found in the action of electromagnetic waves. Over the next thirty years Bose performed hundreds of experiments on electrical signalling in plants. In 1999, what can we make of this research, which its author viewed as his most significant, eclipsing even the discovery of mm-waves and invention of the wireless receiver?

The irritability of plants, the ascent of sap and the nervous mechanism of plants

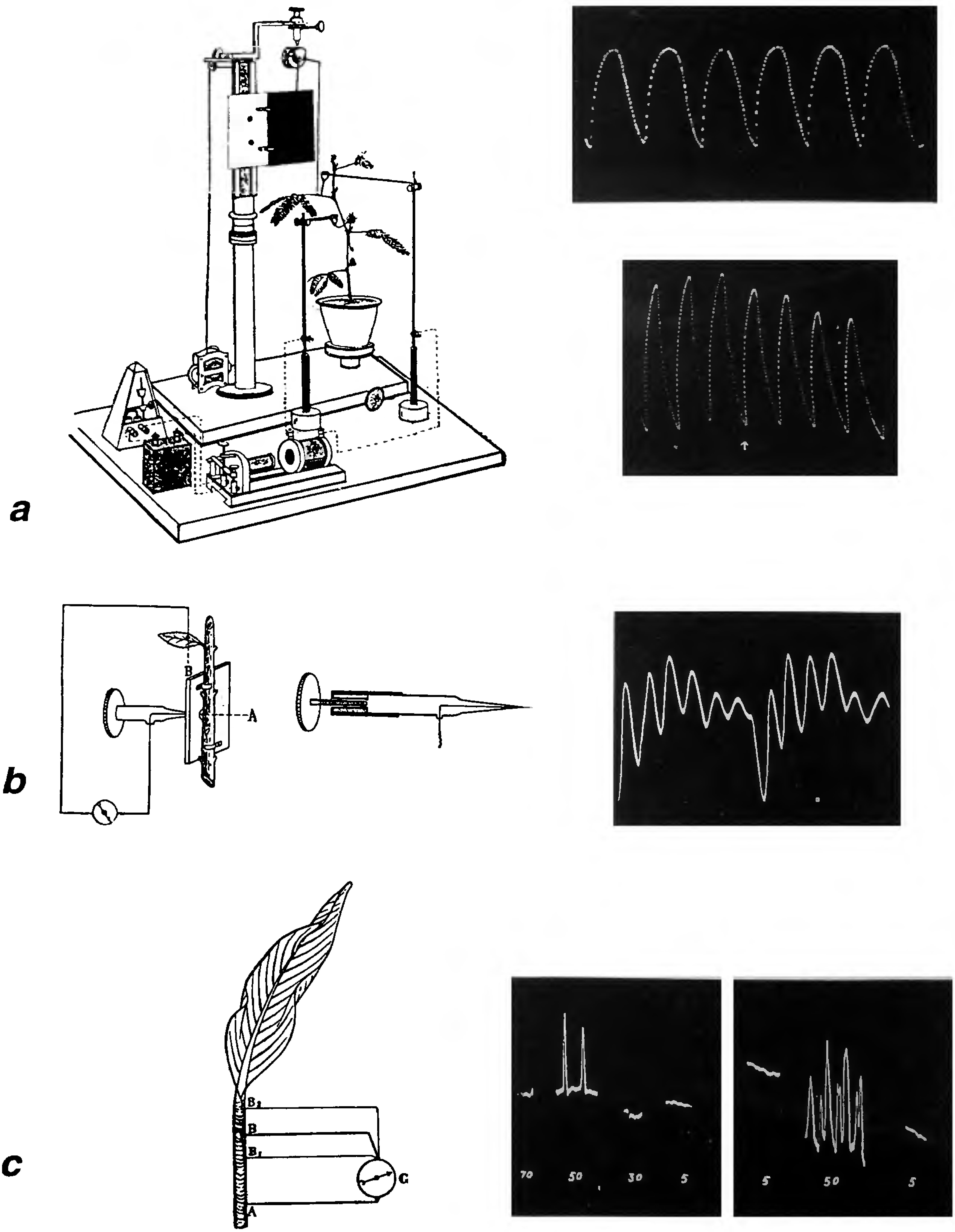
Bose was so prolific a researcher and writer that only three of his books are considered here – '*Researches into the Irritability of Plants*'[11], '*The Ascent of Sap*'[12] and '*The Nervous Mechanisms of Plants*'[13]. These books are read as an inseparable, nonlinear whole, with methods, results and discussion interspersed between them, in a style very different from the modern short paper with its standardized format.

Materials

We have only to look into the nearest garden to be impressed with the fact that plants respond to changes in their environment. A time-lapse camera shows that all plants move, through growth, but at so slow a rate we can scarcely detect it. Bose selected plants which gave dramatic responses to stimuli or displayed obvious intrinsic rhythms. The sensitive plant *Mimosa* folds its leaflets or dips the entire leaf when stimulated. The telegraph plant, *Desmodium*, exhibits a remarkable 'spontaneous' gyration of the lateral leaflets, resulting from rhythmic up and down movements. Bose also examined a range of other species including other plants capable of obvious movements e.g. beans (*Phaseolus* sp) and *Biophytum*, as well as favourites of plant physiology such as *Impatiens*, and *Chrysanthemum*, trees such as *Ficus* and the mango, and monocotyledons including palms. The difficult experiments required sophisticated apparatus, some of which Bose adapted from his earlier physical research.

Methods for measurement of the mechanical response in Mimosa and Desmodium, and measurement of electric potentials in plant tissues

Mechanical responses (dropping of leaves, leaf movements) were measured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using a device akin to the modern chart-recorder, the resonant recorder, and the oscillating recorder (Figure1 *a*; Bose[11]). With these Bose measured very small (mm) leaf movements at narrow (< 1 to 2 sec) time intervals.

Bose compared the effects of mechanical stimulation (scratching, touching, heating, and chilling) with those produced by electrical stimulus via miniature electrodes (Figure 1 *a*) which he connected with the plant in various arrangements (e.g. petiole/leaf, or pulvinus/stem, or leaf/pulvinus in *Mimosa*). Currents were measured with a 'microamperemetre', with a 'feeble' stimulating current pulse being about 8 μA (Bose[11]), so feeble that the sensitive tip of the human tongue could not detect it (Bose[13]). He apparently tested this on himself.

The electrical responses of the plant itself, in response to mechanical or other stimulation were recorded with an electric probe (Figure 1 *b*; Bose[13]). He made careful anatomical drawings of stained sections of *Mimosa* and other tissues, which he related, by size, to the positioning of the electric probe.

Bose had previously solved frustrating technical problems such as degradation of metallic contact surfaces in the hot and humid climate of Bengal, but this was nothing compared to living material, which he quickly found varied in responsiveness according to season, vigour, water status, temperature, age and previous history of stimulation. Such variability might have stumped a less astute and persistent researcher but Bose turned it to advantage, systematically investigated these effects, and established as a general principle the inseparability of bioelectric and environmental phenomena. e.g. '... It is impossible to dissociate ... from ... the age of a given leaf its past history as regards the stimulus of sunlight' (Bose[11], p. 267).

Having selected an 'ideal' plant material, with an established experimental set-up, and having eliminated the obfuscating effects of biological variability, Bose compared the effects of electrical and mechanical stimuli in *Mimosa*, *Desmodium* and numerous other plants. He experimented on the effects of changes in turgor pressure (by varying hydrostatic pressure with a U-tube, or using osmotically active chemicals), sudden changes of temperature (with an electrically regulated thermal chamber, a hot probe or chilled water), and inhibitory poisons such as KCN or anaesthetics such as chloroform and ether.

His main results and conclusions with Mimosa and Desmodium

The major conclusion of Bose[11,13] was radical. As animals had receptors where stimuli were received, a conductor (the nerve) which electrically propagated the stimulus, and an effector, or terminal motor organ, so too did plants. A stimulus was transmitted electrically to the motor organ, the pulvinus in both *Desmodium* and *Mimosa*. The major conduction pathway (established with electric probe) for transmitting the electrical excitation was the phloem. Mechanical stimulation could be mimicked by electrical stimulation. Strong electric stimulus of the pulvinus made *Mimosa* leaves dip, without mechanical stimulation, and a cut in *Desmodium* stalk prevented the rhythmic leaf movements, but these were restored by an electric current passing through the pulvinus. Transmission of the response was strongly temperature-dependent and influenced by light-levels. Repeated stimuli meant fatiguing and loss of excitatory response.

The excitatory response was a wave of protoplasmic, electrotonic excitation, which depended on living cells. The response in *Mimosa*, and rhythmic movements in *Desmodium* were blocked by KCN, $CuSO_4$, sudden application of ice water and chloroform.

Transmission of stimulus was electrotonic since an electrotonic block (two electrodes placed 5 mm apart in between the pulvinus and the point of stimulation, with a constant current maintained between them) stopped the response.

Velocity of transmission was affected by season, temperature, light, vigour of the plants, and age of the organ where it

Figure 1. Some of Bose's equipment and some measurements he made with it.

a, The resonant and oscillating recorder (reproduced from Bose[11]). This device had 'frictionless' jewelled bearings, a fine lightweight horizontal lever connected to the pulvinus or leaf, and a vertical lever for writing the response on a smoked glass plate, which moved at a uniform rate using a clockwork mechanism. The illustration shows a *Mimosa* plant ready for measurement of leaf movements.

The records to the right show, first, the up and down movements of the leaflets of the telegraph plant *Desmodium* (reproduced from Figure 145, Bose[11]). Individual dots are 2 sec apart. The *x* axis shows time, the *y* axis shows displacement, measured with oscillating recorder. This leaf was measured in summer and the whole period is about a minute, although in winter this increased to 4–5 min. The graph below this shows the effect of increasing the hydrostatic pressure using a U-tube (arrow). The *Desmodium* leaflet erected in response (reproduced from Figure 146, Bose[11]).

Currents were produced in plant tissues via miniature electrodes connected with parts of the plant via a saline kaolin paste or saline thread. Stimulation was produced using an induction coil, with a primary coil (some turns of soft iron wire) and a secondary coil (with a large number of wire turns – see bottom of illustration) connected to the stimulating electrode. A current in the primary coil (by pressing a key) induced a 'make' current in the secondary coil. A 'break' induction current of opposite direction was initiated by removing pressure from a key. The current intensity was changed by moving the primary and secondary coils closer or further apart using a slide, giving a graduated range of 12 V EMF (Bose[11]). He also used a Pohls reverser (Bose[13]) so that he could generate a constant current, make the current enter through the stem and exit through the pulvinus, or enter the pulvinus and exit through the stem. Currents were measured with a 'microamperemetre', with a 'feeble' stimulating current being about 8 μA (Bose[11]).

b, The electric probe (EP) (reproduced from Bose[13]). The tip of the probe was in circuit with a sensitive Einthoven galvanometer, and the device could be driven, by small (0.1 mm) increments into the tissue by turning the screw (Bose[13]). The accompanying graph shows periodic groupings of the electrical pulsations in *Desmodium* (reproduced from Figure 69, Bose[13] – not to scale with Figure 1). These accompanied the mechanical oscillations of leaflet position shown in Figure 1. The *x* axis shows time, the *y* axis shows potential difference (PD). The period of each pulsation is about 1 min – the same as the period of leaf movements shown in ***a***.

c, The method for measuring the pulse width of cellular 'pulsations' in the inner layer of cortical cells abutting the endodermis (reproduced from Figure 78, Bose[13]). By careful positioning of the EP, Bose calculated that the length of pulsations was in the mm range. One electrode of the EP was in a fixed position, the other moveable. There was little PD when the electrodes were close together, but when they were progressively moved apart up the stem, a maximum PD was found between them that corresponded to half the width of the pulsation. The accompanying records show the measurement of pulse width in *Chrysanthemum* (100 mm). The numbers below the graphs (*x* axis) refer to the distance between electrodes. The maximum PD (the *y* axis) was found at 50 mm, half the pulse width (reproduced from Figures 79 and 80, Bose[13]).

was measured. In summer, the electrotonic excitation in *Mimosa* was 30 mm/sec, in winter, it was 5 mm/sec. In a thick petiole, it was 55 mm/sec, in a thin petiole, it could reach 400 mm/sec. In winter, the period of 'leaf-clapping' rhythm of *Desmodium* was ~4 min, in summer this increased to 1 min.

Turgor decrease and cell contraction, accompanied by an electrical response of 'galvanometric negativity' followed stimulation, electrical or mechanical, and led to leaf-dipping in *Mimosa* and the 'downstroke' of the *Desmodium* leaflet (Figure 1 *a*). Restoration of leaf position was due to an increase in turgor of the pulvinus, and an intrinsic electrical response of 'galvanometric positivity'. Although the measurements were qualitative (deflection of the galvanometer needle) what matters is the opposite polarity. 'Galvanometric negativity' might have occurred as groups of cells depolarized, and 'galvanometric positivity' when cells hyperpolarized.

The mechanical up and down gyrations of the *Desmodium* leaflet (Figure 1 *a*) were associated with rhythmic alternations between 'galvanometric negativity' and 'galvanometric positivity' of the pulvinus (Figure 1 *b*). The electrical pulsations had the same period as the upstroke ('galvanometrically positive') and downstroke ('galvanometrically negative') of the leaflet and the alternations in cell turgor, contraction and expansion.

From these results, Bose generalized that all strong stimuli produced a decrease in turgor pressure, a contraction of cells, a transient diminution of growth rate, a negative mechanical response (such as dropping of leaves) and an electric response of 'galvanometric negativity'[13]. Feeble stimuli produced directly opposite effects, increase of turgor, expansion of cells, transient increase in growth rate and an electric response of 'galvanometric positivity'.

A theory of ascent of sap

Inspired by his results with *Desmodium*, Bose used electric probes to measure periodic electrical 'pulsations', from 0.4 to several mV, in the inner layer of cortical cells abutting the endodermis of the herbaceous plants *Impatiens*, *Chrysanthemum*, *Canna*, tomato, grapevine and potato; in bananas and palms, and in mango, fig and *Nauclea* trees. The electrical 'pulsations' were recorded on a smoked glass plate, resulting in a 'galvanograph' (Figure 1 *c*). As with *Desmodium*, these were periodic electromechanical pulsations with cell contraction and turgor loss associated with the electrically 'galvanonegative' part of the pulse, and the expansion and swelling of the cells with the 'galvanopositive' part. The sap was injected into the xylem by expulsive contraction, and the xylem was '... viewed as a reservoir, water being pumped in or withdrawn according to circumstance' (Bose[12], p. 221). The ascent of sap was caused by a propagated hydraulic wave of contraction preceded by expansion, squeezing the sap forward.

Bose applied the treatments (e.g. variation in hydrostatic pressure, tonic condition, and temperature, application of anaesthetics and poisons) he had used with *Mimosa* and *Desmodium*. Passage of constant current, or increased temperature, enhanced pulsations. Plasmolyzing agents (e.g. KNO_3) added to the roots arrested the pulsations, as did diminished turgor and poisons such as KCN. The pulsations were maximal at noon and changed in amplitude during the course of a day.

Bose reasoned that if all the inner cortical cells pulsed or contracted at the same moment, there would be no injection of water through into the xylem. Thus there had to be a phase difference. He found that pulsations had very long pulse-widths (e.g. 100 mm in *Chrysanthemum*, 50 mm in *Musa* and 40 mm in *Canna*), small amplitudes (0.4 to a few mV, in *Nauclea*) and a period of 14 sec to several minutes (Figure 1 *c*). We can only wonder what the discovery of these waves in living things meant to Bose, who had generated and detected 5 mm waves using decidedly inanimate materials.

The relevance of Bose's plant research today

Seasonal effects, effects of light and temperature on plant cell electrophysiology

Today, intracellular microelectrodes allow us to measure the actual electric potentials across the plasmalemma of plant cells, and giant characean algal cells have been particularly suitable for such studies. It is now clear that electrophysiological properties can change seasonally and with cell age. For example, in the giant alga *Chara*, the cell membrane potential difference (PD) is significantly less hyperpolarized (less negative) in winter, when plants are vegetative, and hyperpolarizes again immediately before fructification in the spring, which is associated with changes in patterns of cell-to-cell communication[14,15]. Sucrose concentration and ion content, particularly of K^+, varies seasonally in *Chara vulgaris*, again associated with the reproductive cycle[16]. This is not restricted to charophytes – cells of the excitable insectivorous plant *Dionea* also have lower PDs over winter[17]. The action potential shows a definite temperature dependency in *Nitella*[18]. In another alga, the unicell *Eremosphaera*, darkening after illumination causes a transient hyperpolarization of the cell PD due to divalent cation, and anion currents[19]. Turgor pressure and electrophysiology are indeed linked. Hypotonic shock in the cells of *Lamprothamnium*, a salt-tolerant charophyte, results in depolarization, opening of Ca^{2+} channels, efflux of Cl^- and then of K^+, resulting in turgor pressure regulation[20]. The process differs in cells of different age or from different environments[21,22].

Excitability of plant cells

Excellent comprehensive reviews of plant action potentials are found in literature[1–4,23]. The weight of arguments that electrical signalling is of vital importance in plant responses[2–4] is now undeniable following the experiments of Wildon *et al*[5]. Bose argued all along the importance of electrical signalling in plants, and the world has now come around to this view.

Bose conceived of the plant's response to strong stimulus as consisting of associated electrical and mechanical phenomena – turgor loss coupled with electric response (galvanometric negativity) and contraction of cells. This is reflected in modern concepts of plant action potentials. Today a plant action potential is understood as an abrupt depolarization of cell membrane PD followed by a slower decay to the negative resting PD, and can be described by the co-operative kinetics of Ca^{2+}, Cl^- and K^+ ion channels in plasmalemma and tonoplast[1,24,25]. It can be produced mechanically (by touch, injury, chilling, heating) or electrically (by introducing a depolarizing current). Depolarization results from an influx of Ca^{2+}, which stimulates an efflux of Cl^-, followed by a voltage-dependent K^+ efflux[23]. Depolarization is coupled with water efflux and loss of turgor[26] and a transitory contraction of the cell, measured by laser interferometry in single characean cells[27]. Bose presented evidence that action potentials travelled predominantly in the phloem, and today it is understood that action potentials travel both intracellularly and extracellularly (apoplastically). Eschrich *et al.*[28] found that an electrical signal transmitted through the phloem moves between fruit and petiole in zucchini, with the PD in the fruit related to that in the petiole. Patterns of light-induced 'spiking' were transmitted through the apoplast to unilluminated parts of several different plant species[29].

Apoplastic potentials and electrophytograms

Bose was probably measuring extracellular (apoplastic) potentials. Gensler and Diaz-Munoz[30] simultaneously measured apoplastic electropotentials and cotton stem diameter before and after rainfall and irrigation. Stems contracted during the day and expanded at night. Stem expansion followed irrigation, and this was associated with a sudden immediate large drop in electropotential. This resembles the galvanopositive response measured by Bose. Gensler and Yan[31] placed a palladium electrode in the stem and a reference palladium electrode in the root zone of tomato plants. They found a stable, reproducible large negative potential (~ – 400 mV), which gave characteristic potential/time fluctuations. These were directly related to the condition of the plant, its water status, and atmospheric changes. The potential/ time fluctuations were presented as 'electrophytograms', because they resembled cardiograms or encephalograms. The results were interpreted in the light of changes in oxygen concentrations in the apoplast, due to changes in metabolic activity of the cells[31]. They may represent the same phenomena as Bose's galvanographs.

Electrical oscillations in Desmodium, and their association with rhythmic leaf movements

Desmodium has continued to fascinate plant cell electrophysiologists. The elegant experiments of Antkowiak *et al.*[32,33] and other earlier studies[34,35] support Bose's much earlier work. These authors show that gyration of leaflets is indeed caused by rhythmic changes in the turgor pressure of pulvinar cells, which are coupled with periodic oscillations of membrane PD. Antkowiak and Engelmann[32] found that the leaflet moved downwards when the motor cells were depolarized (intracellular PD was ~ – 36 mV), the extracellular PD was negative, and the cells were contracted, losing turgor. By contrast, leaflets moved upward when the motor cells were hyperpolarized (– 136 mV), the extracellular PD was positive, the cells expanded, and turgor pressure increased[32,33]. Like Bose, Antkowiak *et al.*[33] found that increased temperature shortened the period of oscillations. Furthermore, an anaesthetic (enflurane) abolished the movements[32], as Bose had found with chloroform. Interest in the role played by intrinsic electrical oscillations in plant cells is increasing and some of the research is summarized in Table 1.

Bose viewed electromagnetic radiation as the fundamental link between inanimate and animate parts of the world. Of great interest with respect to his emphasis on intrinsic pulsations with their own specific wavelength is the finding[36] that pulsed radiofrequency fields transiently alter the amplitude, period and phase of the leaflet rhythms in *Desmodium*.

Today there is increasing interest in the effects on living things of radiofrequency and mm-wave irradiation, and pulsed electric fields on living systems. Some examples are summarized in Table 2. Whilst it might be expected that some thermal effects on cells would be found, Pickard and Barsoum[37] argued that nonthermal effects also occur. Bose's con-

Table 1. Some documented electrical oscillations in plant, and other cells

Organism or system	Type of oscillation	Effect of oscillations	Authors
Corn roots	H^+ and Ca^{2+} ion concentrations	Associated with ion transport in elongating roots	Shabala *et al.*[43]
Commelina guard cells	Cytosolic Ca^{2+} ion concentration	Control of stomatal aperture	McAinsh *et al.*[44]
Phaseolus (bean) roots	Spontaneous electrical oscillations	Oscillation frequency directly related to rate of growth	Souda *et al.*[45]
Lepidium sativum roots	Spontaneous oscillations in electrical potential	Oscillation occurrence and frequency related to growth	Hecks *et al.*[46]
Phaseolus (bean) roots	Extracellular oscillations in electric potential, intracellular oscillations at interface of xylem and parenchyma	Oscillations have largest amplitude in growth zone	Toko *et al.*[47]
Oat protoplasts	Red and far-red illumination induces oscillations in Ca^{2+}	Not specified	Volotovski *et al.*
Papaver (poppy) pollen tubes	Pulsatile Ca^{2+} spikes	Gradient in Ca^{2+} oscillations and concentration associated with tip growth	Calder *et al.*[48]
Enzymes, animal, plant and fungal cells	Review of cellular oscillators		Rapp[49]

Table 2. Some documented effects of electromagnetic radiation of living organisms

Type of electromagnetic radiation	Organism or system	Effect	Authors
Radiofrequency (RF) bursts	*Chara braunii, Nitella flexilis*	Athermal rectifier response of cell membrane	Pickard and Barsoum[37]
50 Hz magnetic fields	Mammalian cell monolayers and spheroids	Change in cAMP, stimulation of intercellular communication through gap junctions	Schimmelpfeng *et al.*[50]
2450 MHz	Cabbage plants and cabbage maggots	Lethal effects	Biron *et al.*[51]
2450 MHz	Colorado potato beetle, potato plants	Lethal effects	Colpitts *et al.*[52]
2450 MHz	Rat brain cells	DNA single-strand breaks	Lai and Singh[53]
2450 MHz	Cultured mammalian cells	No effects	Malyapa *et al.*[54]
835.62 and 847.74 MHz (*cellular phone frequencies*)	Cultured mammalian cells	No effects	Malapaya *et al.*[55]
High rate of stimulation, low intensity mm waves (41–51 GHz)	Frog nerves	Change in amplitude and velocity of action potential	Pakhamov *et al.*[56]
Induced 27 or 2450 MHz RF fields	Theoretical cell model	Effects on membrane and cell water	Liu and Cleary[57]
DC electric fields	*Mytilus* immunocytes	Immunocyte activation, increased membrane permeability to Ca^{2+}	Stefano *et al.*[58]
Pulsed mm microwaves (54–76 GHz)	Lipid bilayer membranes	Change in membrane capacitance	Alekseev and Ziskin[59]
Rectangular radiopulses	Balsam leaves	Change in cell membrane potential	Petrov and Betskii[60]
Pulsed electric fields	Theoretical tissue cells	Change in cell membrane potential	Cooper[61]
Pulsed electric fields	Bone fractures	Promotion of healing	Basset *et al.*[62]
Constant electric field, 5 V cm^{-1}	Cultured *Xenopus* cells	Change in cell shape, actin distribution	Luther *et al.*[63]
Pulsed RF (21.12 MHz) radiation	*Desmodium* leaflets	Perturbation of amplitude, period and phase of endogenous leaflet rhythm	Ellingsrud and Johnsson[36]

tention that electromechanical waves were intrinsic to signal transmission in plants could be re-considered in the light of new data (Tables 1 and 2). Electromagnetic radiation could potentially influence living cells by perturbing the endogenous rhythms proposed by Bose.

The ascent of sap

Bose's theory of the ascent of sap depended on electromechanical pulsations of living cells. Bose contradicted, and was frankly dismissive of, the 'tension-cohesion' theory of Dixon and Joly, first proposed in 1894, and widely accepted[38] from about 1925. It is still the most accepted theory[39]. Bose considered it 'inconceivable'[12], 'far-fetched'[13] and did not believe evidence that '... the water columns ... could possess the necessary tensile strength ... the cavities of the wood vessels and tracheids contain air bubbles which must impair their cohesion' (Bose[12], p. 2). In the theory, the xylem functions like a wick, with the force pulling the water to the tree-tops originating in the large evaporative surface of the leaves. Here, small (3–5 nm) pores between cellulose microfibrils sustain large negative pressures (tensions) in the water columns, which resist cavitation.

Recently, Canny proposed an alternative theory (the compensating-pressure theory) backed by strong experimental evidence, where living cells do play a crucial role[40–42]. In brief, living cells close to the xylem provide 'compensating pressure' (CP) which refills the xylem when it cavitates, as it begins to do early in the day. Large tensions do not exist in the xylem. Their reported measurements are instead measurements of CP which is matched to the increasing rate of transpiration (and of embolism) by hydrolysis of starch to sugar in living cells, increasing osmotic pressure, and providing a 'squeeze' which refi embolizing vessels when needed. . is required in the roots, and located in the endodermis, whicl as a one-way valve, due to the sn (~ 5 nm) of pores traversing it, a barrier containing the pressure. If the CP theory promises to rew understanding of plant water r and start a flood of new experimei

The CP theory owes nothing t but it does validate his skepticisı the ability of water columns to substantial tensions without ca' and his view that living cell essential to the ascent of sap. His concept that water was injected xylem by the definite electri mechanical pulsations or oscilla the living cells differs from theory, but, like the CP theor located crucial 'valving' or 'p cells at the junction with the end It might be fruitful to attempt t some of his technically difficult experiments, and determine whether such periodic electrical oscillations, with wavelengths varying according to environmental conditions, and coupled to the rate of transpiration, do indeed occur.

Conclusion

J. C. Bose died in 1937 and his theories of electrical signalling and electromechanical oscillations in plant cells became obscure. Today, electrical oscillations in plant cells are of great interest (Table 1). There is also considerable interest in effects of microwaves on living things (Table 2). Bose's contention that coupled electrical and mechanical pulsations or oscillations are fundamental to life-processes in plants seems less far-fetched in 1999 than in the decades immediately after his death, when the discovery of chemical signalling through auxin and wide acceptance of the tension–cohesion theory pushed Bose's work to the far fringes of orthodox plant physiology.

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V. A. Shepherd is in the Department of Biophysics, School of Physics, The University of NSW, 2052, Australia.