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ACKNOWLEDGEMENT. We thank Sri Lanka Institute of Nanotechnology and Hayleys Agro Ltd, Sri Lanka for financial support.

Received 7 February 2011; revised accepted 19 May 2011

Long distance electrical signalling in jute plant

Prajjal Datta and P. Palit*

Plant Physiology Section, Central Research Institute for Jute and Allied Fibres, Barrackpore 700 120, India

To gain an understanding of the velocity and mechanism of electrical signalling for long-distance communication in plants, a slender jute (*Corchorus capsularis* L.) stem was provided with a train of electrical pulses through a specially designed microelectrode at the phloem region. The propagated electric signal was detected at a distance 150 cm above the input region. The applied square pulses were reduced considerably and modified to curved ones at the output point. The signal moved extracellular with a measured velocity of almost nanoseconds from input to output electrode. Several hypotheses for such rapid electrical signalling are proposed.

Keywords: Electrical signal, jute plant, long-distance communication, square and curved waves.

*For correspondence. (e-mail: palitpratip@gmail.com)

CULTIVATED jute (*Corchorus* spp.) is a C3 dicotyledonous woody annual herb¹. It produces a commercially important natural lignocellulose fibre from the stem bark². Under commercial cultivation jute plants grow unbranched, erect and often attain a height of 3 m at maturity. During vegetative growth it behaves like a steady-state plant, where the source and sinks are well compensated³.

In every multicellular plant, growth of the various plant parts requires coordinated signalling between plant cells⁴. Almost 100 years ago, Jagadis Chandra Bose⁵ viewed the electrical signalling between plant cells as of primary significance in response to external stimuli. In subsequent years most plant biologists emphasized on the transduction of stimuli into some form of chemical signal and their transport to the responsive parts⁶⁻⁸. Some others argued that multifunctional electric signals (action potentials (APs)) rather than chemicals could be primarily responsible for long-distance signal transmission in plants⁹⁻¹⁷. Wildon *et al.*¹¹ showed the chemical signals evoked by wounding in the phloem to be significantly slower than the rapid changes in membrane potential. Electrical signals that were generated and transmitted from distant plant parts arrived at responding tissues well before the initiation of transcript accumulation.

Bose¹⁸ used a variety of plant species, including sensitive plants like *Desmodium*, *Mimosa*, *Biophytum*, and others like *Impatiens*, *Chrysanthemum*, banana, *Phaseolas*, *Ficus*, etc. to show electrical signalling and nervous mechanism in plants. Considering the slender, unbranched structure of a jute plant, we started experimenting with jute to reinvestigate some of Bose's propositions on rapid, systemic, long distance electrical signalling across large volume of cells in intact plants¹⁹. In this communication, we provide evidence on the rapid systemic transmission of applied electrical signal through the phloem tissue of a growing jute plant and try to ascribe a mechanism for such rapid signalling.

We used well-irrigated and properly managed, field-grown or potted jute plants (var. JRC 212 and its X-ray-induced mutant *dlpf*, INGR No. 04107) of 85–90 days age. At that stage jute plants grow to a height of about 225 cm and show maximum metabolic and growth activity²⁰.

Since the useful signal of the plant is generally a low-frequency signal and the noisy signal of the surroundings is of much higher frequency, the plants were put inside a locally built Faraday cage before each measurement.

Following Bose's idea, we made a fine (less than 0.2 mm diameter) but stiff copper electrodes mounted on a micrometer (see details in Datta and Palit¹⁹). The electrodes were inserted up to the phloem region (about 150 μm from the stem surface) of the growing stems at least 12 h before measurements for stabilization. One of the electrodes was inserted near the base (37 cm above the soil surface) of the stem (input electrode) and the other at 187 cm above the soil surface, near the top of the

stem (output electrode). A separate electrode was impaled into the soil close to the plant as the common reference or ground electrode in all cases.

For measurement of electrical signals, the electrodes were connected to channel 1 or channel 2 of a two-channel digital real time oscilloscope – 100 MHz, 1 GS/s (Tektronix, TDS 220, Tec-Inc, USA) depending on the requirement of the experiment. A train of pulses was provided through the input electrode at the basal region of the plant by a microprocessor (8085 Intel)-controlled pulse generator. Pulses of different frequencies, viz. 500 Hz, 6 kHz and 1 MHz were applied with respective time durations of 2 s, 166 μs and 1 μs of equal on-time and off-time periods. In all cases, except one when sine waves of 6 kHz with 166 μs time duration were applied for comparison, the applied pulses were square waves. The nature and the time duration of the propagating pulses through the plant were recorded by the oscilloscope connected to the output electrode. To understand the nature and direction of pulse movement, the polarity of the electrodes was reversed by applying input pulse through the top electrode and detecting the output pulses through the bottom electrode.

Using the same experimental arrangement, transmission of electric signal was studied in the following systems:

(i) Through a 90-day-old mutant of JRC 212 designated as *dlpf* with deficiency in secondary cell-wall formation²¹.

(ii) Through a 90-day-old water-stressed (by withholding irrigation for 10 days) JRC 212 plant grown in glazed tile pot under a polythene shed (average PPFD 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and ambient temperature 38°C). The plant showed distinct signs of water stress with droopy and slightly scorched leaves.

(iii) Through an intact jute plant whose bark (phloem) had been removed along with the lateral leaves, leaving the naked stick (wood or xylem) and a few top leaves. The electrodes were impaled deep inside the xylem tissue but not up to the pith.

(iv) Through 2 m long dry and wet jute fibre strands stretched and tied on a wooden clamp stand. Conducting metal clips were used as electrodes.

(v) Through a highly conducting metal (nichrome) wire held vertically. Conducting metal clips were used as electrodes.

(vi) Through a 2 m long and 0.5 cm diameter soft rubber (electrically bad conductor) tube, closed at one end and filled with either de-ionized double-distilled water or 0.2 M NaCl solution, and held upright by clamping on a wooden stand. Fine copper wires as described above were inserted into the lumen of the tube to serve as the electrodes.

In all cases a separate electrode was placed below the lower electrode to serve as the reference electrode and a train of square wave pulses of 6 kHz frequency with

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90 μs on-time and 50 μs off-time were provided through the lower electrode.

Impedance and capacitance of the growing plant were measured with the help of an impedance analyser (5 Hz–13 MHz; Hewlett Packard, USA; model 4192 ALF) keeping the same electrode arrangement. Impedance was measured at different frequencies, viz. 1 kHz, 10 kHz, 100 kHz and 1 MHz.

Extracellular measurements are well known from animal electrophysiology and are based upon measurements of the total of bioelectrical activity in large groups of cells. For example, electrocardiogram (ECG) and electroencephalogram (EEG) are widely used in medical practice¹⁵. When external electric pulses were provided in the phloem region of the living jute plant, the pulses transmitted through the tissue were detected at a distal point (150 cm upstream) practically within nano-seconds (Figure 1). But the magnitude of the output pulse showed considerable reduction from that applied through the input electrode. For example, Figure 1 indicates that the 6 kHz input pulse of 2 V magnitude was reduced to 500 mV at the detecting point. Also, the nature of the input and output waves was quite different. The square waves of the input pulse were transformed to curved waves at the output point, in spite of the fact that the rise time and the decay time were more or less equal in both the terminals (Figure 1). The transmission velocity and nature of the output waves were the same in a severely water-stressed plant (Figure 2), though the amplitude of the output pulse was slightly reduced. This indicates that turgidity may be important but not essential for long-

distance communication by electric signalling. Surprisingly, an exactly similar nature of output curve was recorded by Bose¹⁸ when he illuminated a frog's retina. Chen and Lee²² suggested that this change of form of trans-membrane current from a square to curved one could be the result of capacitance and leakage currents of the cell membrane. Presence of nanofarad to picofarad range of capacitance along the transmitting path (sum total of large groups of cells) was observed in our study (Table 1). We propose that this could be due to the presence of a considerable number of protein molecules in the propagation route (plasmodesmatal connection of the cells) that behave like capacitors in absorbing and slowly releasing the current, and thus changing the form of the signal from a square to curved one. Several putative plasmodesmata-localized proteins of non-specific role have been discovered^{23,24}.

How to obtain the main character of plant electric wave signals is a difficult problem in the field of the signal processing of plant electric wave signals. Although a unique wavelet transform theory to analyse the plant electric wave signal has been proposed²⁵, multi-resolution wavelet analysis as a signal processing technology is already widely applied to many fields, especially to biomedical signals²⁶. But it is seldom put to use for the processing of electric signals of plants. Also, it was noticed that impedances were proportional to the distance between input and output electrodes, except for a very high

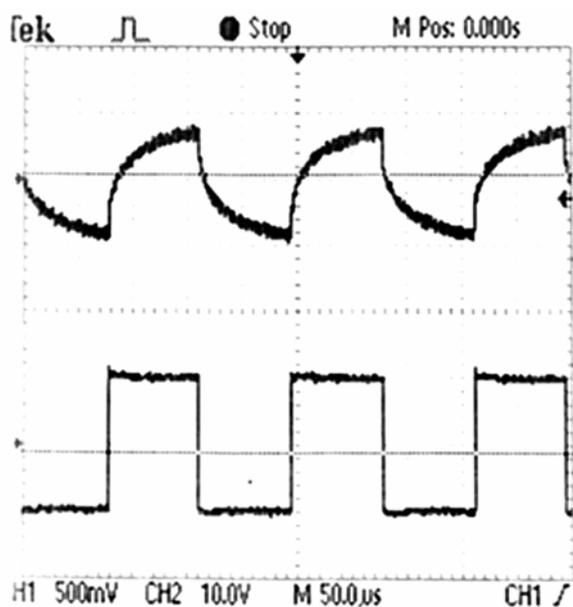


Figure 1. Printout of oscilloscope measurements showing input (channel 2, below) and output (channel 1, above) waves. Input pulse was provided near a normal jute plant (JRC 212) base and output measured at 150 cm above. Frequency is 6 kHz.

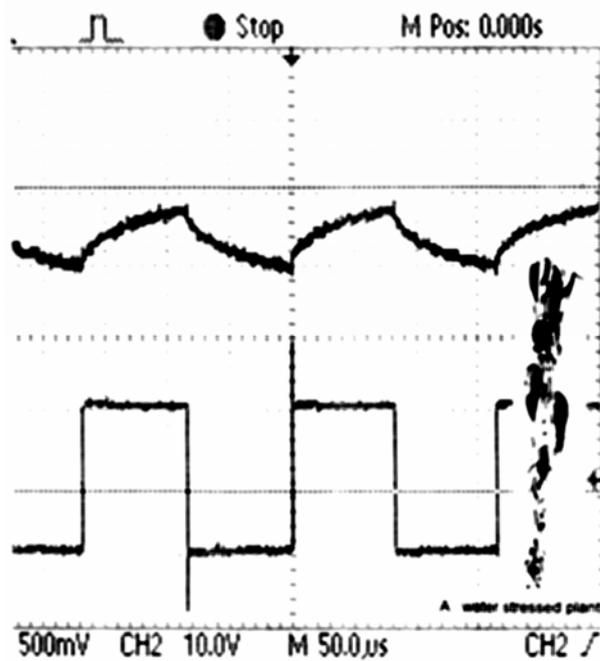
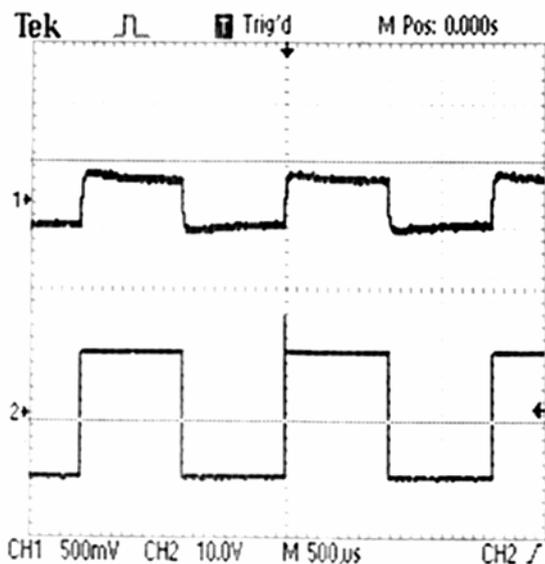


Figure 2. Printout of oscilloscope measurements showing input (channel 2, below) and output (channel 1, above) waves. Input pulse was provided near a water-stressed jute plant (JRC 212) base and output measured at 150 cm above. Frequency is 6 kHz.

Table 1. Measured impedance (Z), capacitance (C) and related parameters internal to a growing jute plant (JRC 212) at various frequencies (F)

F	Z	Phase angle ($^{\circ}$)	In series		In parallel	
			C	Loss factor	C	Loss factor
1 kHz	0.74 M Ω	-28	0.45 nF	1.8	0.1 nF	1.8
10 kHz	0.35 M Ω	-32.5	84 pF	1.5	23 pF	1.5
100 kHz	105.2 k Ω	-69	15 pF	0.42	13 pF	0.42
1 MHz	15 k Ω	-83	9.6 pF	0.14	9.4 pF	0.14

**Figure 3.** Printout of oscilloscope measurements when the square pulse input (channel 2) was near the top of a JRC 212 plant and output was detected (channel 1) near the base of the plant. Frequency is 6 kHz.

frequency of applied current (e.g. 1 MHz). This observation points to a probability that when the excitation/stimulus is extremely intense, the transmission of the electrical signal may jump over the cumulative impedance imposed by the tissue distance. A novel form of electrical signalling in plants, called 'system signalling' has been proposed²⁷. This signalling cannot be compared to the classic AP as present in the nerves of animals and also in plants. APs follow all-or-none characteristics: they are activated if a certain stimulus threshold is reached and then spread constantly. The 'system potential', however, can carry different information at the same time. The strength of the inducing stimulus can influence the amplitude of the systemic signal and the effect of different ions.

It is interesting to note that with the same volume of tissue, electrical signal of any frequency did not show the expected change in the form of the propagated pulses when it was applied from the top of the plant and detected at the base (Figure 3). This observation implies that the transmission of electrical signal may have a definite polarity. This is apparently in disagreement with the

observations of Stankovic *et al.*²⁸. They observed that electrical responses to an apical stimulus (APs and variation potentials (VPs)) can go in any direction throughout the plant. But the propagation of APs and VPs is mostly intracellular (symplastic, requiring a change in membrane potential) rather than extracellular²⁹. Polarity in cell-cell communication has been documented in root cells, which are inherently polar with signal input and signal output³⁰.

Nearly no delay in the transmission of the applied electric signal through the jute stem indicates the possibility of almost an electronic velocity of signalling in plants. Most early workers from Bose¹⁸ to Pickard³¹ and Rousset *et al.*³², measured essentially the AP generated within the plant body as a result of various external stimuli. The velocity of propagation of this AP could be at rates of 10–40 mm/s, which resembles primitive nerve APs³³. Pickard³¹, however, proposed an unfamiliar class of electrical events with less than 200 μ s rise time in tomato shoots as a result of imposing water stress. He stressed that this electric event was extracellular. His result implies that the passage of electric signal could be faster if it routes through the plasmodesmatal connection bypassing entry into the cell, and hence extracellular. The present study indicates that when electric signal was directly imposed over the cellular body (phloem region; see Bose and Das³⁴), transmission of the signal was even faster, being less than a microsecond per 150 cm. This rapidity of electric signal transmission through a living jute plant was comparable only to that through a highly conducting metal wire (Figure 4c). Interestingly, this fast movement was only through the phloem region but not through the woody tissue (dead cells of xylem element, Figure 5c). Also, the velocity in the phloem fibre cell-wall deficient mutant and its wild parent of jute was identical (Figure 6). This signifies that the electrical signal is not propagated by the dead cells (fibre) or their cell wall. This observation was further corroborated by the failure of electrical signal propagation through the isolated, washed and dried jute fibre strands (Figure 5a and b). Bose¹⁸, however, found that isolated vascular bundles of fern can transmit electrical signal. But this could be due to the presence of several ions over the surface of the freshly isolated vascular tissues. In this experiment, a non-conducting tube containing NaCl solution, but not the one containing pure water showed a high rate of transmission

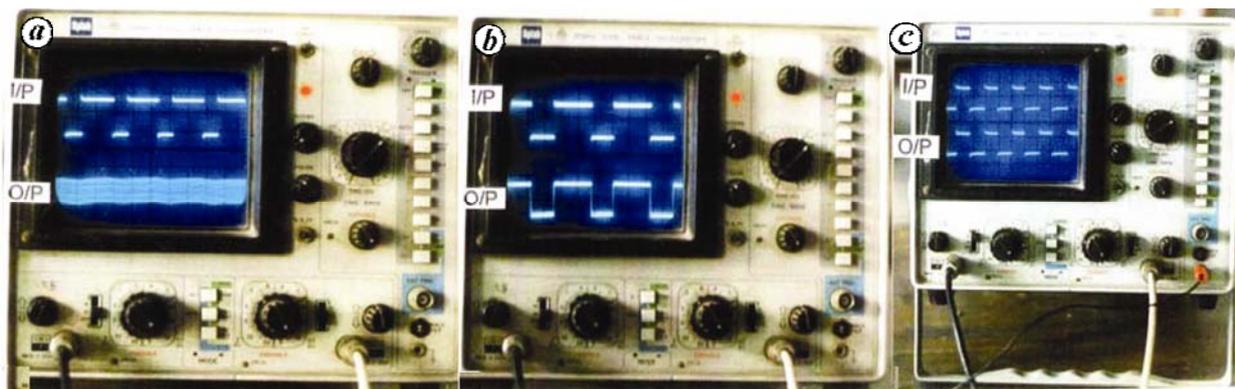


Figure 4. Images of the input (I/P) and output (O/P) signal waves on an oscilloscope screen. Signalling through distilled water column (a), NaCl solution (b) and a nichrome wire (c). Note the extensive noise in O/P through distilled water column only. The shape of the O/P waveforms through the NaCl column and nichrome wire are similar to the respective I/Ps.

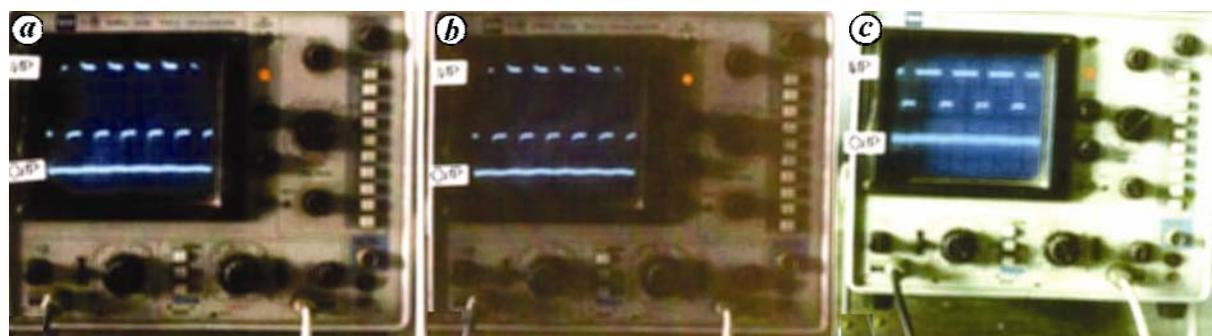


Figure 5. Images of input (I/P) and output (O/P) signal waves on the oscilloscope screen. Signalling through dry jute fibre (a), wet jute fibre (b) and naked stick (xylem) (c). Note: no detectable signal transmission, only noises as O/P.

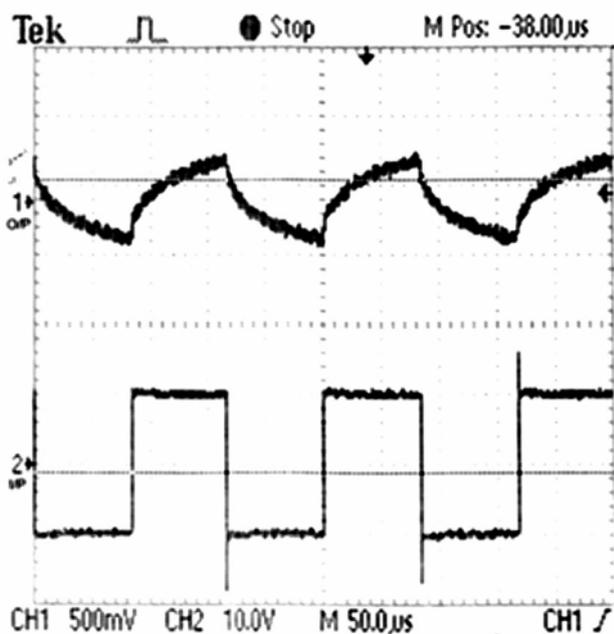


Figure 6. Printout of oscilloscope measurements showing input (channel 2, below) and output (channel 1, above) waves. Input pulse was provided near the mutant plant (*dlpf*) base and output measured at 150 cm above. Frequency is 6 kHz.

(Figure 4 a and b). Apparently, electrolytes dissolved in water might have supported ionic conductivity. Therefore, signal transmission appears to be an ionic event. Pico-second events are common in electron transfer during light harvesting in living systems. The sensitive plant *Mimosa* also responds to the signal by ion efflux via the plasmodesmata, which leads to leaf movement³⁵. It must be remembered that high velocity of electrical signal movement is common in the animal world. For example, *Octopus* and mammalian nerves often show a transmission rate of 3 and 100 m/s respectively³⁶.

Not only the fast movement of the applied electric signals, but also the plant electric wave signals could be a reflection of plants response to the changes of environment. Environmental stimuli spontaneously generate APs which convey electric signalling across tissues. For example, the bioelectric potential of a jute plant varied considerably with the time of the day that experienced constant changes in incident light and temperature¹⁹.

Signal movement through the plasmodesmata is important, as the plasmodesmata allow adjacent cells to communicate with each other across their intervening walls³⁷. Thus like the neurons in animals, the plasmodesmata interconnect the entire body of a plant and help in rapid

transfer of signals. This suggests that plants do have a system of communication analogous to animal neurobiology. Presence of a brain and central nervous system is not always a prerequisite for rapid interpretation and response to stimuli in living creatures³⁸.

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ACKNOWLEDGEMENT. We thank Prof. S. P. Sen, for his encouragement and useful suggestions.

Received 23 February 2011; accepted 23 May 2011