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BRIEF COMMUNICATION

Characteristics of Current Passage through Plant Tissue

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Abstract. **Plant tissue connected in a d.c. circuit behaves as a capacitor, short-circuited through a resistor. Using a saw-tooth voltage (T = 2 ms, U_{max} = +13 V), structural and physiological conditions in a plant tissue can be analyzed on the basis of changes in the current character.**

Plant tissue connected in a d.c. electric circuit behaves as a capacitor, short-circuited through a second-order conductor with a linear current-voltage dependence (Fig. 1a). Cytoplasmatic membranes (m, chiefly plasmalemma) are considered to be capacitance elements (C); conductive connection can be provided by ionic solutions in the free space (FS, stable structure) and by the symplast (SP) interconnected through plasmodesmata (the variable component). The conductance of plasmodesmata is rather high (SPANSWICK 1972). The conductance through the plasmalemma is also not negligible (passive ion fluxes, accelerated by a potential gradient).

It can be assumed that the electric circuit is closed chiefly through highly mobile ions, such as K^+ and Cl^- in both the connected systems (FS, SP), and that the character of the current depends on their concentration, the relative distribution between the FS and cytoplasma (cyt) and possibly the xylem, whereas the vacuolar pool need not be affected. The various pathways between the electrodes and to the capacitance elements exhibit considerable resistance toward the ion movement, as can be seen in Fig. 1b (R, R_l).

The current source is a saw-tooth voltage generator (linear increase of a ⊕-voltage in time; T = 2 ms, U_{max} = 13 V). The plant is connected in the circuit by inserting Pt-electrodes (with a diameter of 0.3 or 0.5 mm, and at a spacing of 2.5 or 5 mm), arranged either in a pair (linearly), or in a triplet (at right angles). The current characteristic was monitored on an

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oscilloscope as the voltage on a resistor (1 kΩ) connected in series; the value of this resistor is more than one order of magnitude lower than those of the measured resistors and thus is not a source of substantial error. The principal types of current curve correspond to the sum of a current with an ohmic dependence ($i_R = k_1 \cdot t$) and a capacity component [$i_C = k_2 (1 - e^{-t/\tau})$], where t is the time of increase of the voltage on the electrodes, k_1, k_2 and τ are constants whose significance follows from the theoretical equation for a system with one capacitance being charged:

$$i = \frac{U_{max}}{T}\left[C(1 - e^{-\frac{t}{R_i C}}) + \frac{1}{R} t\right] \tag{1}$$

A real curve can be briefly expressed as

$$i \cdot \text{const} = C(1 - e^{-at}) + Gt \tag{2}$$

where $a = (R_i C)^{-1}$ and $G = R^{-1}$; the former value is obtained by calculation from the i value for $t = 0.05T$ and k_1 as $i_R \cdot t^{-1}$. However, experimental curves often do not obey this simple concept and can be explained by assuming a series of capacitors charged in parallel, with various R and C values in the individual branches (Fig. 1c). If the importance of the parallel elements in the circuit increases, then the current dependence flattens and the transfer to the linear part does not correspond to the exponential form of the basic equation.

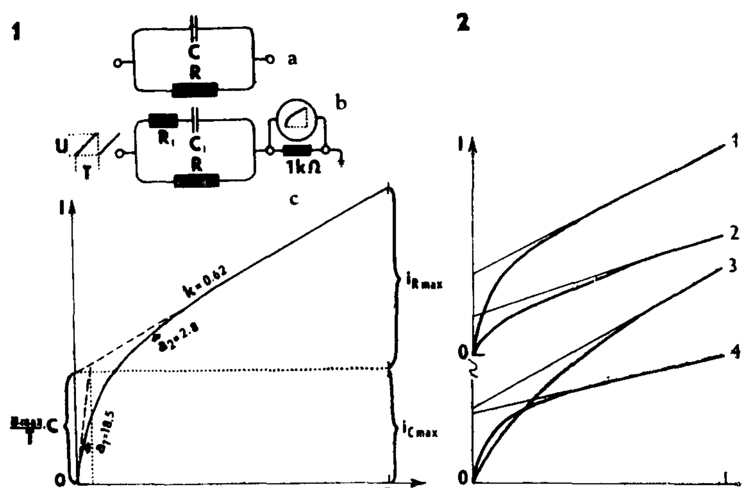

Fig. 1. Scheme of plant electric function and the corresponding conductance characteristic: a — scheme of the electric circuit in a plant (according to SCHREIBER and KREEB, 1977); b — the circuit used in this paper; on the left — input of a saw-tooth voltage, on the right — output to the oscilloscope; c — the basic type of I—U—t curve; for the principal equations see the text. Fig. 2. Current *vs* voltage curves measured on plants: 1 — longitudinal and 2 — diagonal conductance of a *Phalangium comosum* leaf; 3 — the effect of ether (8 min) on the longitudinal conductance in the hypocotylus of *Cucurbita pepo*; 4 — the state before application of ether. x-axis — time, t; y-axis — current, I.

In plant tissues the resistor values depend on structural and physiological factors, such as the orientation and frequency of plasmodesmata, the presence of intercellulars, the spatial orientation and longitudinal dimensions of the cells, *etc.* and the relationship between $[K^+]_{FS}$ and $[K^+]_{cyt}$, *etc.* This effect is marked in measurements of the current characteristics of leaves with respect to the vein orientation (especially with monocotyledonous plants, Fig. 2). Curves 1 and 2 indicate that some readily monitorable electric characteristics differ in dependence on the current direction with respect to the leaf structure (longitudinal $\gtrless$ diagonal); for example, with a *Phalangium* leaf the values of $i_{R_{max}}$, $i_{C_{max}}$, their ratio $i_{C_{max}}/i_{R_{max}}$, and coefficient a are greater in the longitudinal direction. These relationships differ for various plants:

Plant leaf	$i_{R_{max}}$	$i_{C_{max}}$	$i_{C_{max}} \cdot (i_{R_{max}})^{-1}$	a	$a \cdot C$
Zea mays	>	>	>	>	>
Dactylis glomerata	>	>	<	~	>
Phalangium comosum	>	>	>	>	>

the $\gtrless$ sign expresses the orientation at which the value is greater; ~ denotes that there is no pronounced relationship.

The current values passing through the resistance branch relative to the total current, $k = i_{R_{max}} \cdot (i_{max})^{-1}$, are between 0.5 and 0.8. The relative a values determining the slope of the tangent to the initial part of the curve attain values of 15 to 40 ($\tau = 50$ to 150 μs) and the product $a \cdot C$ expresses the relative conductance of the capacitance branch (R_i^{-1}) provided that the simple equation is valid. We assume that an increase in this value can be given both by an increase in $[K^+]_{cyt}$ and by greater effective cross-section of the plasmodesmata. The R values in our measurements varied between 30 and 50 kΩ, but they are important only for evaluation of the measuring system (the leaf thickness, the quality of contact with the electrode, *etc.*, are naturally important).

An example of physiological changes measurable using the conductance parameters described here is the effect of application of ether (Fig. 2, curves 3, 4). Within 8 min, the shape of the curve changes from that denoted as 3 to that denoted as 4, coefficient a changing considerably; as the capacitance is almost unchanged, the time change in a corresponds to a change in the conductance in the branches of the capacitance component. The summary expression for current in this system with various values of R_i and C_i is given by the expression

$$\sum_{n} i_C = I_C = \frac{U_{max}}{T} \sum_{n} C_i \left(1 - e^{-\frac{t}{R_i C_i}}\right) \tag{3}$$

Real calculation of the values in the individual branches and their relationships is impossible, but correction coefficient a_2 (for $t = 0.9\, i_{C_{max}}$) can be calculated when determining principal coefficient a_1, by means of which the i_C value for the middle part of the curve can be corrected empirically (introducing $n = 2$). If the ratio, $\overline{C} \cdot C_i^{-1}$ (where $\overline{C}$ is the average capacitance of the two branches), is not very different from unity, Eq. (3) can be converted into the approximate form,

$$I_C = \frac{U_{max}}{T} \sum_n \overline{C}\left(1 - e^{-\frac{t}{R_i C_i}}\right) \quad (4)$$

and the empirical correction coefficients would characterize the slope of the i_C curve of the parallel sum branch. It is, however, chiefly used as a significant parameter describing the deviation from the current response according to Eq. (1). On application of ether, the a_1 value decreased from 21.5 to 5.6 and the a_2 value from 2.0 to 0.8. When assuming a circuit with two parallel capacitance branches, a similar situation would occur provided that the plasmalemma is not destroyed, but that K^+ flows into the FS and in the short-circuiting branch $(R_{FS})^{-1}$ increases, as well as the permeability of membranes as $(R_m + R_{cyt})^{-1}$, perhaps characterized by coefficient a_2. Only an indirect basis exists for these considerations. Similar changes occur on freezing or heating of tissues. The current dependence parameters change in a manner analogous to curves 3 and 4 (Fig. 2) on freezing a leaf or stalk; it is known (BANGE 1979) that K^+ flows into the FS and the conductance of the tissues increases (MACDONALD *et al.* 1974, *etc.*). In unbalanced mineral nutrition of plants, the *a* value also decreases, among other things, which will be the subject of other studies.

There have been various attempts to use simple electrometric methods for monitoring various characteristics of plant tissues and organs described in the literature. Tissue hydration was measured by SCHREIBER and KREEB (1977) in a high-frequency field. The vitality of woody plants was evaluated by GLERUM (1970) according to the resistance at frequencies of 1 Hz and 1 MHz. NISSILA and FUCHIGAMI (1978) measured the degree of ripeness of *Cornus stolnifera* shoots from the capacitance ratio at frequencies of 1 kHz and 1 MHz after previous freezing, thus separating the capacitance component (non-conductive at lower frequencies) from the ohmic one. Measurement of the capacitance between the soil and the plant base (CHLOUPEK 1972, 1976) permits evaluation of the development of the root system, *etc.*

The present paper documents in several points that, when a standard procedure is maintained and with simple mathematical treatment, further very sensitive information on the state of a plant (tissue) is yielded by the described method, which can serve as a diagnostic test for the biological condition of the plant. With a linear change in the voltage, a number of further characteristics can be found from a single recording (differences in the ionic concentrations in FS and FP, ion-transport efficiency of the plasmalemma, *etc.*), which are manifested in the basic constants of the curve.

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BOOK REVIEW

Seemann, J., Chirkov, Y. I., Lomas, J., Primault, B.: Agrometeorology. — Springer Verlag, Berlin—Heidelberg—New York 1979. 324 pp., cloth DM 98,—; US $ 53.90.

This monograph is neither a textbook nor a handbook as the authors themselves state in the preface: In view of the fact that it is written as a series of separate accounts it has to be looked upon rather as an introduction to the present-day problems of agrometeorology. The book bridges the existing gaps in contemporary knowledge of interactions between the biological and climatic events by accumulating materials concerning interrelated plant and weather observations. About one half of the book is devoted to physical and meteorological principles of agrometeorology. In thirteen chapters the effect of the most important macroclimatic factors (*e.g.* solar radiation, heat, mass and momentum transfer) on plant cover are discussed and the corresponding measuring techniques are specified. The secong half of the book (twenty-four chapters) deals with the applied agrometeorology both in the open field (soil climate, climate of meadows and pastures, grain crops, trees, orchards and forests), and in the greenhouse. Attention is also paid to water requirements of plants (the effects of drought, dry winds, dust storms and hails, irrigation, *etc.*). The authors do not content themselves with simple descriptions of exact observations but they also try to systematize information on plant-climate interactions in order to stimulate the more efficient use of climatic resources and thus increase productivity throughout the world. They also discuss the requirements on further development of measuring methods and the application of agrometeorological statistics and models. They estimate the usefulness of agroclimatology in planning and in crop distribution and weigh possibilities of improving climate for agricultural purposes, inclusive of agrometeorological forecast systems.

The book is well printed and arranged, supplied with numerous figures, tables and schemes and complemented with the subject index. It is only to be regretted that in the literature recent references are not often quoted. The interpretation of the problems was not intended to be exhaustive. The analysis is concentrated prevalently on the plant-macroclimate interactions so that the reader who will look up the topics on micrometeorology of different plant stands will meet with failure. Nevertheless, the book is of high theoretical and practical value for researchers in agronomy, ecology, agrometeorology, plant physiology, forestry, biogeography and related disciplines.

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