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ELECTRICAL PROPERTIES OF PLANT TISSUES. RESISTANCE OF A MAIZE LEAF

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Abstract. In the framework of the investigations of electrical phenomena in plants, the DC resistance of plant tissues was studied. Objects of study were the leaves of monocot plant *Zea mays indurata.* The DC resistance of leaves is related almost exclusively to the continual system of apoplast. Effective resistance of apoplast measured along the midrib was found to be in inverse proportion to the width of a leaf. Taking into account the macroscopic structural anisotropy of a leaf, measurements of resistance were carried out in different directions with respect to the midrib. The degree of anisotropy of apoplast conductive system was found to be marked feebly. Local incisions of leaf tissue increase the resistance insufficiently due to bypass current routes.

The resistance of a leaf was measured in the course of progressive water deficit. As the leaf is dried up, the DC resistance of its living part decreases, whereas the resistance of the "dead zone" rises sharply. The observed decrease in resistance of leaf tissue in the course of water starvation seems unexpected. It may be caused by the entry of water and salts from vacuoles through membranes into apoplast.

Keywords: apoplast, DC resistance, leaf, maize, water starvation

INTRODUCTION

Green plants show different electrical activity. This fact has been known long ago [1,2]. However, intense studies in this field began only in the last decades of the former century along with the elaboration of contemporary experimental methods [3-5]. Electrical phenomena in plants have complicated character. In plants,

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along with the effects induced by the action of various natural factors or artificial impacts, numerous spontaneous variation of potential may be registered. At present, a vast deal of information concerning electrical effects in plants is accumulated, although neither their physiological role in plant's life nor the biophysical mechanisms, which generate them, can be considered as being studied satisfactorily.

A clear notion of plant tissue passive electrical properties, e.g. their electrical resistance, is needed to apprehend the specificity of plant electrical processes. Plant tissues are very complicated, highly structured, anisotropic systems comprising of both conductive and insulative elements. Because of that the resistance of different plant tissues is not purely ohmic and is frequency dependent. Electrical resistance of plant tissues varies within rather wide limits. It depends on the physiological state of the plant.

The particular objective of the present work is a study of DC resistance of plant tissues. Such experiments have not been conducted earlier. The passage of direct current through the tissue of a leaf occurs almost exclusively via apoplast as a continual system. The paths through symplast and vacuoles are intersected with a great number of membranes and have therefore very high resistance for DC. On the other hand, the presence of capacitive components along with these paths should manifest itself in the alternative current measurements.

For the study, leaves of monocot plant maize with relatively simple macroscopic structure were chosen.

MATERIALS AND METHODS

Maize (*Zea mays indurata*) was grown under illumination of about 100 W/m^2 produced by luminescent lamps LD-20 and LB-20 in a 16/8 light/dark period. Plants were given water every second day. Conditions of water starvation in some experiments were provided by cessation of watering.

Electrical measurements were conducted in a Faraday cage. To avoid damaging the plant tissue we have elaborated a new technique of electrode-leaf connection that was found to be rather convenient and efficient. The Ag/AgCl electrodes prepared from a silver wire (0.5 mm in diameter) were fixed at definite points of the leaf surface with the help of small (1.5-2 mm in diameter) drops of honey, to which dry potassium chloride (1:25 by weight) was added. Electrical resistance of such electrodes was about 3-5 kΩ.

The measuring circuit included a length of a leaf between two electrodes, a resistor of known nominal (R_n) connected in series, and an external voltage source. A potential step of about 20 mV (ΔE) from the latter was applied to the circuit, and the voltage drop (ΔU) across the resistor R_n was amplified and recorded by the storage oscilloscope C9-8 (input impendence of preamplifier > 10^{10} Ω). The resistance of the leaf length under measurement (R_x) was found as:

$$R_x = R_n \times [(\Delta E / \Delta U) - 1].$$

The described measuring system allowed registering rather large arrays of data (up to 2048 readings), which were then transmitted to a computer for filtration and statistical software treatment. Each experimental point on the curves shown in the figures below, was the result of averaging ten measurements made at different *Rn* values. The standard deviation of measured *Rx*-value almost entirely corresponds to the size of symbols (circles) shown in the Figures.

Measurements were started about an hour after electrodes mechanical appliance to a leaf. Such an interval was found to be adequate for all induced processes in plant tissue to be completed. Application of a potential step (about 20 mV) or interruption of circuit caused practically instantaneous response (hundredths of a second). Thus, the plant tissue responded as a passive matter possessing certain conductance, even to a feeble impact.

RESULTS AND DISCUSSION

Fig. 1 shows the results of measurements on differing in their width maize leaves of the same plant. Curves 1-3 represent the resistance of the leaf length as a function of the distance between the measuring electrodes: $R = f(x)$. Both electrodes were placed on the midrib of the leaf, the position of one of them fixed (base electrode), the position of the other - variable. The resistance increases almost linearly with the increase of the distance between electrodes, except for the apical part of the leaf, where its cross-section diminishes. DC resistance is mainly that of apoplast, therefore, the analysis of *R(x)*–curve enables some conclusions about the distribution of efficient cross-section of apoplast along the length of a leaf to be made.

Assuming the Ohm's Law applicable to the object under study, the specific resistance of apoplast could be defined as follows:

$$\rho_{ap} = S_{ap}(x) * \left(\frac{dR}{dx}\right), \quad (1),$$

where $S_{ap}(x)$ is the cross-sectional area of apoplast in section x.

The latter value is difficult to measure. Therefore, it seems reasonable to introduce a certain characteristic of apoplast resistance independent from the peculiarities of macroscopic structure of a leaf and related to one of its easily measurable dimensions, its width, for example. Such a characteristic can be defined as the "efficient specific resistance" of apoplast - ρ_{eff}. Assuming the cross-section of apoplast as a certain function of the leaf width (b), for example: $S_{ap} \approx b^n$, it can be represented this way:

$$\rho_{eff} = k * b(x)^n * \frac{dR}{dx}, \text{(2)},$$

where the coefficient (k) and the exponent (n) depend upon the structure of the paths of electric current in apoplast.

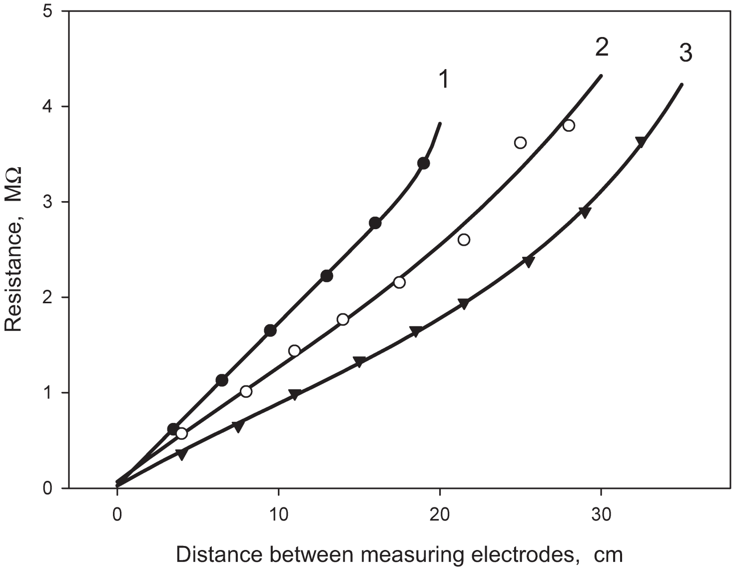


Fig1. Dependence of leaf resistance on the distance between measuring electrodes, the position of one of them fixed (base electrode). Both electrodes were placed on the midrib. The size of symbols (circles) approximately corresponds to the standard deviation of experimental data. Object of measurements: leaves of *Z.mays indurata,* 50 days old. **1** – fifth (second alive) leaf; l= 29 cm, b_{max} = 1.3 cm. **2** –seventh leaf; l =58 cm, b_{max} = 1.8 cm; **3** – ninth leaf; l= =50cm, b_{max} = 2.4 cm. Position of base electrode (zero point on X-line), cm from the stem: **1** – 6, **2** – 22, **3** – 13.5.

Supposing that electric current flows uniformly throughout the cross-section, and its configuration maintains the similitude along the length, the efficient specific resistance should be proportionate to the square of the width (n = 2). If a leaf becomes relatively thinner towards its apex, the dependence should be weaker: $2>n>1$. However, cells adjacent to the longitudinal ribs of a leaf play an essential role in the passage of the current through the apoplast. If the longitudinal ribs are distributed almost alike throughout the width and their number decreases as the leaf narrows, the resistance is in inverse ratio to the width, and therefore: $n \approx 1$. If the number of ribs remains invariable, but they come together when approaching the apex, then $n < 1$. As it is evident from photomicrographs of maize leaf, the distance between the ribs remains approximately constant, and their number diminishes toward the end. Thus, $n \approx 1$ could be expected.

Analysis of $R(x)$-curves enables us to gain some insight into the real structure of the leaf conducting system. Fig. 2 shows an example of such an approach. The base curve, $R = f(x)$, corresponds to curve (3) in Fig. 1. The dotted line is its derivative - dR / dx. Curve $b(x)$ depicts the longitudinal profile of the leaf. Curves $\rho_{eff}(x)$ are calculated according to equation (2) at different values of n. The condition of constancy of $\rho_{eff}(x)$ is met most satisfactorily at $n = 1$, thus the resistance of a leaf is in inverse proportion to its width (except the very apical part).

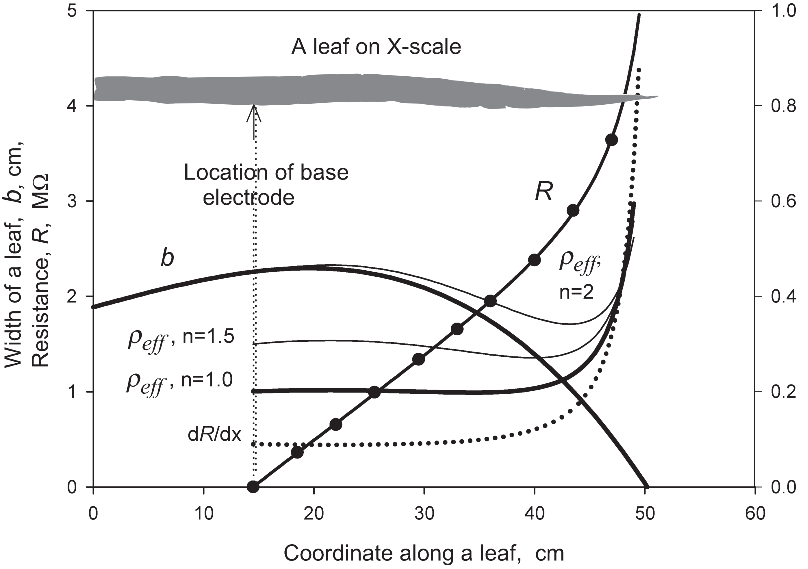
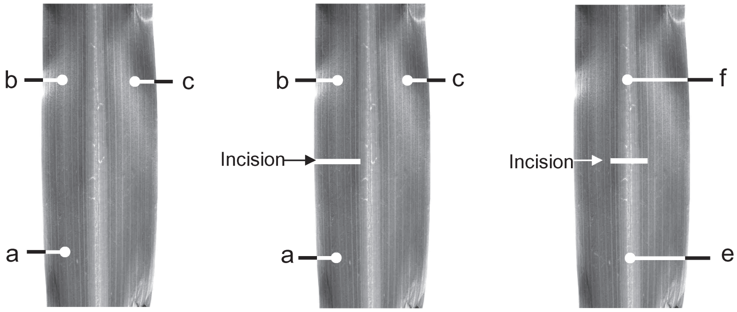


Fig.2. Evaluation of the efficient specific resistance of apoplast (ρ_{eff}). R – measured value of resistance along a leaf (corresponds to curve 3 in Fig.1); dR / dx - differential resistance of a leaf; b – width of a leaf. Functions $\rho_{eff}(x)$ are calculated at n–values 1, 1.5, 2.

In the present study, we estimate not the absolute value of the efficient resistance but the values $\rho_{eff}(x) / k$. That is ample for our purpose, however.

A maize leaf has an elongated structure. It seems significant to estimate to what a degree this macroscopic structural anisotropy manifests itself in electrical properties of apoplast, and whether there is a noticeable difference of resistance along and across the leaf. A series of experiments was carried out for this purpose. The results are shown in Fig. 3. The resistance was measured transversely and diagonally along the side ribs of an intact leaf. Data obtained are summarized in Table I under the corresponding image of the leaf. The value of resistance per unit length measured across the leaf is about twice as great as that measured along the leaf:



I	
a - b	0.83/0.16*
b - c	0.58/0.29*
a - c	0.91/0.17*

II	
a – b before incising	0.83/0.16*
a – b after incising	1.06/0.20*

III	
e – f before incising	0.55/0.11*
e – f after incising	0.71/0.14*

Fig.3. The dependence of resistance on the relative position of measuring electrodes and the influence of incision. *a,b,…f* – points of electrode location on the leaf. Figures in tables – values of resistance between corresponding points (MΩ); those denoted with * - values of resistance per unit distance (MΩ/cm).

0.29 and 0.16 MΩ/cm, respectively. The resistance in diagonal direction (0.17 MΩ/cm) is nearly the same as that along the leaf. An incision of the side ribs resulted in an increase of resistance only by 25 per cent - from 0.16 to 0.20 MΩ/cm (Table II). An incising of the midrib had even smaller effect: 0.11 and 0.14 MΩ/cm, respectively (Table III). Thus, local injuries do not affect substantially the conducting system of apoplast. It may be concluded that apoplast conductive system is characterized with rather low degree of anisotropy. Most conductive is the midrib, whereas the longitudinal side ribs and especially transverse ribs are somewhat less conductive.

The resistance of apoplast depends on the physiological state of the leaf, on its water regime in particular. Leaf electrical resistance was measured under progressive water deficit conditions. Curves 1 to 6 in Fig. 4 show the distribution of resistance along the midrib of the same maize leaf after 4, 6, 8, 10, 11, and 12 days of water starvation, respectively.

As the leaf being dried up, the DC resistance of its living part decreases (the slope of initial part of curves 1-5 diminishes). After several days of starvation, a “dead zone” appears at the apex of the leaf and expands gradually toward the stem. The resistance of the “dead zone” exceeds that of the living part (steeply ascending tails of curves 3-6). The observed decrease in resistance of leaf tissue in the course of water starvation seems unexpected. This effect may be caused by the entry of water and salts from vacuoles through membranes into the apoplast.

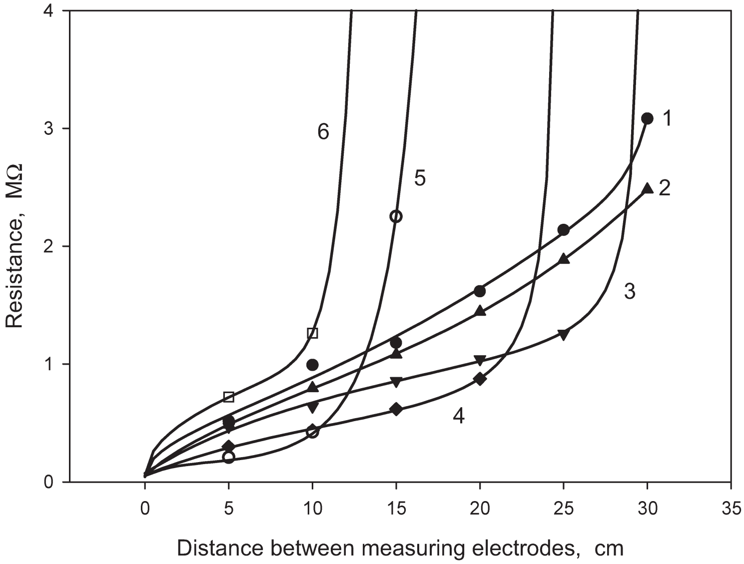


Fig.4. Variation of *R(x)* – function of a leaf in the course of water starvation. Object of measurements: the eleventh (fourth alive) leaf of *Z.mays indurata,* 106 days old; l = 38 cm, b_{max}= 2.6 cm. Position of base electrode (zero point on X-line) – 5 cm from the stem. Both electrodes located on the midrib. Days of water starvation: **1** – 4; **2** – 6; **3** – 8; **4** – 10; **5** –11; **6** – 12.

Comprehension of electrical processes in plants may contribute to the elaboration of new approaches and means of objective diagnostics of physiological state of plants.

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