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Passive electrical properties of *Lupinus angustifolius* L. stem
IV. The core-conductor theory parametres: space constant λ and time constant τ

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Abstract

On the basis of the core-conductor theory and the method described by Hodgkin and Rushton (1946) for the axon, the space constant λ and the time constant τ have been determined for the stem of *Lupinus*. Electrotonic potentials were recorded in the extrapolar region in the vicinity of the cathode along the longitudinal axis of the stem. Extracellular recording electrodes were applied. It was found that the steady-state distribution of potential along the stem surface is of exponential character. The calculated space constant λ has a value of 2.0 to 2.4 mm (average 2.1 mm) and is almost identical with the λ values for nerves and muscles (mean 1.5—2.0 mm). The values of the time constants ("half-time") of electrotonic potentials increase linearly with the distance from the cathode. The time constant τ calculated on this basis is on the average 5.2 sec and as compared with τ for nerves and muscles is 10^3 times higher. The phenomena observed in the *Lupinus* stem fulfill the equations of the core-conductor theory (Appendix). Their character is identical to that of the phenomena noted in nerves or muscles. It is probable that they occur on the membrane of excitable cells of the stem. The results here presented are a convincing argument indicating that in higher plants an excitable system may exist, subjected to the same laws as that in animal organisms.

INTRODUCTION

It results from up-to-date investigations in this Laboratory, concerning the arising and propagation of excitation in the *Lupinus* stem, that the characteristic of the results obtained is identical with that noted in animal excitable systems (axons, nerve, muscle). These characteristics are: the action potential (AP) of typical shape propagating without decay, the all-or-nothing law, Pflüger's laws of contraction, the strength-duration relation, refractory periods, accommodation and anode break excitation, latency, electrotonic potentials and local responses (Paszewski and Zawadzki, 1973, 1974, 1976a; Zawadzki, 1979a, b; Zawadzki and Dziubińska 1979). As demonstrated by Hodgkin and Rushton (1946), beside studies of the active state, an important role is played by investigations of passive (electrotonic) properties of the membrane in gaining a better knowledge of the excitable structures. The resistance-capacitance properties of the axon established in investigations on electrotonic potentials, served as basis for elaboration of an electric model of the axon. The assumption that the axon can be represented by a system of resistances and capacitances is known as the core-conductor theory, since it implies that the axon behaves like a poorly insulated cable (Fig. 1A). In such a system, voltage V applied at a given point varies with the distance x and time t (because of the capacitance in the system) according to the equation

$$V=\lambda^2 \frac{\delta^2 V}{\delta x^2} - \tau \frac{\delta V}{\delta t}$$

This equation contains two coefficients designated as space constant λ and time constant τ (Aidley, 1971). A more extensive discussion of the problem is given in the Appendix.

The resistance-capacitance properties of the *Lupinus* stem have been described by Zawadzki (1979b). A single RC circuit is shown there as a simple model corresponding approximately to the passive electrical properties of the *Lupinus* stem. The present paper is a continuation of the above mentioned investigations and an attempt at demonstrating that the core-conductor theory may find application in the description of electrical properties of plants.

MATERIAL AND METHODS

The material (40 — 70-day-old plants of *Lupinus angustifolius* L.), the apparatus and methods have been described in an earlier paper (Paszewski and Zawadzki, 1973). The electrotonic potentials were measured by the method described by Zawadzki (1979a) with the use of a stimulus corresponding to 0.4 of the rheobase. For determining the steady-state distribution of potential along the surface of the *Lupinus* stem, the electrotonic potentials were measured at points lying at a distance of 0.0, 0.5, 1.0, 1.5, ..., 6.5 and 7.0 mm from the cathode along the longitudinal stem axis. Contact with the stem surface was established by way of calomel electrodes ending in a pipette 0.3

mm in diametre. Successive stimulations were applied at 30-min intervals. The experimental arrangement is shown in Fig. 2. The space constant λ and the time constant τ were determined by the method described by Hodgkin and Rushton (1946) for axons. The experiments were performed in daylight (about 1.5 $W \cdot m^{-2}$) at 21—23°C.

RESULTS AND DISCUSSION

The space constant λ

As compared to a single RC circuit (Zawadzki, 1979b) the electric model resulting from the core-conductor theory (cable model — Fig. 1A) takes into account an essential geometrical parametre depending on length of the system (axon, nerve, muscle) — the space constant λ. Let us consider the results obtained for *Lupinus* stem according to the method used by Hodgkin and Rushton (1946) for the axon. Fig. 2 shows as example electrotonic potential records observed at various sites of the extrapolar region along the longitudinal axis of the stem. The records were obtained with the application of a rectangular cathodal stimulus of 20 sec duration and 0.4 of the rheobase value. The potentials are typical exponentially rising and

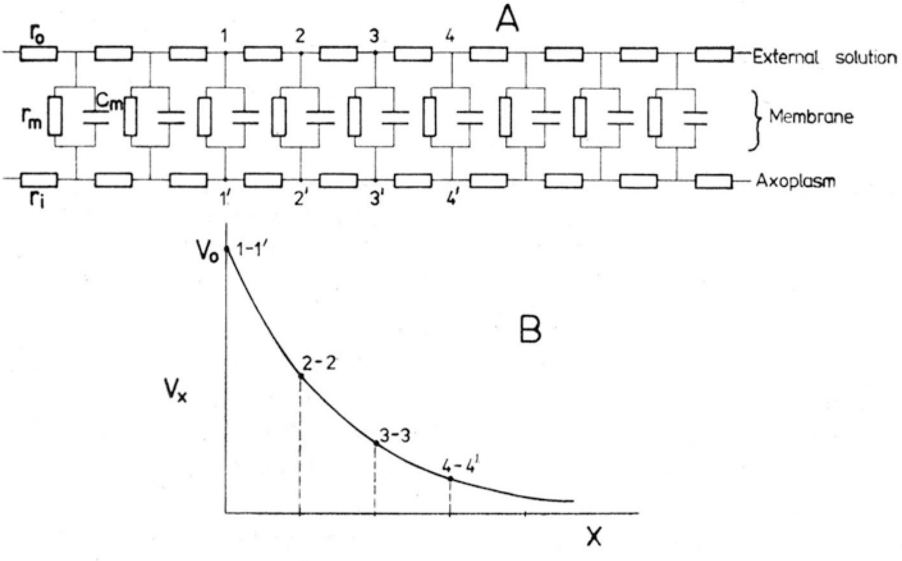

Fig. 1. A. Electrical model of the passive (electrotonic) properties of a length of axon (explanation in Appendix). B. Steady-state distribution of potential along the model. The voltage V_x across the "membrane" falls exponentially with the distance x from points 1—1′ at which the voltage V_0 is applied

falling electrotonic potentials with amplitude decreasing with distance from cathode. They were obtained for a highly excitable plant, that is with a low rheobase. It should be noted that the amplitudes of these electrotonic potentials as responses to a stimulus of 0.4 rheobase are almost identical as those in the case of axons (Hodgkin and Rushton, 1946) or of muscles (Kamiyama and Matsuda, 1966), and they are of the value of several mV. On the other hand the time of potential rise and fall is about 10^3 times longer in the plant.

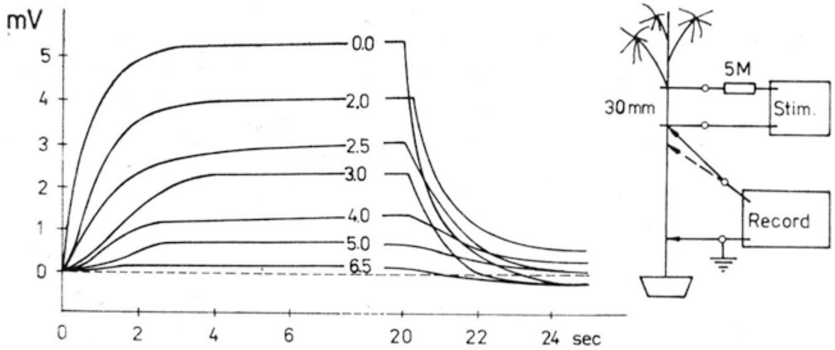

Fig. 2. Electrotonic potentials in *Lupinus* stem recorded in extrapolar region. Records obtained for one of the plants after application of a stimulus of 20 sec duration and 0.4 value of the rheobase (experiment no. 1 — Table 1). Distance from the cathode is shown by the figures on each record. Experimental arrangement on right side

Equation (1.7) shows that there should be an exponential relation between the steady potential in the extrapolar region and the distance from the cathode. This relation is shown in Fig. 3A on the example of three series of measurement obtained on three *Lupinus* plants with different rheobase values. Deviations from the exponential potential fall are visible in the region closest to the cathode (up to about 1.5—2 mm). In this area the potential remains at an approximately unchanged level. This is the border area where the assumptions of the core-conductor theory are not fulfilled because the length of this border area is comparable to the stem diametre (about 2 mm) and the cathode thickness (0.4 mm). This has probably an essential influence on the distribution of electric field force lines in the vicinity of the cathode. An identical phenomenon was observed for the axon by Hodgkin and Rushton (1946) and for the muscle by Kamiyama and Matsuda (1966). Thus, the data obtained from the area up to 1.5 mm distant from the cathode will be disregarded in the elaboration of the results. Let us consider the results within the range shown by the continuous lines in Fig. 3A. The interpolation here presented

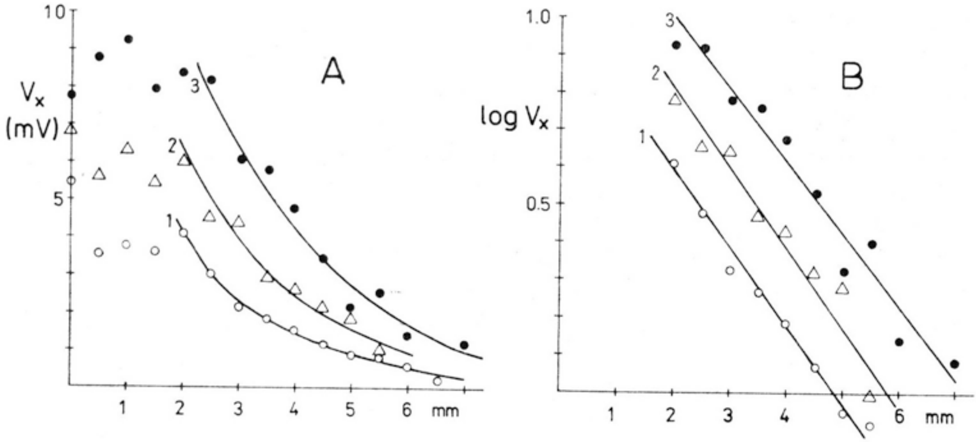

Fig. 3. Equilibrium distribution of extrapolar potential in *Lupinus* stem.

A. Relation between the steady potential in the extrapolar region and the distance from the cathode. Stimulus 0.4 of the rheobase. Three measurement series obtained on three plants with different rheobase values. Experiment no. 1 — curve ○, 2 — curve △, 3 — curve ●. At a distance of about 2 mm from the cathode (border area) the steady potential has an almost constant value. The exponential fall of this potential occurs at a distance of 2 to about 7 mm as marked by continuous lines.

B. The same results as in Fig. 3A shown in logarithmic scale. The space constant λ for experiments no. 1, 2 and 3 calculated from slope of lines (slope = (log e)/λ) are 2.0, 2.0 and 2.2 mm, respectively (Table 1).

indicates that the potential distribution in the extrapolar region is of exponential character (with the exclusion of the area closest to the cathode). A straight line with slope (log e)/λ should result when the log of the potential is plotted against the distance. This method was used in all the experiments and is illustrated in Fig. 3B. The λ values calculated in this way for five *Lupinus* plants are 2.0, 2.0, 2.2, 2.1 and 2.2 mm (Table 1). Fig. 4 proves that this procedure gave satisfactory results. The results of five experiments are plotted on a linear scale; the ordinates giving the potential as a fraction of the potential at the cathode (distance 2 mm) and the abscissae the distance as a fraction of

Table 1

Space constant λ and time constant τ determined for *Lupinus* stem

Time constant τ in A determined from time constants of rise of electrotonic potentials, in B from time constants of fall of electrotonic potentials in extrapolar region

No of experiment		1	2	3	4	5	mean
Space constant λ, (mm)		2.0	2.0	2.2	2.1	2.2	2.1
Time constant τ, (sec)	A	5.7	4.7	6.7	4.7	4.2	5.2
	B	5.0	5.0	4.3	6.0	5.5	

the space constant. If equation (1.7) is fulfilled perfectly, all the points should fall on an exponential curve drawn as a continuous line. This curve was determined for a mean value of $\lambda = 2.1$ mm. In practice there are deviations, nevertheless the exponential character of distribution of the experimental points is distinctly noticeable. The space constants λ calculated from formula (1.7) for the data in Fig. 3A as the length over which the voltage falls to 1/e of its original value amount to 2.0, 2.1 and 2.4 mm, respectively, and are in agreement with the values calculated from the slopes of the logarithmic curves. A tendency is visible towards a somewhat higher value of space constant for plants characterized by a lower excitability. This set of observations demonstrates the validity of the theory and of the method of measurement employed.

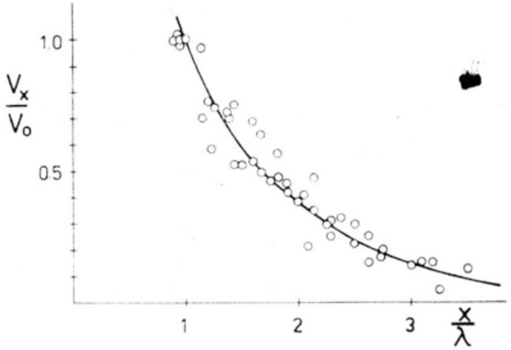

Fig. 4. Equilibrium distribution of extrapolar potential in five experiments. Ordinates: potential as a fraction of the potential at the cathode (at a distance of 2 mm). Abscissae: distance as a fraction of the measured space constant λ. The continuous line is drawn according to equation (1.7)

It also results from the diagrams in Fig. 3A that when electrical stimulation is applied, the maximal voltage value appears at a certain distance from the cathode (about 2 mm). A threshold (rheobase) stimulus may, therefore, evoke excitation at points about 1—2 mm distant from the cathode. This excitation will be recorded by further lying electrodes. On the other hand, an electrode applied at the cathode (distance 0.0 mm) can only show local responses. Such cases of "development" of excitation at a certain distance from the cathode into an action potential are shown in the paper by Zawadzki (1979a). Hodgkin (1939) described this phenomenon in axons.

Time constant τ

As mentioned by Hodgkin and Rushton (1946), determination of the time constant of the membrane is a more complicated problem than that of the space constant. One of the methods suggested by these authors is determination of the time constant of the membrane on the basis of the rate of rise and/or fall of electrotonic potentials in the extrapolar region in the vicinity of the cathode. According to their observation on nerve fibres, the time constants of electrotonic potentials increase linearly with the distance from the current source, and the slope of linearity is nearly equal to $2\lambda/\tau$, where τ denotes the time constant of the membrane. This method found also application in the determination of the time constant of the muscle cell membrane (Kamiyama and Matsuda, 1966).

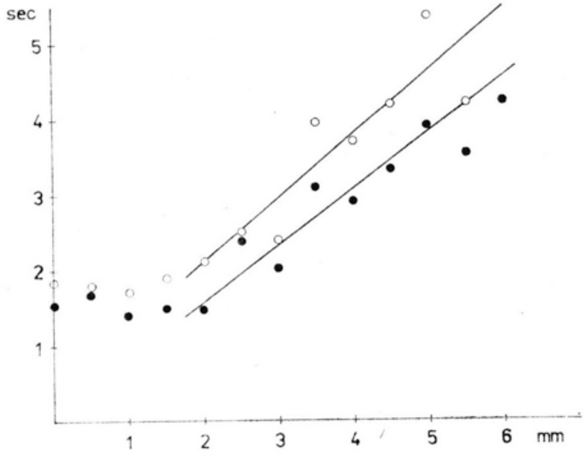

Fig. 5. Distribution of time constants of rise and fall of electrotonic potentials in extrapolar region for *Lupinus* stem.

Ordinates: time constant ("half-time") of rise and fall of electrotonic potentials. Abscissae: distance from cathode. Points ○ denote the time constant of rise and points ○ the time constant of fall of the electrotonic potentials. Each point represents the mean value of five experiments. The linear rise starts at a distance of about 2 mm from the cathode, as indicated by continuous lines (slope = $2\lambda/\tau$)

It results from the exemplary records in Fig. 2 obtained for the *Lupinus* stem that the time constants of electrotonic potentials increase with the distance from the cathode. This relation is illustrated by Fig. 5 which presents the distribution of mean time constants of rise and fall of electrotonic potentials in the extrapolar region, obtained in measurements on five *Lupinus* plants. The time constant τ calculated from these curves (with mean value $\lambda = 2.1$ mm) is 5.2 sec. The time constant τ calculated by the same method (from the slope of the curves) for the particular plants are shown in Table 1. It results from the diagrams in Fig. 5 that the time constants of rise and fall of electrotonic potentials exhibit the lowest values in the vicinity of the cathode. Similarly as in the case of determination of potential distribution in the extrapolar region, these values remain at an almost constant level in the area up to about 2 mm distant from the cathode. The observed variations of these time constants in this area amounted to about 0.8 to 2.8 sec for various *Lupinus* plants. For similar reasons as mentioned above, the results from the area 2 to about 6 mm distant from the cathode were taken for calculations. It should be borne in mind that in the case of determination of the time constant τ, the character of the observed phenomena is identical as in the case of the axon or muscle, the absolute τ value reaching, however, in *Lupinus* stem on the average 5.2 sec is higher by about $2 \cdot 10^3$ times.

To sum up the results it may be affirmed that within the range of the space constant λ and the time constant τ the core-conductor theory describes the passive electrical properties of the *Lupinus* stem. It results from the theory that the determined parametres refer to 1 cm of the object length and result in the first place from the cell membrane properties.

The investigations do not, however, give any indication as to which structural element of the stem tissues these properties might be ascribed. This is an important problem which has been also discussed in our earlier papers. It requires further investigations leading to a better knowledge of the structures and pathways responsible for excitation in higher plants. On the other hand, Hodgkin and Rushton (1946) used extracellular electrodes, the voltage changes were measured on the outside of the axon membrane. These authors demonstrated that the changes are proportional to the change in potential across the membrane so that the core-conductor equations can still be applied. Like in muscle studies extracellular electrodes are used or a combination of extra- and intracellular leads (e.g. extracellular stimulation of a muscle — Kamiyama and Matsuda, 1966), and the results are referred to the cell membranes. It may, therefore, be assumed that in the case of *Lupinus* stem the determined parametres also refer to the excitable cell membranes. This supposition finds support in the studies of Sibaoka (1962) on *Mimosa* with the use of microelectrodes, those of Stuhlman and Darden (1950), DiPalma, Mohl and Best (1961) on *Dionaea muscipula,* Williams and Pickard (1972), Williams and Spanswick (1972) on *Drosera,* Mamulashvili, Krasavina and Lialin (1973) on pumpkins, cucumbers and sunflowers, and those of Paszewski and Zawadzki (1976b) on *Lupinus.*

It results unequivocally from our investigations to date that the phenomenon observed in *Lupinus* stem connected with a state of excitation and also those resulting from passive (electrotonic) properties are all fully governed by the basic laws of excitability (Aidley, 1971). It is also essential that the values of all these parametres independent of time (e.g. amplitude of AP, electrotonic potentials and threshold potential, space constant λ) are the same as or very similar to those occurring in nerves or muscles. Time-dependent parametres exhibit the same characteristic as those in animal systems, only their course is slower. As compared with the characteristic times of transients in the axon of *Carcinus* those in the *Lupinus* stem occur about 10^3 times slower. These relations between various kinds of nerves and muscles are easy to demonstrate. According to the author's opinion, the here presented results are a conclusive argument proving that in higher plants an excitable system exists, subject to the same laws as in animal organisms.

APPENDIX

A full mathematical elaboration of the core-conductor theory may be found in the works of Hodgkin and Rushton (1946) and Taylor (1963). The present abridged elaboration taken from Aidley (1971) calls the reader's attention to the essence of the problem and may serve as a model of attempts at elaboration of an equation for such a complex system as is the *Lupinus* stem.

It is assumed that there occur in the axon: a transverse resistance of the membrane (r_m), transverse capacitance of the membrane (c_m), a longitudinal resistance of the external medium (r_o) and a longitudinal resistance of the axoplasm (r_i). These quantities refer to unit lengths (e.g. 1 cm) of the axon and do not change along its length, and the axon is infinitely long. The complete network is shown in Fig. 1A. Let us apply voltage V_o accross the membrane at a certain point. The question arises how V varies with distance x and time t (because of the capacitance in the system). The transverse current flowing through the membrane (i_m) will be the sum of the currents flowing through r_m and c_m, i.e.

$$i_m = \frac{V}{r_m} + c_m \frac{dV}{dt} \tag{1.1}$$

The current (i) flowing through a longitudinal resistance r_o and r_i may be represented as

$$i = -\frac{dV}{dx}\left(\frac{1}{r_o + r_i}\right) \tag{1.2}$$

and

$$i_m = -\frac{di}{dx} \tag{1.3}$$

Hence

$$i_m = \left(\frac{1}{r_o + r_i}\right) \frac{d^2V}{dx^2} \tag{1.4}$$

Equating (1.4) with (1.1),

$$\frac{V}{r_m} + c_m \frac{dV}{dt} = \left(\frac{1}{r_o + r_i}\right) \frac{d^2V}{dx^2}$$

or

$$V = \left(\frac{r_m}{r_o + r_i}\right) \frac{\delta^2 V}{\delta x^2} - r_m c_m \frac{\delta V}{\delta t} \tag{1.5}$$

After inroduction of the two constants, the space constant λ and the time constant τ, since

$$\lambda^2 = \frac{r_m}{r_o + r_i}$$

and

$$\tau = r_m \ c_m$$

we get from (1.5)

$$V = \lambda^2 \frac{\delta^2 V}{\delta x^2} - \tau \frac{\delta V}{\delta t} \tag{1.6}$$

This is the relation between V, x and t.
If a constant current is applied for a long (effectively infinite) time, (the (1.6) simplifies to

$$V = \lambda^2 \frac{\delta^2 V}{\delta x^2}$$

The solution of this equation is

$$V_x = V_o e^{-x/\lambda} \tag{1.7}$$

This means that the voltage across the membrane falls exponentially with the distance from the point at which the current is applied. This is shown in Fig. 1B and λ can be defined as the length over which the voltage across the membrane falls to 1/e of its original value V_o.

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Bierne elektryczne własności łodygi Lupinus angustifolius L.

Streszczenie

W oparciu o teorię kablową (the core-conductor theory) i metody badawcze opisane przez **Hodgkina** i **Rushtona** (1946) dla aksonu, wyznaczono dla łodygi *Lupinus* wartości stałej przestrzennej λ i stałej czasowej τ. Stosowano zewnątrzkomórkowe elektrody pomiarowe. Potencjały elektrotoniczne rejestrowano w zewnątrzelektrodowym obszarze w pobliżu katody wzdłuż podłużnej osi łodygi. Stwierdzono, że stacjonarny rozkład potencjału wzdłuż powierzchni łodygi ma charakter wykładniczy. Obliczona na tej podstawie stała przestrzenna λ ma średnią wartość 2.1 mm i jest prawie identyczna z wartościami λ dla nerwów i mięśni (średnio 1.5—2.0 mm). Wartości stałych czasowych potencjałów elektrotonicznych wzrastają liniowo z odległością od katody. Stała czasowa τ

określona na tej podstawie wynosi średnio 5.2 sek i w porównaniu do τ dla nerwów i mięśni jest większa około 10^3 razy.

Zjawiska obserwowane w łodydze *Lupinus* w pełni podlegają równaniom teorii kablowej. Mają identyczną charakterystykę jak zjawiska zachodzące w zwierzęcych układach pobudliwych. Można przypuszczać, że zachodzą na błonach komórek pobudliwych łodygi.

Przedstawione wyniki stanowią zdaniem autora istotny argument na to, że u roślin wyższych może istnieć system pobudliwy podlegający tym samym prawom co w organizmach zwierzęcych.