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Electrical properties of *Lupinus angustifolius* L. stem

III. RC model, time constant, latency and threshold charge

TADEUSZ ZAWADZKI

Department of Plant Physiology, Maria Curie-Skłodowska University, Lublin, Poland

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Abstract

The changes of potential in the stem of *Lupinus* were characterized on the basis of the strength-duration relation and of electrotonic potentials. It was found that the stimulated stem behaves like an electrical RC circuit. The time constants of electrotonic potential rise and decay were determined. A simple electrical model characterizing the passive electrical properties of the *Lupinus* stem is suggested. The values of resistance and capacitance of the *Lupinus* stem were determined on the basis of the RC circuit.

The resistance-capacitance properties of the stem tissues serve as basis to gain a better knowledge of the parametres describing excitation, such as the strength-duration relation or latency. These properties in the stem of *Lupinus* are of the same nature as those in nerves or muscles. The values of the threshold charge of the order of 10^{-6} C were calculated. It is suggested that the regularities occurring here may be connected with accommodation and processes regulating the resting potential of cells.

INTRODUCTION

It results from the strength-duration relation (Rushton, 1935; Aidley, 1971) that the threshold stimulus intensity (square constant current pulse) rises as the pulse length is reduced. Thus, the time factor plays an important role as does the intensity of the stimulus. The necessity of applying an electrical stimulus for a certain time period may be explained by the capacitance of the cell membrane. The stimulating voltage must, for evoking excitation, depolarize the membrane until its potential attains the threshold value. Since the axon membrane behaves electrically like a resistance and capacitance in parallel (Hodgkin and Rushton, 1946; Aidley, 1971), the rate of changes in the membrane potential, i.e. the depolarization is determined by the time of capacitance charging. This phenomenon can be characterized by reference to a simple electrical model (Fig. 1). The exponential rise of voltage can be expressed by the equation

$$V_0 = V_m\left(1 - e^{-\frac{t}{RC}}\right) \tag{1}$$

It has been demonstrated in previous papers that electrical stimulation parametres (e.g. all-or-nothing law, strength-duration relation, refractory periods, electrotonic potentials, local responses, accommodation) characterize the arising and propagation of impulses in the *Lupinus* stem in the same way as in nerves (Paszewski and Zawadzki, 1973, 1974, 1976; Zawadzki, 1979; Zawadzki and Dziubińska, 1979). The present paper is an attempt to demonstrate that the role of the time factor in electrical stimulation and excitation of the *Lupinus* stem may be interpreted in the same way as it is in animal excitable tissues, and the resistance-capacitance properties may be represented by a simple RC model.

MATERIAL AND METHODS

The material (40—70-day-old plants of *Lupinus angustifolius* L.), the apparatus and methods are described in an earlier paper (Paszewski and Zawadzki, 1973). The strength-duration relation was determined by the method used by Paszewski and Zawadzki (1974). The RC time constants τ_1 and τ_2 were determined from the strength-duration relation and also graphically from the electrotonic potential records obtained at the cathode with the use of a stimulus of the value of 0.5 of the rheobase. It was essential in these investigation to apply an external resistance R_o of various value (from 0 to 15 Mohm) connected into the stimulating circuit in series with the plant. The resistance values (R_m and R_i) and capacitance (C) values were determined by means of formulae (3) and (4). The experiments were performed under daylight (1.5 $W \cdot m^{-2}$) at 21—23°C.

RESULTS AND DISCUSSION

Strength-duration relation and RC properties of *Lupinus* stem

The strength-duration relation (Paszewski and Zawadzki, 1974) is described by the empirical equation

$$\frac{I_m}{I_0} = \frac{1}{1 - e^{-t/k}} \tag{2}$$

where I_m is the pulse intensity (voltage), t is the pulse duration, I_o is the threshold stimulus intensity when t is long (rheobase) and k is a constant (Aidley, 1971). Equation (2) is equivalent to equation (1). The constant k has a time dimension and is the time constant RC. The threshold voltage stimulus for long duration is called the rheobase and is designated by V_{rh}. Equation (1) can be written in the form

$$\frac{V_m}{V_{rh}} = \frac{1}{1-e^{-t/RC}} \tag{1.1}$$

where V_m is the pulse voltage, V_{rh} the rheobase, t is the pulse duration, R is the resistance of the circuit and C is the capacitance. The equivalence of equations (1) and (2) indicates that the strength-duration relation occurring in the *Lupinus* stem is the result of the resistance-capacitance properties of the stem.

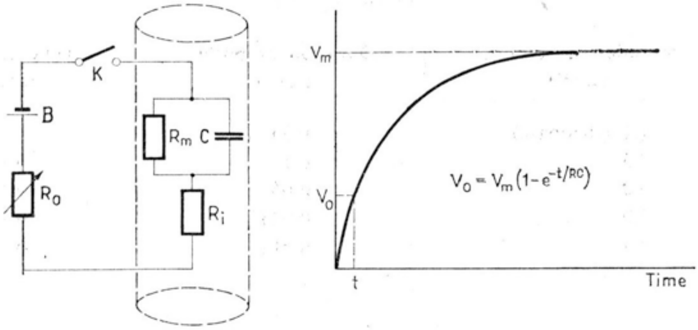

Fig. 1. Electrical RC circuit presented in the form of an experimental arrangement. R_m, R_i and C are resistances and capacitance of the stem tissues and constitute the proposed RC model of the *Lupinus* stem

R_o — external variable resistance (0—15 Mohm), B — battery, K — key. The externally applied voltage V_m (rectangular pulse) reaches accross the capacitor the given value V_o after time t. Circuit resistance $R = R_m (R_i + R_o) / (R_m + R_i + R_o)$ and in the case when $R_o = 0$; $R = R_m R_i / (R_m + R_i)$

For a circuit as in Fig. 1, $R = R_m(R_i+R_o)/(R_m+R_i+R_o)$. Let us denote the RC of potential rise as τ_1. We then get from (1.1)

$$\tau_1 = -\frac{t}{\ln(1-V_{rh}/V_m)} \tag{1.2}$$

The experimental data for the strength-duration relation and calculated values of τ_1 are presented in Table 1. Since the differences in τ_1 values are small, the strength-duration curve plotted for the mean value of $\tau_1 = 0.14$ sec differs but slightly from the experimental curve and does not exceed the limits of measurement error (Fig. 2).

Thus, electrical (rectangular voltage) pulses applied externally rise exponentially in the *Lupinus* stem. The stem behaves in this case like an RC circuit and it is obvious that the successive 8.8, 7.0, 5.0, 2.5 and 1.2 V stimuli will reach the rheobase value ($V_{rh} = 1.2$ V), and will thus evoke excitation after a time of 0.018, 0,025, 0.04, 0.1 and about 0.35 sec, respectively. Further duration of the stimulus is no more essential for the excitation phenomenon (Paszewski and Zawadzki, 1973). It results there from that a stronger stimulus causes the rheobase value to be reached ealier. A regular tendency of increase of RC with diminution of the stimulus value may, however, be evidence that the phenomenon does not occur in the *Lupinus* stem strictly according to equations (1) and (2).

Table 1

Results obtained in determination of strength-duration relation in *Lupinus* stem

Data from investigation of one of the plants with stem cross-section 3 mm^2. Time constants calculated by means of equation (1.2). The measurements were taken without extarnal resistance ($R_0 = 0$)

	Stimulating voltage, V_m (V)	Duration of pulse, t (sec)	Time constant τ_1 (sec)
1	1.2 (rheobase)	0.35	—
2	2.5	0.1	0.15
3	5.0	0.04	0.14
4	7.0	0.025	0.13
5	8.8	0.018	0.12

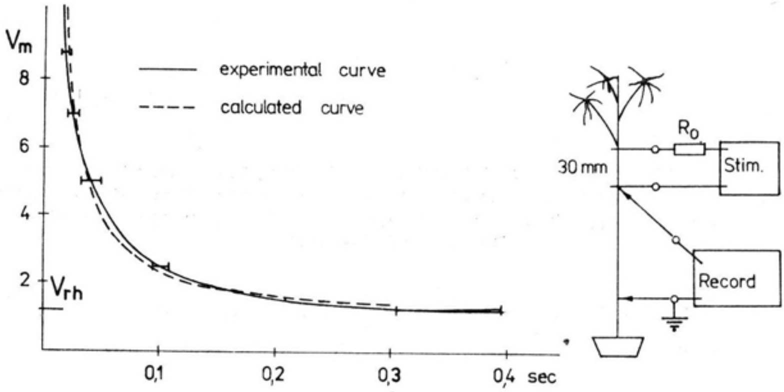

Fig. 2. Strength-duration curves plotted for *Lupinus* stem. Continuous line — experimental curve

Interrupted line — calculated curve determined from equation (2) for the mean time constant $\tau_1 = 0.14$ sec and $V_{rh} = 1.2$ V. Experimental data give in Table 1. Experimental arrangement on right side. Experiment performed at $R_0 = 0$

When the strength-duration relation is determined with the use of large external resistance R_o (above 3—5 Mohm) a significant deviation from equation (2) is observed in the case of weak stimuli. The utilization times are then longer and the rheobase higher than it would result from the strength-duration curve for stronger stimuli. This may be due to the fact that the large resistance R_o increases the time constant τ_1. In this way a stimulus of rheobase value grows in the stem slowly (particularly in the last phase of rise) according to the exponential curve (Fig. 1). It is easy to prove that at $\tau_1 \approx 1$ sec the rate of rise of a stimulus of value similar to that of the rheobase corresponds to the accommodation rate in the *Lupinus* stem (Zawadzki and Dziubińska, 1979). In other words, in view of the RC properties of the stem, the stimulus rises so slowly that accommodation begins to play an essential role. With the increase of stimulus value this regularity rapidly disappears.

Electrotonic potentials and the RC model

The exponential character of rise and fall of the potential in the stem of *Lupinus* also results from the records of electrotonic potential and local responses. The subthreshold responses have been described by Zawadzki (1979). Let us consider the electrotonic potentials from the aspect of their exponential character. Fig. 3 shows records of three electrotonic potentials obtained at the cathode, chosen as example. If the *Lupinus* stem behaves as the RC circuit shown above (Fig. 1), the additional external resistance R_o will influence the value of the time constant τ_1 of potential rise (charging of capacitance C) according to the formula

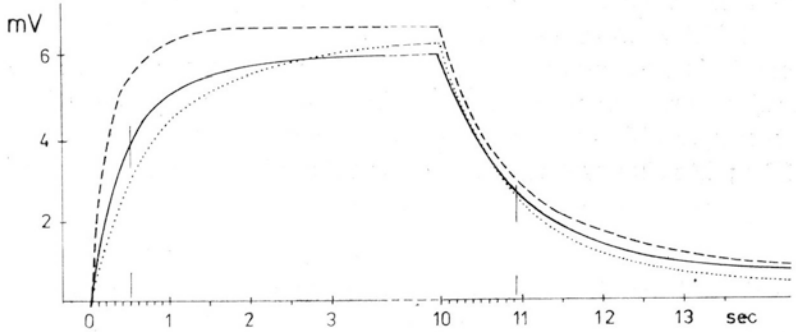

Fig. 3. Three records of electrotonic potentials chosen as examples and taken at various R_0 values for a stimulus corresponding to 0.5 of the rheobase value. Records obtained in experimental arrangement as in Fig. 2

Interrupted line — record at $R_O = 10^3$ Ohms, continuous line — record at $R_O = 5 \cdot 10^5$ Ohms, dotted line — record at $R_O = 5 \cdot 10^6$ Ohms. Time constants of rise (τ_1) and fall (τ_2) determined graphically (time for the voltage to reach 1 — 1/e of its final value). For instance for continuous line $\tau_1 = 0.5$ sec and τ_2 0.92 sec (see equations (1) and (2) and Table 2)

$$\frac{R_m(R_i+R_0)}{R_m+R_i+R_0}C=\tau_1 \tag{3}$$

and will have no influence on the value of the time constant τ_2 of potential fall corresponding to the formula

$$R_m C = \tau_2 \tag{4}$$

because discharge of capacitance C on opening key K occurs only through resistance R_m. Introduction into the model RC of resistance R_i results from the following reasons. If resistance R_i did not exist and $R_o = 0$, the τ_1 would practically be equal to zero. Since in the case of measurement with $R_o = 0$ (see Fig. 2. and Table 1) a certain RC value occurs, it may be concluded that, beside the resistance connected parallelly with the capacitance, there must exist an additional resistance R_i. It results from the records of electrotonic potentials (Fig. 3) that when R_o increases, τ_1 also increases till it reaches the value of τ_2. This value is not dependent on the R_o value and is constant. The observed regularities are in agreement with equations (3) and (4). The τ_1 and τ_2 values may be determined graphically from electrotonic potential records taken at various R_o values. From formulae (3) and (4) a system of equations is obtained, the solution of which gives the R_m, R_i and C values. The results obtained in this way are listed in Table 2. Data for a typical *Lupinus* plant with a rather high excitability were determined. They concern one element of the stem and it is not possible to present them per unit (e.g. in reference to a surface area or volume unit), because the structure of the stem elements responsible for excitation is not well known as yet (Sibaoka, 1962, 1966; Paszewski and Zawadzki, 1976b). The results for other *Lupinus* plants may, in extreme cases, differ from those here reported up to two times. It should also be noted that the electrotonic potentials are not ideally exponential transients. The deviations from this course, however, are slight. Therefore, the error in determination of the time constants is also very small.

Table 2

Results obtained with graphically determined time constants from electrotonic potential records (as in Fig. 3)

Each value of time constants τ_1 of potential rise and time constants τ_2 of potential fall is an arithmetic mean of 5—7 replications on the same plant. Values R_m, R_i and C were obtained by solving the set of equations (3) and (4)

	Stimulus intensity as fraction of threshold	R_o (Ohm)	τ_1 (sec)	τ_2 (sec)	R_m (Ohm)	R_i (Ohm)	C (μF)
1	0.5	10^3	0.25 ± 0.05	0.9 ± 0.07	$6.5 \cdot 10^5$	$2.5 \cdot 10^5$	1.4
2	0.5	$5 \cdot 10^5$	0.5 ± 0.06	0.9 ± 0.06			
3	0.5	$5 \cdot 10^6$	0.8 ± 0.05	0.9 ± 0.06			

The RC model and latency

It is an important property of the local response that its time relation determines latency. Latency is defined as the time between the onset of a stimulus and the peak of the ensuing AP. It is closely connected with the resistance-capacitance properties of the membrane (Aidley, 1971). The latency in the stem of *Lupinus* is shown in Fig. 4A. This phenomenon is also visible on local response records (Zawadzki, 1979). The maximal latency value appears when the stimulus has the threshold value (rheobase) and for the *Lupinus* stem it amounts to about 25 sec. Above the threshold the latency diminishes more or less exponentially together with the increase in the intensity of the stimulus (Fig. 4B). The latency phenomenon may be observed at any resistance R_o value, the highest values, however, are obtained when a high R_o (above 3—5 Mohm) is applied, thus when the time constant τ_1 of potential rise is large.

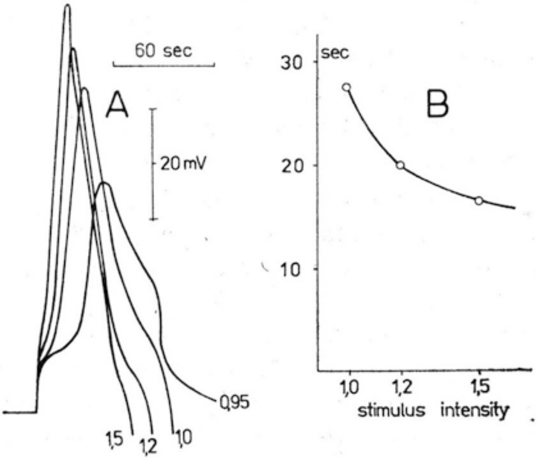

Fig. 4. Latency in *Lupinus* stem

A. Curves represented so as to allow determination of latency. The figures in each record give the value of the stimulus as a fraction of the rheobase. Record 0.95 — local response, records 1.0, 1.2 and 1.5 lead to excitation. Experiment performed with resistance $R_o = 3$ Mohm. B. Latency plotted versus stimulus intensity. Curve derived from records in Fig. 4A

The RC model and the threshold charge

The resting potential as membrane polarization is the result of separation of electrical charges on the membrane, arising and maintained at the cost of metabolic energy. On the basis of the proposed RC model (Fig. 1), the value of the threshold charge may be calculated, that is the value of the charge which must be supplied in order to depolarize the membrane to the threshold potential at which excitation occurs. The formula describing the charge accumulated on capacitance C after time t when the voltage V is applied, is as follows

$$q=\frac{VCR_m}{R_i+R_m}\left(1-e^{-\frac{R_i+R_m}{CR_iR_m}t}\right) \tag{5}$$

The derivation of the formula is shown in Appendix. If we introduce into this formula the R_m, R_i and C values from Table 2 and the successive voltages V as well as the corresponding times t from Table 1, we obtain the respective values of the threshold charge: $0.9\cdot10^{-6}$, $0.8\cdot10^{-6}$, $0.7\cdot10^{-6}$, $0.6\cdot10^{-6}$ and $0.6\cdot10^{-6}$ C. These results were obtained for a plant with rheobase $V_{rh} = 1.2$ V. For less excitable *Lupinus* plants, that is with a 2—3 times higher rheobase, correspondingly (several times) higher values of the threshold charge are obtained.

It results from threshold charge values shown here that the higher the stimulating voltage the lower is the threshold charge with a tendency to stabilization at a certain level around $0.6\cdot10^{-6}$ C. On the other hand, the closer the stimulating voltage to the rheobase value the more the threshold charge increases. This phenomenon may be interpreted as follows. After application of the stimulus the depolarizing voltage increases exponentially. When the voltage is close to the rheobase, it rises in the final phase very slowly according to the course of the exponential curve. In this way the supplied charge depolarizing the cell membrane also changes slowly. It is possible that it may begin to be counter-balanced by forces tending to bring the membrane polarization to a state of rest (e.g. electrogenic pumps). Thus, when threshold depolarization is reached slowly, transgression of the threshold requires the supply of a larger charge. This problem with its mathematical approach will be discussed in forthcoming papers. It may be that it constitutes the essence of the accommodation phenomenon, and that it may serve for estimation of the efficiency of the processes establishing the resting potential of the membrane.

The here presented results may be summed up as follows. Under the experimental conditions, analogous to those in the case of axons, resistance-capacitance properties appear in the stem of *Lupinus*. Their characteristic is identical as in the axon. Only the duration of the phenomena in plants is about 10^3—10^4 times longer. The RC model here presented is identical with that used in neuroelectrophysiology and very similar to the model of plant tissue proposed by Hayden, Moyse, Calder, Crawford and Fensom (1969).

The results here described like those of earlier studies (Parts I—VI) bring evidence that excitation of animal and plant excitable systems occurs and may be described in a similar way. This is also true for the passive electrical properties.

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APPENDIX

According to the theory of electrical circuits (Fig. 5) the dependence of current intensity on time (in a quasistationary case) may be calculated from the following equations

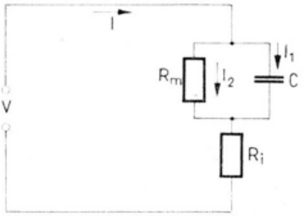

Fig. 5. Diagram for deriving equation (5) in Appendix

$$R_i\, I + R_m\, I_2 = V \tag{5.1}$$

$$-R_m\, I_2 + \frac{1}{C}\int_0^t I_1\, dt = 0 \tag{5.2}$$

$$I_1 + I_2 = I \tag{5.3}$$

With the use of (5.1) and (5.3) equation (5.2) may be transformed so as to contain only one unknown I_1

$$\frac{R_i\, R_m}{R_i + R_m}\, I_1 + \frac{1}{C}\int_0^t I_1\, dt - \frac{R_m\, V}{R_i + R_m} = 0 \tag{5.4}$$

We find the solution of this equation in the form

$$I_1 = A e^{-\alpha t} \tag{5.5}$$

After substituting (5.5) into (5.4) we get

$$A\left(\frac{R_i\, R_m}{R_i + R_m} - \frac{1}{C\alpha}\right) e^{-\alpha t} + \left(-\frac{R_m\, V}{R_i + R_m} + \frac{A}{C\alpha}\right) = 0 \tag{5.6}$$

which should be brought to identity.

Hence

$$\alpha=\frac{R_i+R_m}{CR_i\,R_m}$$

$$A=\frac{V}{R_i}$$

Thus

$$I_1=\frac{V}{R_i}\,e^{-\frac{R_i+R_m}{CR_i\,R_m}\,t} \tag{5.7}$$

The charge present at moment t on the plates of the capacitance is calculated by means of the formula

$$q\,(t)=\int_0^t I_1\,(t)\,dt \tag{5.8}$$

hence

$$q=\frac{VCR_m}{R_i+R_m}\left(1-e^{-\frac{R_i+R_m}{CR_i\,R_m}\,t}\right) \tag{5}$$

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Author's address:
Dr. Tadeusz Zawadzki
Department of Plant Physiology
Maria Curie-Skłodowska University
Akademicka str. 19, 20-033 Lublin,
Poland

Elektryczne własności łodygi Lupinus angustifolius

Model RC, stała czasowa, latencja i ładunek progowy

Streszczenie

W oparciu o zależność siła-czas trwania i potencjały elektrotoniczne scharakteryzowano zmiany potencjału w łodydze *Lupinus*. Stwierdzono, że stymulowana łodyga zachowuje się jak elektryczny obwód RC. Określono stałe czasowe na-

rastania i zaniku potencjałów elektrotonicznych. Zaproponowano prosty model elektryczny RC charakteryzujący bierne elektryczne własności łodygi *Lupinus*. W oparciu o ten model określono wartości oporu i pojemności łodygi *Lupinus* oraz obliczono, że progowa wartość ładunku elektrycznego wynosi około 10^{-6} C.

Oporowo-pojemnościowe własności tkanek łodygi mogą stanowić podstawę do lepszego zrozumienia parametrów opisujących pobudzenie, podobnie jak ma to miejsce w zwierzęcych układach pobudliwych. Można przypuszczać, że obserwowane prawidłowości mają związek z akomodacją i procesami regulującymi potencjał spoczynkowy komórek.