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An oscillatory component of propagated fluctuation electric potential in lupine shoot

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Abstract

Application of a drop of auxin solution to a cut surface on the petiole in lupine shoot elicits a travelling pulse of electric potential decrease. This pulse was simultaneously recorded by means of a DC amplifier and band-pass amplifier 0.1-100 Hz, both connected to the same exploring AgCl electrode driven into the stem. The DC record shows a pulse 20-80 mV in height of about 30 s duration at its height with smooth slopes. The band-pass amplifier shows one to a few pairs of spikes (negative and positive) whose amplitude is at least of an order lower than that of the DC pulse. These spikes are interpreted as the action potential of certain excitable cells recorded in a "volume conductor". The pulse is interpreted as a wave of cooperative depolarization of excitable and a mass of inexcitable cells.

Key words: action potential, oscillatory component, Lupinus spp.

INTRODUCTION

It is a well-known fact that propagated action potential may be induced in shoots (Paszewski and Zawadzki 1973, Pickard 1973, Zawadzki and Trębacz 1982). Action potential (AP) means a temporary, regenerative (explosive) decrease or reversion of the transmembrane potential difference (E_n) (Gradmann and Mummert 1980). Intrinsic properties of AP are: all-or-none i.e. explosive behaviour, summation of subthreshold stimuli to a triggering one, a refractory period, possibility of oscillation, selfpropagation due to a current flow from a region undergoing explosive change through an adjacent region of the membrane which is triggered to firing by discharging.

Propagation of AP in a plant organ means that a wave of AP spreads along electrically coupled cells. It should be taken into account that protoplasts of a plant organ are connected by plasmodesmata resulting in a symplast — a continuous membrane bound cytoplasmic network, which is interspaced with the apoplast — a continuous network consisting of the organ structures outside the plasmalemma. The interior of a cell undergoing AP (referred to below as an excited cell) is on higher potential than the interior of neighbouring still resting cells. Since the protoplasts connected by plasmodesmata are electrically coupled (Goodwin 1976), the current must flow from the excited cell to the resting cells through the plasmodesmata. An unavoidable consequence is the discharging of the membrane capacitor which partially depolarizes the membrane. Typically, depolarization increases the permeability of the membrane, and this has two consequences: 1) the increase of the conductance of the membrane, 2) the current created by the ions whose concentrations on both sides of the membrane are not in balance with the electric potentials there in the resting state. The return current flows as an ionic current in the conducting medium, mainly in the apoplast — closing the circuit as an ionic current through the permeable plasmalemma of the excited cell. It is natural to expect that this current, if strong enough, in the proximity of the excited cell, triggers the neighbouring cells to firing if they are excitable. The AP is propagated then through the symplast. Sibaoka (1962) has shown that a critical number of cells must be excited to assure propagation of AP down a bundle in the *Mimosa* leaf, and it may be generalized that for the propagation of AP in a symplast, a summation of currents from an adequate number of cells which are undergoing depolarization is necessary.

It is very probable that not all cells in a plant organ are excitable.

What can be expected if besides excitable cells in an symplast, there also are inexcitable cells which are able to depolarize in a graded way in response to the current generated by the AP of excitable cells? It can be easily envisaged that there will be a wave of AP accompanied by a wave of nonexplosive depolarization in neighbouring inexcitable cells which, by increasing the plasmalemma permeability of these cells, increases the current, and triggers the next excitable cells to fire. Thus we should take into account a variant of AP propagation in a symplast where two waves of depolarization — AP in excitable cells and a nonexplosive, graded depolarization in neighbouring cells — beget mutually. We propose the term cooperative action-graded potential or shortly AGP as referring to such a compound wave. It seems that many electrical fluctuations observed in plants are of the AGP type, especially those characterized by slow travelling and long duration.

It is known that in plant organs there may be travelling fluctuations of the electrie potential called variation potential (Houwink 1935, Pickard

1973, Van Sambeek and Pickard 1976). A substance released from injured cells is transported with water in the xylem from which it leaks into neighbouring living cells and stimulates them to a depolarization of either the AP or the graded type. Since the velocity of substance transport and the pattern of its leaking from xylem can be highly variable, the variation potential differs from AP and presumably from AGP by variable velocity and variable shape (in the same plant). The variation potential can also be distinguished from genuine propagated AP by its long duration, and the nonreturning of the potential to the baseline (Pickard 1973). The variation potential rather than the AP is often suspected in case of a slow propagation. There are many reports in literature on a relatively slow travelling fluctuation of potential which did not always return promptly to the baseline, but without the variability in shape and velocity as can be expected in the case of variation potential (Umrath 1959). We would postulate that these fluctuations are of the cooperative action – graded potential-type.

Typically, the recording of AP in a plant organ is done with both electrodes of a pair located in the apoplast or in contact with it. This is obvious when the electrodes are on the organ's surface, but it is also true for electrodes driven into an organ.

The apoplast represents the external conducting medium in which the voltage source – the differential E_m along the membrane is immersed. If the volume of the medium is small in comparison with the volume of the part of the symplast which is the voltage source, and one electrode (exploring electrode) is close to the source while the other is far from it, the peak of potential fluctuation recorded is comparable to the E_m change, both with regard to height and shape. In such cases, the exploring electrode simply measures the change of electrochemical potential in the apoplast due to the change in the ion concentration following the change of membrane permeability. However, since the change of concentration is a local phenomenon, the amplitude of the fluctuation decreases sharply with the distance between the electrode and the source. When the exploring electrode is beyond the region of concentration change, it "sees" the source through the volume conductor. The shape of the fluctuation peak differs significantlly from the E_m change, the recording is of the volume conductor (VC) type.

The interpretation of such a recording is based on treating the source as a dipole with respect to the electrode. The spatio-temporal pattern of the dipole change determines the shape of the record (Patton and Woodbury 1965, Scher 1965). How different the peaks representing AP on the VC record from the E_m change may be, can be illustrated by an electrocardiogram on which the action potential in ventricles, which lasts about 300 ms is

represented by two narrow spikes (known as QRS and T waves), the shape of which depends on the position of the electrodes. During the main part of the ventricle AP (maximal depolarization) the potential on the electrocardiogram is on the baseline.

The external potential of a resting cell is of course zero everywhere in the medium. Also, a depolarized cell is not a source of voltage in the volume conductor. If a cell is depolarizing as a whole, it is not a source as well. The source of voltage in VC is that which shows dipolar properties with respect to the electrode. A membrane in which there is a sufficient E_m gradient (i.e. change of E_m along the membrane) has such a property.

The electrical space constant of a plant cell is so large in comparison with the cell diameter that the cell must behave as a unit during depolarization, even during explosive depolarization of the AP type. However, it can be expected that the plasmodesmata have the space constant less then their length, and should show dipolar properties when AP develops in the cells. Action potential in a plant cell joined with other cells by plasmodesmata may thus be a source of potential change in VC recording. However, because we know neither the spatial nor the temporal pattern of E_m change and of other changes in plasmodesmata, we cannot predict anything about the VC records of AP. An analogy would be an electroencephalogram which seems to result from dendritic activity (Towe 1965). However, it can be predicted that the duration of potential fluctuation in VC recording should be much shorter than that of the depolarization of the cell involved, i.e. the fluctuations should represent a sort of oscillation during the depolarization.

Paszewski and Zawadzki (1973, 1976) and Zawadzki (1980), described propagated AP induced in lupine stems. They used a DC amplifier and surface contact electrodes. The AP appeared as a negative pulse of voltage about 80 mV with rather smooth slopes, travelling at a rate of 2-10 cm per minute. Its duration, indexed as the time between attainment of and return to half peak height, was about half a minute, which corresponds in length to a few cm of the depolarized segment.

The high amplitude of the pulse indicates that a considerable portion of the symplast is depolarized close to the electrode. In fact the depolarization embraces the cortex (Zawadzki and Trębacz 1982). The recording of the depolarized portion in Paszewski's and his collaborators' works must thus be classified as in a small volume of conducting medium. The authors have clearly showed that the pulse as a whole is an all-or-none reaction and inferred that it represents AP, but we can ask whether the whole pulse is due to an AP type of depolarization. Zawadzki and Trębacz (1982) on the basis of experiments with a mechanical block applied to the cortex, concluded that "all or almost all cells of the primary cortex participate in

normal AP propagation". However, it appears to us that a more correct conclusion would be that all cortical cells undergo depolarization, but the depolarization in all cells is not necessarily of AP-type.

We are tempted to interpret Paszewski's and Zawadzki's pulse as being of an AGP type. If so, the AP component should be recognizable as a relatively short oscillation according to the principle of VC recording, and therefore by using a proper band-pass filter could be separated from the general depolarization cycle of much longer duration. We have done simultaneous recordings of Paszewski's and Zawadzki's pulse in its original shape, and with a band-pass amplifier to remove the graded depolarization.

MATERIAL AND METHODS

PLANT MATERIAL

Lupine plants (*Lupinus* cv. Wat) were grown in pots in a greenhouse at a temperature of 20-30°C. The plants were 20-40 cm high with approximately a dozen leaves. The potted plants were transferred to the measuring cage 1 day before recording.

MEASURING EQUIPMENT

Two kinds of amplifiers were used. One was a pH amplifier (Meratronik N517) — called a DC amplifier, with digital readout and analog output. Input resistance was more than $10^{12}\Omega$, input bias current was no more than about 10^{-14}A. Band width was from 0 to 1 Hz, the amplification factor was usually 1. The other one, was a type WSB-4 band-pass amplifier (AC amplifier) with symmetrical input and nonsymmetrical output. Input resistance was no less than $2 \times 10^{9}\Omega$, the discrimination factor was no less than 100 dB. Band width was 0.1-100 Hz, programmable amplification was in the range of 500 to 10^{6}, usually 10^{3}. The noise was less than 1.5 μV RMS. The signals were recorded by means of x, t recorders (Goerz RE 555) and were monitored on a quadruple trace oscilloscope (OD4A).

Electrodes. Silver-chloride electrodes were used. They were made of 10-15 mm long segments of sharpened silver wire (0.3 mm, 99.9% Ag) covered with AgCl (Meyer-Waarden 1980). Electrodes were driven into the stem or petiole to a depth of about 1 mm. The contact between plant and electrodes was good for a period of a few days. The recording started several hours or the next day after driving the electrode in. Any movement of the electrodes with respect to plants was avoided, changes in connections were achieved by means of electrical switches.

Measuring cage. A Faraday's cage made of steel plates and steel open-work 2×2×2 m in a laboratory room was used to provide enough signal to noise ratio in AC recording. There were mercury bulbs with a total power of 0.75 kW above the cage roof, which provided about 1600 lux on plant level in the cage. The light period was from 8 to 16 h daily adjusted to the season, the temperature was about 20°C, the humidity —70%.

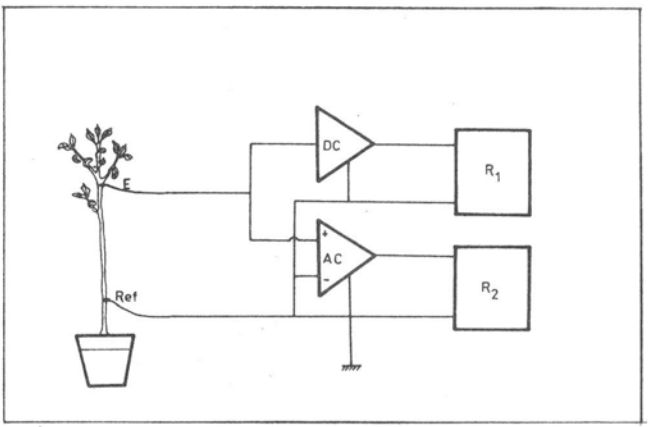

Fig. 1. The scheme of the measuring system. E — measuring Ag-AgCl electrode, Ref — reference electrode, DC — direct current amplifier, AC — band-pass amplifier, R_1, R_2 — recorders (x, t)

Electrical connections. Measuring electrodes were located along the shoot starting with the petiole, otherwise they were arranged in a whorl on the stem. The reference electrode usually was at the bottom of stem. DC and AC amplifiers were used in pairs, each connected to the same measuring electrode. The measuring and reference electrodes were connected to the amplifiers nonsymmetrically (Fig. 1).

STIMULATION

AP was induced by applying a drop of NAA solution to a cut petiole, 1.5 min after cutting the leaf blade from the petiole. The cut was 30-50 mm above the uppermost electrode which was either at the petiole base or on the stem at the median trace from the cut leaf. The NAA concentration was 10^{-3} $M \cdot dm^{-3}$ and the drop volume was in the range of 1-5 mm^3.

RESULTS

Sometimes cutting of the petiole already evoked a propagated pulse which in the DC recording had all of the features of the pulse known

from Paszewski's and his collaborators' studies on lupine. The most reproducible way of evoking such a pulse was application of an NAA drop on the cut surface: the propagated pulse appeared in more than 50% of the stimulations, not counting the fluctuations which can be considered as variation potential. A typical recording with 3 electrodes is shown on Fig. 2. The DC records show first (after stimulation) a negative pulse followed by an inverted pulse. The first represents depolarization in the region of the corresponding "exploring" electrode, the second originates from lowering of the potential at the reference electrode. The inverted pulse on the record from electrode 2 is low -- the decrease of potential at the reference electrode -- so clear with respect to electrode 1 -- was counteracted by prolongated lowering of potential at electrode 2. A comparison of the temporal distance between the negative and positive pulses on one curve and between the exploring and reference electrodes gives the rate of travelling about 7 $cm \cdot min^{-1}$.

The AC records (a_1, a_2) show groups of spikes (D) which, according to experience gained, are directly related to the pulses. Since the AC amplifier reacts only to oscillatory components of potential fluctuation, the group of spikes on the AC record is referred to as the -- oscillatory component or in short OC. The amplitude of the OC is very small in comparison with the pulse height. There are two cycles in the OC shown in Fig. 2. The first spike in the group is negative. There are also other groups of signals on the AC records in Fig. 2. Group A is due to the manipulation involved with cutting. Group B contains simultaneous and identical signals on both records which means that they are related to something which was seen by the reference electrode. Group C is related to the manipulation during putting the drop of NAA on the cut surface and indicates the time of stimulation. Group E contains signals from the reference electrode. Usually in this group there was an OC related to the pulse in the region of the reference electrode, however when this electrode was located at the stem bottom, the OC were often unpronounced as in the case shown on Fig. 2.

The characteristics of the signals related to the pulse are as follows.

DC RECORDS

The pulse height was variable, however in all cases in which travelling occured, it was in the range 20-80 mV. The height may be different even on closely located electrodes. Figure 3 shows records from 3 exploring electrodes located in a whorl. The highest negative pulse was in this case about 40 mV, the lowest only slightly above 10 mV. The pulse had reached the level of the whorl, however it did not reach the reference electrode.

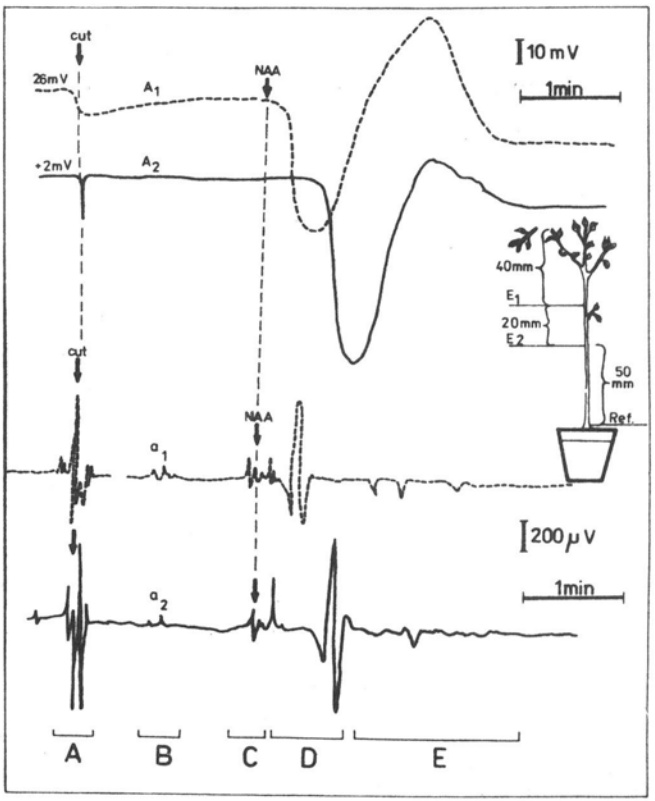

Fig. 2. The arrangements of the electrodes E_1, E_2 and Ref are shown on the right. The deflection of the curves down means lowering of potential. Moment of cutting and putting NAA drop indicated by dashed lines marked "cut" and "NAA", respectively. A_1 and A_2 — DC records, a_1 and a_2 — AC records. Explanation of the spike groups A-D in the text

Our interpretation of the pulse height variation is the following: In the case of a high pulse (about 80 mV) the electrode is within the region undergoing depolarization. In the case of a low pulse a considerable part of the symplast at the electrode level is depolarized, however, the electrode is slightly outside this part. Different sectors of the stem at a particular level may differ in degree of depolarization; typically the most depolarized sector is that which contains the median leaf trace from the stimulated leaf.

The slopes of the pulse are smooth and do not reveal any superposed peaks which could be related to the OC on AC record. Nevertheless there may be smoothly outlined projections (shoulders) especially on the back slope. The duration of the pulse at its half height is usually about 30 s — which usually corresponds to about 3 cm of stem length. The duration of the front slope is shorter than that of the back slope, especially

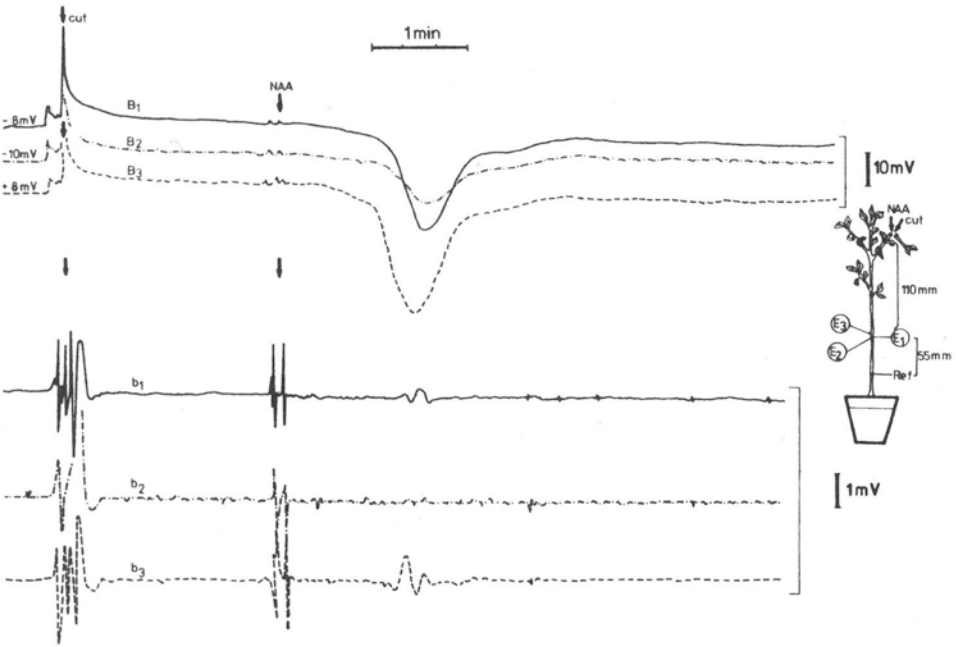

Fig. 3. Simultaneous record from three electrodes placed in the whorl. The curves B_1, B_2 and B_3 derive from the DC amplifier. The oscillating component of observed AP is seen on curves b_1, b_2 and b_3, respectively

there may be a prolonged phase of final restoration of the potential to the baseline. Sometimes there is no return to the baseline (Fig. 4).

AC RECORDS

The spikes of OC have an amplitude in the range of 40-1000 μV (sporadically to 3 mV). They occur usually in the early part of the upstroke phase of the pulse. The number of cycles (1 cycle is considered to consist of oppositely directed spikes) varies from 1 to more than 4 (Fig. 4), but if there are more than three cycles, the remaining ones are less pronounced. The first spike usually is negative. The temporal distance between two spikes directed in the same way is mostly in the range of 7-15 s. The spikes may have projections on their slopes (Fig. 5). In general, the shape of the OC group is very variable in recordings from different plants or from the same plant on different days or periods separated by a few hours. However, it is remarkable that the shape of OC in the same pulse but on different electrodes (Figs. 2, 5) or in different pulses from different leaves on the same plant, is often similar (Fig. 4). In any case, the variation is in such instances much less than the general variation.

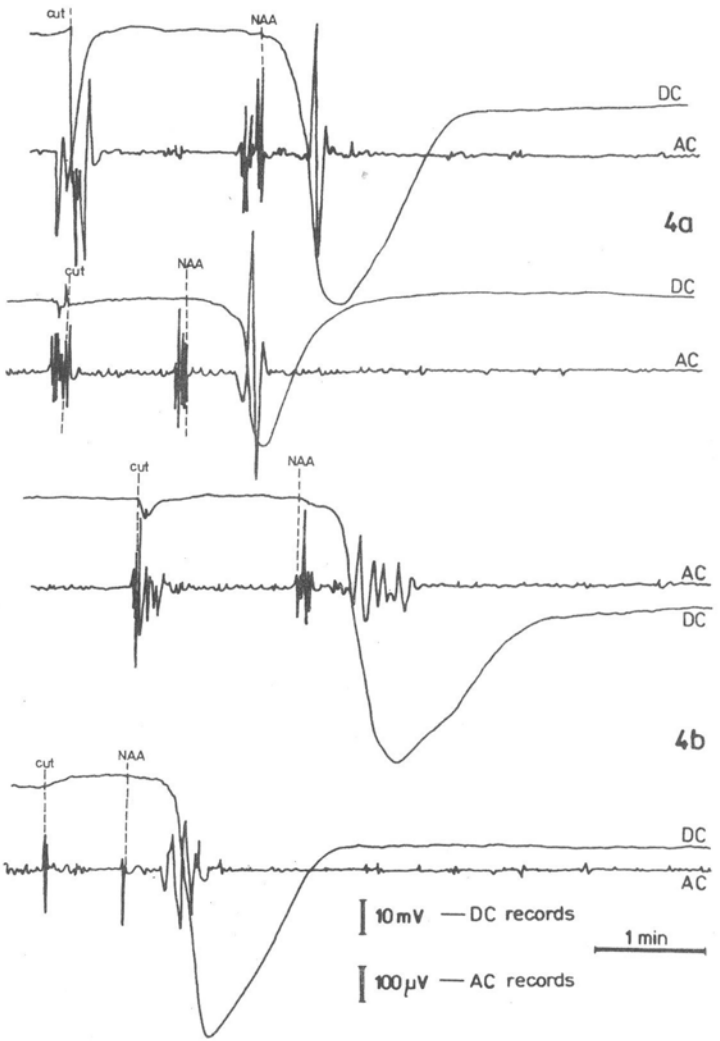

Fig. 4. AP and its OC observed in the petioles of lupine. The records on Fig. 4a derive from two petioles of one plant, those on Fig. 4b, from the other plant

The OC is travelling without changing its temporal position with respect to the pulse on DC record, thus it can serve as a marker of the travelling pulse. In general, the height of the pulse on the DC record and the amplitude of OC spikes are approximately proportional, except from the stem base where the pulse may be high but OC spikes are usually low. In the case of a dampened pulse the amplitude of OC spikes may be relatively high in the region where the pulse is dampened.

The DC and AC records do not depend on the connection of the electrode to only one type of amplifier or to both.

It should be added that analogical signals to those evoked may appear spontaneously. Figure 5 shows a propagated spontaneous signal of the OC

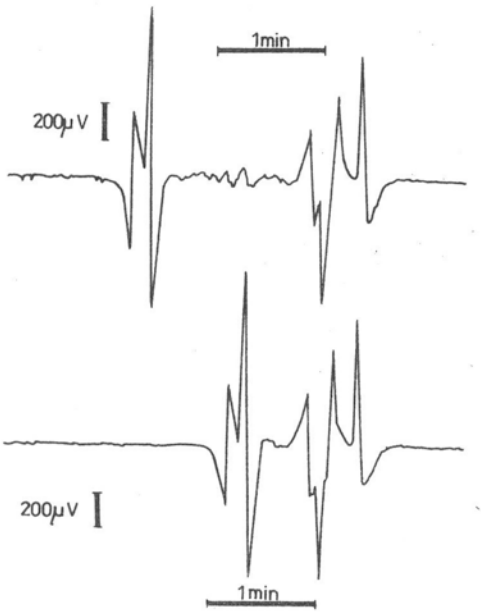

Fig. 5. Spontaneous, propagating OC observed on the three electrodes. The OC on the 3rd (reference) electrode produces simultaneous signals on both recorders but with inverted polarity with respect to the signals from the measuring electrodes

type recorded successively by three electrodes. Whether this signal was accompanied by the pulse of extensive depolarization cannot be known because the electrodes were connected to the AC amplifier only.

DISCUSSION

In our experiment, the appearance of the variation potential was undoubtedly possible. In fact, we observed many cases of potential fluctuation of a different shape than the typical pulse. Probably, these were the cases where the "wound hormone" plus auxin had reached the level of the exploring electrode i.e. cases of variation potential. They were not taken into consideration. That which was studied was similar to the pulses described by Paszewski and his collaborators. Their studies do not leave any doubts that the propagating pulse is not a variation potential. However, it is quite possible

that the pulses in our studies originated from the variation potential in the proximal part of the cut petiole: the "wound substance" plus auxin reached a certain level inside the petiole via xylem triggering variation potential in the live tissue up to this level, and then a self-sustaining wave of depolarization (the pulse) was propagated basipetally.

According to our interpretation there is only a relatively small portion of excitable cells in the lupine stem. The situation is similar to that in the petiole of *Mimosa* (Sibaoka 1966, Samejima and Sibaoka 1983), where excitable cells occur as a strand of protoxylem and protophloem parenchyma and all other cells, epidermis, cortex, sclerenchyma sheats and pith are inexcitable. The AP is transmitted electrically from one excitable cell to another excitable cell which results in a relatively fast velocity 2-3 $cm \cdot s^{-1}$. However, if one strand of excitable cells is surgically disconnected between the points of stimulation and recording, intracellular AP in this strand occurs at the same time as in the intact strand. This is interpreted by Sibaoka (1966) as due to current transmitted from the intact strand, where it is generated by AP, to the disconnected strand through the inexcitable cells. The very rapid transmission across the inexcitable cells indicates that the current is generated solely by the excitable cells without addition to it by depolarization of inexcitable cells. Direct intracellular recording of the latter cells indicates only a light, transient change of E_m upon transmission of the AP through the petiole.

If in *Mimosa* the cortical cells are inexcitable, it would be rather strange to expect that all cortical cells are excitable in lupine. We should rather expect that also in this plant only certain cells are excitable and this seems to be supported by the present study (if our interpretation that OC represent AP recorded in volume conductor is proper). Similarly as in *Mimosa*, cooperation in many cells should be expected. In fact, our concept that the pulse in lupine is a wave of cooperative depolarization of action type in excitable cells and graded type in inexcitable cells, stresses the cooperation phenomenon: the inexcitable cells cooperate not only passively as in *Mimosa* but also actively, adding to the current which triggers the next excitable cells. It is reasonable to relate the relatively very slow velocity of the pulse, to the fact that there is an active component of the inexcitable cells which probably correctly can be considered "slow". Per analogia we can envisage a wave of fire spreading in a row of matches arranged in a line. The burning of the combustible mixture fires explosively — the wood burns gradually (though completely). The longer the wooden parts in comparison to the combustible parts, the slower the wave. We would also like to offer this analogy for visualisation of how cooperation of graded and explosive processes produces a phenomenon which, as a whole, shows the behavior of the all-or-none type. It appears thus that our hypothesis

stating that there is not solely action potential in the lupine stem, is not in conflict with the properties of the pulse which were established by Paszewski and his collaborators and which allowed them to treat the pulse as the action potential. It is known that elicitation of a propagating action potential in ordinary plants is fortuitous event, even if its probability is high by selecting the proper species and defining the proper conditions for growing and stimulation (Pickard 1973). We feel that this low safety factor may be just the participation of inexcitable cells in AP propagation. Firing of excitable cells, if proper stimulation is provided, is safe, however propagation of AP through a line of such cells may be unsafe, when cells without regenerative positive feedback between current and depolarization cooperate in this process. We are fully aware that there is a possibility of a radically different hypothesis about the origin of OC, namely that depolarization of the plasmalemma does not run smoothly but in an oscilatory way, i.e. the OC represents the oscillation in the kinetics of plasmalemma depolarization, and is a feature of every part of the symplast undergoing depolarization. According to this hypothesis the AC amplifier would simply filter the fast enough oscillations of the depolarization. Since the supposed oscillation though faster than the pulse is still probably not fast enough to be perceived in a volume conductor it would have to occur in the proximity of the electrode. It should be taken into account that Głębicki et al. (1986) have shown occurance of fluctuations similar to OC but originating from sources which may be distant from the electrode, and thus recorded in a volume conductor.

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Składowa oscylacyjna zaburzenia potencjału elektrycznego propagowanego w pędach łubinu

Streszczenie

Działanie kropli roztworu auksyny na ucięty ogonek liściowy powoduje wystąpienie spadku potencjału propagowanego wzdłuż ogonka liściowego i łodygi. Zaburzenie to było jednocześnie rejestrowane przez dwa wzmacniacze: wzmacniacz stałoprądowy i wzmacniacz z pasmem przenoszenia 0,1-100 Hz. Oba wzmacniacze były połączone z tą samą elektrodą pomiarową. Zaburzenia rejestrowane przez wzmacniacz stałoprądowy miały amplitudę 20-80 mV, a ich czas trwania mierzony w połowie amplitudy wynosił około 30 s. Obraz tego samego zaburzenia rejestrowany przez wzmacniacz z ograniczonym pasmem przenoszenia, zawiera od jednego do kilku ostrych, ujemnych i dodatnich skoków potencjału, których amplituda jest o rząd wielkości mniejsza od zaburzenia rejestrowanego przez wzmacniacz stałoprądowy. Skoki te są interpretowane jako potencjały czynnościowe komórek pobudliwych, rejestrowane w przewodniku objętościowym. Całe zjawisko interpretuje się jako falę depolaryzacji rozchodzącą się dzięki współdziałaniu komórek pobudliwych z otaczającymi je niepobudliwymi.