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Characteristics of Action Potentials in Willow (*Salix viminalis* L.)

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ABSTRACT

After application of electric stimuli (square DC pulses) extra- and intracellular potentials were recorded on willow shoots. The all-or-nothing law, strength–duration relation, and general characteristics of the action potential were investigated. By using inhibitors of ionic channels (tetraethylammonium, $MnCl_2$, $LaCl_3$), the excitability of willow could be completely blocked. Treatment with the phosphorylation uncoupler dinitrophenol induced a depolarization and disappearance of excitability, indicating the participation of a metabolic component of the membrane potential. By using energy-dispersive X-ray microanalysis, the distribution of chloride, potassium and calcium was measured in different tissues of non-stimulated and stimulated willow shoots.

It was shown that stimulation of the plant was followed by ion shifts which were most striking in the phloem cells. While their content of potassium and chloride was diminished after stimulation, the amount of cytoplasmic calcium increased slightly. These displacements lead to the conclusion that Ca^{2+} influx as well as K^+ and Cl^- efflux are involved in the propagation of action potentials.

Key words: Action potential, electrical stimuli, energy-dispersive X-ray microanalysis, ion shifts, *Salix viminalis*.

INTRODUCTION

Electrical activity in plants has been examined since the last century (Burdon-Sanderson, 1873). Most of the investigated plants perform leaf movements like *Mimosa* (Sibaoka, 1950) or use action potentials to catch insects like *Drosera* (Williams and Pickard, 1972; Williams and Spanswick, 1976) or *Dionaea muscipula* (Hodick and Sievers, 1986). However, action potentials have been examined in plants not possessing motor activity, and these include Characean algal cells (Findlay, 1961; Gaffey and Mullins, 1958; Oda, 1976; Shimmen and Tazawa, 1980), *Acetabularia* (Gradmann, 1976), the liverwort *Conocephalum conicum* (Dziubinska *et al.*, 1983) and higher plants like *Lupinus angustifolius* (Paszewski and Zawadzki, 1973; Zawadzki, 1980), *Luffa cylindrica* (Shiina and Tazawa, 1986) and *Helianthus annuus* (Zawadzki *et al.*, 1991). It is suggested that action potentials play a major role in inter- and intracellular communication and for regulation of physiological processes at the molecular and the organism level (Davies, 1987).

While communication over long distances may be achieved through propagated potential changes, local signalling may be caused by changes in the cellular ion concentrations. The ionic mechanism of excitation in plants is based on the observation that chloride carried the inward current (Gaffey and Mullins, 1958) and potassium the outward current. However, calcium also plays a significant role during the action potential (Beilby and Coster, 1979; Kikuyama and Tazawa, 1983). It has been suggested that entry of calcium stimulates the opening of chloride channels (Kikuyama, 1987; Lunevsky *et al.*, 1983; Tsutsui *et al.*, 1986).

As a first step in examining the electrical activity of trees, the characteristics of action potentials of willow plants were investigated. The plants were stimulated electrically and extra- and intracellular potentials were recorded. In order to identify ions that are involved in excitation, effects of some biologically active substances on the excitability were tested and X-ray microanalysis was performed on non-stimulated and stimulated plants.

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MATERIALS AND METHODS

Plant material

Cuttings (10–20 cm long, 2–3 mm in diameter) were made from twigs of 20-year-old willow trees (*Salix viminalis* L.). After keeping the lower ends submerged in aerated nutrient solution (composition in mol m^{-3}: 5 KNO_3, 5 $Ca(NO_3)_2$, 2 $MgSO_4$, 1 KH_2PO_4, in mmol m^{-3}: 50 KCl, 40 Fe-EDTA, 25 H_3BO_3, 5 $MnSO_4$, 2 $ZnSO_4$, 0·5 $CuSO_4$, 0·014 $(NH_4)_6MO_7O_{24}$) they developed roots within 5–14 d. These hydroponically grown plants were cultivated in a greenhouse under daylight conditions and temperatures between 20 °C and 27 °C, normal humidity, and without artificial light. Plants of similar height (20–30 cm) and appearance were selected for the experiments.

Measurement of membrane and action potentials

After the plants were transferred to the measuring stand, two stimulating electrodes (silver wire 0·4 mm in diameter moistened with 0·1% (w/v) KCl in agar) were applied to the apical stem surface with a distance of 1–2 cm between anode and cathode. The stimuli were delivered using a pulse generator (Pulsar 4i, Frederick Haer, Brunswick, Maine, USA), an adjustable source of square voltage and current pulses. Before the measurements started, the plants were placed in the Faraday cage for 1 d. On the following day, the measuring electrodes were attached to the surface of the stem at distances of 5 and 10 cm from the stimulating electrodes (Fig. 1A). They consisted of Ag/AgCl-wire wrapped in cotton which was moistened with 0·1% (w/v) KCl solution and provided the appropriate contact with the plant surface. The reference electrode was brought into contact with the solution of the root system. The measuring electrodes were connected to a differential amplifier (Model 750, WPI, Sarasota, Florida, USA) with an input impedance of 10^{12} ohms. The outputs were displayed on a chart recorder.

For intracellular measurements, glass microelectrodes with tip diameters less than 1 μm were fabricated from microcapillaries (WPI) on a vertical electrode puller (Model 700C, David Kopf, Tujunga, California, USA) and back-filled with 100 mol m^{-3} KCl. The microelectrodes were clamped in Ag–AgCl pellet holders (WPI) and connected to microelectrode preamplifiers (input impedance 10^{12} ohms) to which the WPI-amplifier was attached. The microelectrodes were impaled into the stem cortex using micromanipulators, and the stimulating cathode was connected to one microelectrode (Fig. 1B). By using a long-working distance objective the position of the microelectrode was checked to be in the stem cortex. The anode was brought into contact with the bathing medium. By changing the stimulus strength and duration, the relation between these values was determined.

For measurements in the phloem, 2–3 cm long strips of willow bark were dipped into a medium of 1–10 mol m^{-3} KCl, 0·1 mol m^{-3} $CaCl_2$, 0·1 mol m^{-3} $MgCl_2$, 0·5 mol m^{-3} NaCl, 0·4 mol m^{-3} NaOH, 0·05 mol m^{-3} Na_2SO_4, 1·0 mol m^{-3} morpholinopropane sulphonic acid (pH 7·0) and 100 mol m^{-3} mannitol (to prevent osmotic shock).

Microelectrodes were inserted into the phloem side of the strip (Fig. 1C) and action potentials were generated by connecting the stimulating cathode to one microelectrode and the anode to the bathing medium. The effect of ionic channel inhibitors and substances modifying the excitability was tested during application of the substance to the solution. The measured values are arithmetic means ±s.e.

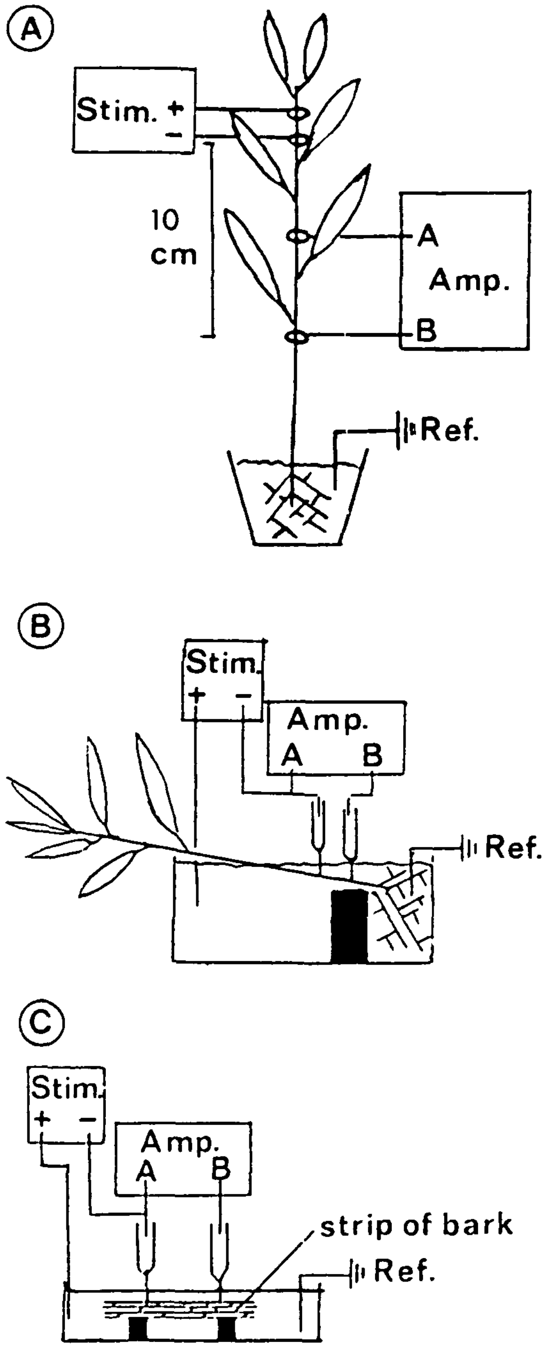


FIG. 1. (A) Measuring arrangement for the recording of extracellular potentials in willow shoots. (B) Measurement of intracellular potentials in the cortex of willow stems. (C) Recording of the resting potentials and action potentials of the phloem cells in a strip of willow bark.

X-ray microanalysis

From non-stimulated and stimulated plants, small samples of about 3 mm^2 were quickly frozen in isopentane, which previously had been cooled to about −175 °C with liquid nitrogen. Non-stimulated plants were slowly cooled to 3 °C before cutting samples. This was necessary to prevent stimulation of the tissue. Stimulated plants were excited by extracellular electrodes. The samples were freeze-dried, infiltrated, and embedded in Spurr's resin medium (Spurr, 1969) by applying the method described by Fritz (1980, 1989). Cross-sections (1 μm thick) were cut with Teflon-coated glass knives, transferred dry to copper sandwich grids, and coated with vaporized carbon. The sections were examined under a Philips EM 420 electron microscope at 120 KeV, equipped with an energy dispersive X-ray microanalytical device (EDAX 9100). All measurements were made at a primary magnification of 6350 ×. The area covered by the electron beam was 200–250 nm in diameter. Data obtained from a large number of histologically identical locations are presented as mean values ±s.e.

RESULTS AND DISCUSSION

Extracellular potentials

Following electrical stimulation of the plant, a propagating action potential with an amplitude of 50 mV was recorded by both electrodes (Fig. 2, upper scheme). The action potential had a constant velocity of 2 cm s^{-1} and was transmitted basipetally without delay. During stimulation, a stimulus artifact, which does not mirror the electrical activity of the plant, was observed. Almost 3 s later, the first electrode (A) measured the action potential which was generated by the plant itself. As shown in the strength–duration relation (lower scheme of Fig. 2), the stimulus required to trigger an action potential increases when the stimulus duration is shortened. The two dashed lines indicate that a stimulus intensity lower than 2 V and a stimulus duration less than 1 s does not evoke action potentials. A stimulus of 3 V and a duration of 2 s was used as standard. Since further increases in the stimulus strength do not change its amplitude and shape, the action potential conforms to the all-or-nothing law. With regard to refractory periods, we found that for 2 min after the action potential has passed it is impossible to elicit a second one, however high the stimulus strength.

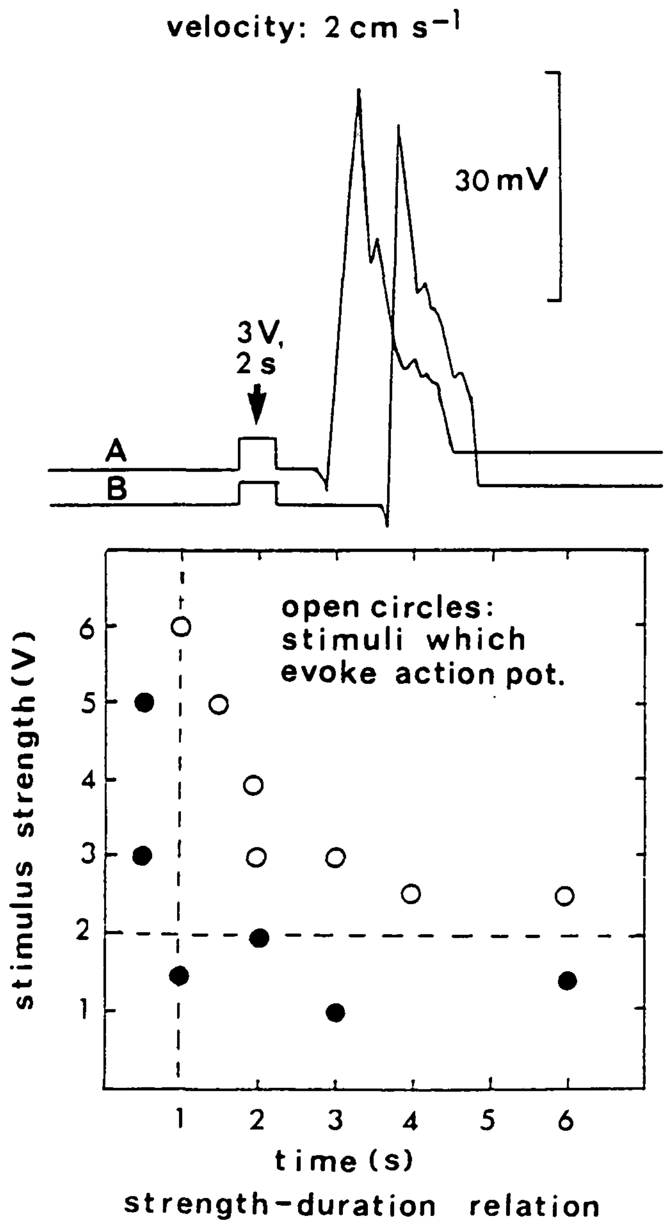


FIG. 2. Recording of extracellular potentials in willow shoots. Stimuli stronger than 2 V and longer than 1 s were able to evoke action potentials (strength–duration relation) which were propagated with a velocity of 2 cm s^{-1} in basipetal direction.

In contrast, the shape and amplitude of the potential change differ between various plants of the same clone. Although the plants were similar in shape, size and age and were grown under identical conditions, their excitability was quite different. Some plants were highly excitable, some were moderately excitable and others were not excitable. Since the degree of excitability of a particular plant could also change during the day, it is likely that excitability depends on rhythmic, diurnal changes.

Intracellular potentials

Action potentials were recorded intracellularly by placing the lower stem of the plant horizontally into saline solution. Then two microelectrodes were inserted into the stem cortex; one of them was connected to the cathode of the stimulator (Fig. 1B). The membrane potential ranged from −100 to −138 mV during six experiments with different plants. The amplitude of the evoked action potentials had values of 30 to 50 mV and the velocity of propagation was 2 cm s^{-1} in both basipetal and acropetal directions (Fig. 3, upper scheme). Stimuli shorter than 1 s and lower than 2 nA did not induce an action potential, regardless of intensity or duration of the second parameter (Fig. 3, lower scheme). The resting and action potentials did not vary significantly in different parts of the cortex.

The intracellular measurements showed that the extracellular recorded signals result from changes in the transmembrane potential difference. Although the amplitudes and shapes of the potential changes differ during both types of methods, the transmission velocity is the same.

The influence of ionic channel inhibitors and phosphorylation uncouplers on the excitability

It is generally known that the ionic mechanism of excitation in the Characeae is based on K^+, Cl^- and Ca^{2+} movements (Tazawa *et al.*, 1987). One method to investigate the excitation mechanism of willow was the

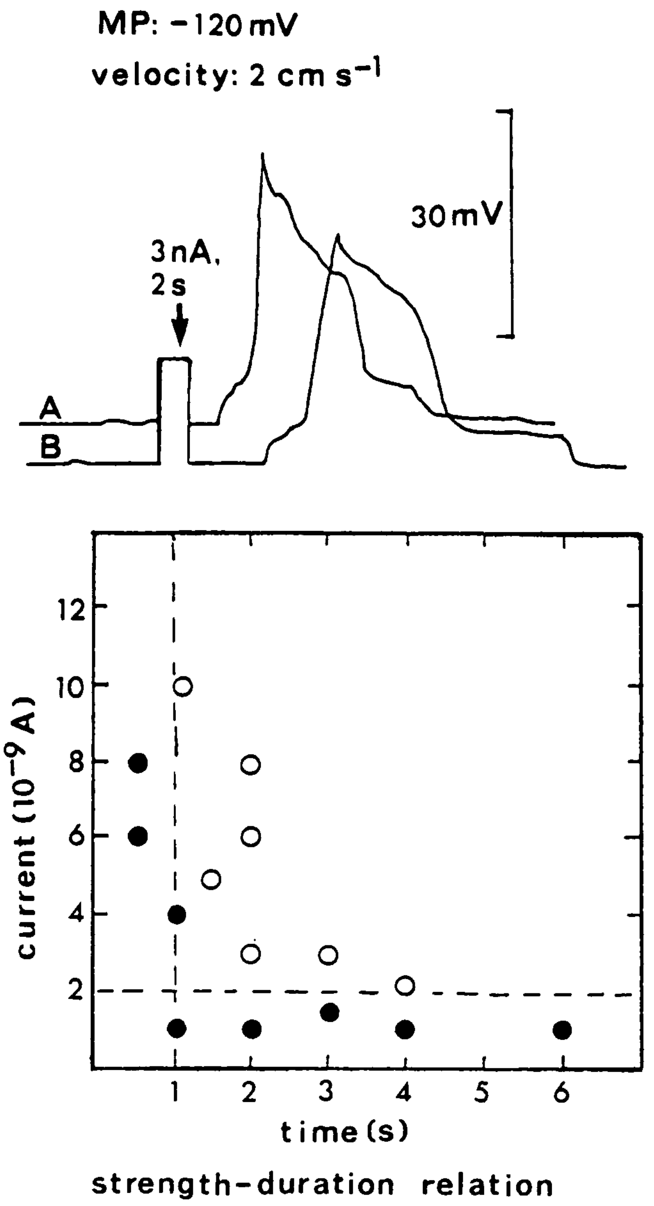


FIG. 3. Measurement of intracellular potentials in the cortex of willow stems. Stimuli stronger than 2 nA and longer than 1 s evoked action potentials with an amplitude of 30–50 mV. The velocity of propagation was 2 cm s^{-1} in both basipetal and apical directions.

TABLE 1. *Recording of the resting potential of the phloem cells and inhibiting effects of different substances on the excitability of willow*

The resting potentials represent the values before the application of the inhibitors. Experiments were repeated five- to seven-fold, data are mean values ± s.e.

Inhibitor	RP (mV)	ΔRP (mV)	Effect on excitability	*n*
TEA (5 mol m^{-3})	-140 ± 18	$+8 \pm 3$	inhibition	7
$MnCl_2$ (5 mol m^{-3})	-135 ± 21	$+10 \pm 5$	inhibition	7
$LaCl_3$ (2 mol m^{-3})	-145 ± 16	$+52 \pm 14$	inhibition	7
DNP (0·1 mol m^{-3})	-140 ± 19	$+50 \pm 17$	inhibition	6
NH_4Cl (3 mol m^{-3})	-145 ± 18	$+40 \pm 13$	inhibition	5

use of inhibitors. Since it is known from experiments with *Mimosa pudica* that phloem cells serve as the transmission pathway for action potentials (Samejima and Sibaoka, 1982; Fromm, 1991), the following measurements were made in the willow phloem by inserting microelectrodes into bark strips from the cambial side (Fig. 1c). After stabilization of the resting potential, mean values from −135 to −145 mV were recorded during this series of experiments (Table 1). The excitability of the phloem was tested by applying electric pulses through one microelectrode and recording the potential changes as shown in Fig. 1c).

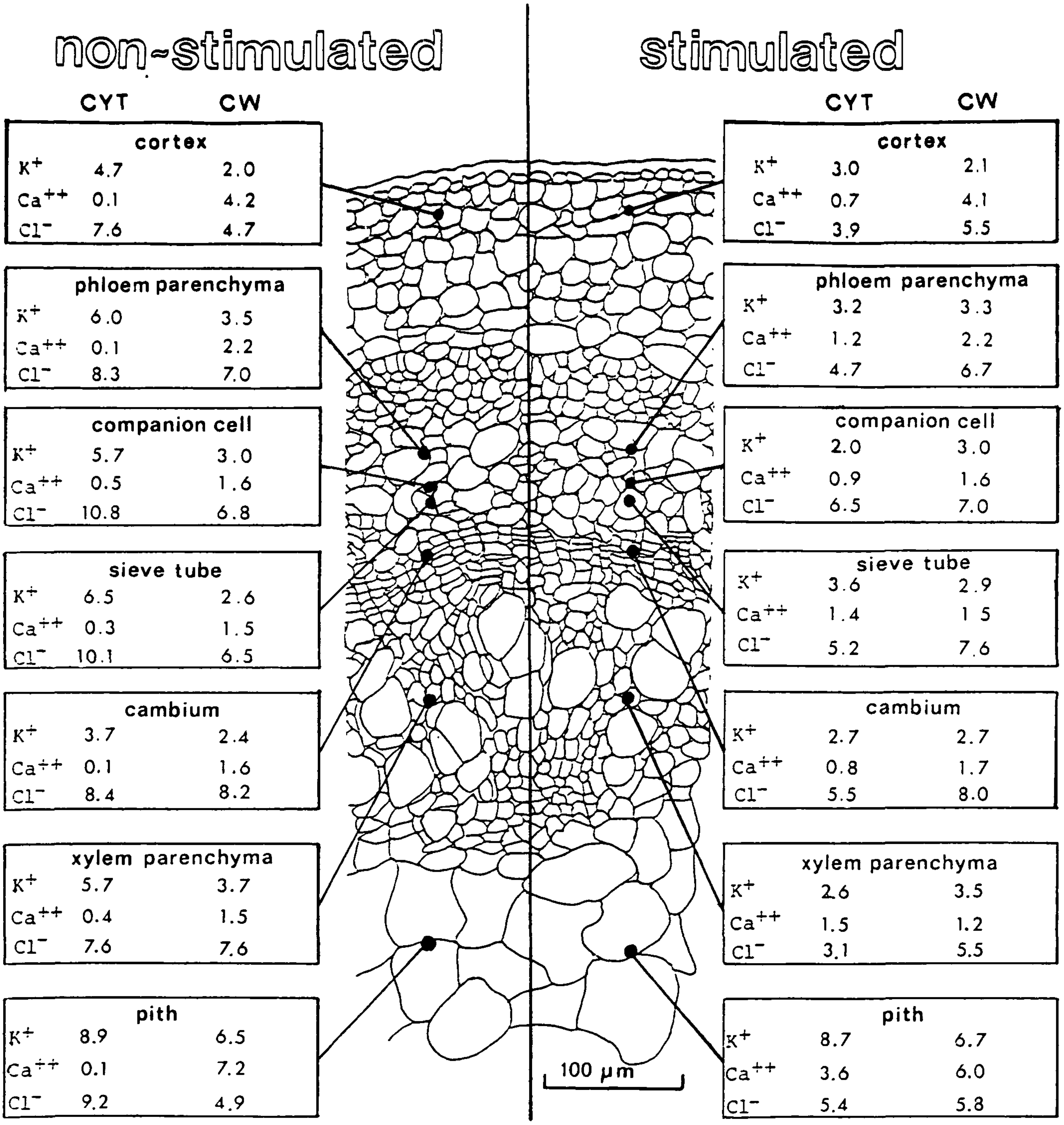
Then several inhibitors were applied, and excitability was tested again. Tetraethylammonium (TEA) is a cation best known as inhibitor of K^+ channels (Tasaki and Hagiwara, 1957; Shimmen and Tazawa, 1983). After application of 5 mol m^{-3} TEA the resting potential depolarized slightly and excitability of the phloem cells was completely inhibited after 15 min (Table 1). The inhibiting effect of TEA did not depend on the K^+ concentration of the bathing solution, which ranged from 1–10 mol m^{-3}. Thus, evidence is provided that K^+ channels play a role in the generation of willow action potentials.

When $MnCl_2$ and $LaCl_3$, which are inhibitors of Ca^{2+}-channels (Trebacz *et al.*, 1989; Shiina and Tazawa, 1987), were applied to the solution, each of them caused a cessation of excitability after 20–30 min (Table 1). These results indicate that Ca^{2+} channels are also involved in the induction of the willow action potential.

Since 2,4-dinitrophenol (DNP) is an uncoupler of both oxidative (Slayman, 1965) and photophosphorylation (Krogmann *et al.*, 1959) it eliminates the metabolic component of the membrane potential. In willow 0·1 mol m^{-3} DNP rapidly depolarized the membrane potential by about 50 mV, and subsequent electrical stimuli were not able to produce action potentials, regardless of their intensity and duration. The interpretation of metabolic inhibitors is more complex. Here the inhibition of the excitation may occur due to either depolarization of the resting potential or by direct effect on the channels involved in excitation. An electrogenic ionic pump might be involved, at least indirectly, in generating the action potential of willow.

Another uncoupler of phosphorylation is ammonium chloride (Krogmann *et al.*, 1959) which eliminates proton gradients because of its transformation to NH_3 and H^+ in a neutral or alkaline medium. When it was applied in a medium with a potassium concentration of 1 mol m^{-3}, a depolarization of 40 mV with an irregular shape occurred, leading to a total absence of excitability after 40 min (Table 1). These results are in accordance with those of Trebacz and coworkers (1989) on the excitability of the liverwort *Conocephalum conicum*. The elimination of the metabolic part of the membrane potential indicates an inhibition of proton pumps in the cell membrane.

However, the effect of ammonium itself is difficult to interpret. Ullrich *et al.* (1984) also demonstrated large effect of ammonium on the membrane potential of *Lemna*. It was shown earlier (Keifer and Spanswick, 1979) that 5 mol m^{-3} NH_4Cl produced only a 15% decline in the ATP level in *Chara*. However, it does depolarize the membrane potential. This may be due to an elevation of cytoplasmic pH because we have unpublished evidence that the effect may be reversed by agents that acidify the cytoplasm.



non-stimulated

	CYT	CW
cortex		
K^+	4.7	2.0
Ca^{++}	0.1	4.2
Cl^-	7.6	4.7
phloem parenchyma		
K^+	6.0	3.5
Ca^{++}	0.1	2.2
Cl^-	8.3	7.0
companion cell		
K^+	5.7	3.0
Ca^{++}	0.5	1.6
Cl^-	10.8	6.8
sieve tube		
K^+	6.5	2.6
Ca^{++}	0.3	1.5
Cl^-	10.1	6.5
cambium		
K^+	3.7	2.4
Ca^{++}	0.1	1.6
Cl^-	8.4	8.2
xylem parenchyma		
K^+	5.7	3.7
Ca^{++}	0.4	1.5
Cl^-	7.6	7.6
pith		
K^+	8.9	6.5
Ca^{++}	0.1	7.2
Cl^-	9.2	4.9

stimulated

	CYT	CW
cortex		
K^+	3.0	2.1
Ca^{++}	0.7	4.1
Cl^-	3.9	5.5
phloem parenchyma		
K^+	3.2	3.3
Ca^{++}	1.2	2.2
Cl^-	4.7	6.7
companion cell		
K^+	2.0	3.0
Ca^{++}	0.9	1.6
Cl^-	6.5	7.0
sieve tube		
K^+	3.6	2.9
Ca^{++}	1.4	1.5
Cl^-	5.2	7.6
cambium		
K^+	2.7	2.7
Ca^{++}	0.8	1.7
Cl^-	5.5	8.0
xylem parenchyma		
K^+	2.6	3.5
Ca^{++}	1.5	1.2
Cl^-	3.1	5.5
pith		
K^+	8.7	6.7
Ca^{++}	3.6	6.0
Cl^-	5.4	5.8

FIG. 4. Concentrations of K^+, Cl^- and Ca^{2+} in twigs of non-stimulated and stimulated willow plants. Emitted X-ray signals are given as peak:background ratio. The data are mean values of 20 measurements taken from three plants with a s.e. lower than 0·5 for K^+, 0·2 for Ca^{2+} and 0·9 for Cl^-. CYT: cytoplasm, CW: cell walls. Units: counts per second.

Ion distributions before and after excitation

Apart from the use of inhibitors, the ionic mechanism of excitation was investigated by X-ray microanalysis in order to determine the ion distribution of excitable cells before and after the plants were stimulated. The peak/background-ratios of cells from willow twigs show that in most cell types the K^+, Ca^{2+} and Cl^- content of the cytoplasm (cyt) differs greatly during stimulation (Fig. 4). In order to be sure that the analysis was performed in the cytoplasm, only cells with visible vacuoles were chosen for the measurements. In all types of cells, with the exception of the pith, the cytoplasmic K^+ and Cl^- content decreased sharply while Ca^{2+} slowly increased during stimulation. In the cell walls, only minor changes of these ions could be observed. In particular, the cortex cells in which action potentials were measured intracellularly and all cells of the phloem showed striking differences.

From these displacements during stimulation, it is assumed that Cl^- also carries the inward and K^+ the outward current in the willow action potential. Since Ca^{2+} is present at lower concentrations than K^+ and Cl^-, its role during excitation might involve stimulation, as was already proposed for the Characeae action potential (Lunevsky *et al.*, 1983). However, one has to keep in mind that there is a difference between the amount of Ca^{2+} measured by X-ray microanalysis and the 'free' Ca^{2+} measured using Ca^{2+} selective microelectrodes, which would be in the submicromolar range.

CONCLUSIONS

This work has shown that action potentials, which occur in many plants, are also generated in willow trees. The investigation of ion displacements led to the conclusion that Ca^{2+} influx as well as K^+ and Cl^- efflux are involved in the transmitted action potential. Since the action potentials were propagated over long distances (10 cm), they may play a key role in intercellular communication. The physiological function of the willow action potential is under current investigation. It has already been shown that electric signals released from willow roots change photosynthesis and transpiration (Fromm and Eschrich, 1993).

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