ACTA SOCIETATIS
BOTANICORUM POLONIAE
Vol. 57, nr 2: 271-278
1988

Mathematical modelling of light-induced electric reaction of *Cucurbita pepo* L. leaves

JAN STOLAREK, WALDEMAR KARCZ, MARIUSZ PIETRUSZKA

Department of Plant Physiology, University of Silesia, Jagiellońska 28, 40-032 Katowice, Poland

(Received: October 22, 1987. Accepted: December 23, 1987)

Abstract

The bioelectric reactions of 14-16 day old plants of pumpkin (*Cucurbita pepo* L.) and internodal cells of *Nitellopsis obtusa* to the action of visible and ultraviolet light (UV-C) were studied. The possibility of analyzing the bioelectric reaction of pumpkin plants induced by visible light by means of mathematical modelling using a linear differential equation of the second order was considered. The solution of this equation (positive and negative functions) can, in a sufficient way, reflect the participation of H^+ and Cl^- ions in the generation of the photoelectric response in green plant cells.

Key words: bioelectric reaction, visible light, mathematical model

INTRODUCTION

The electric reaction of plants in response to the action of light has been studied over many years by various investigators (Waller 1929, Zurzycki 1968, Pallaghy and Lüttge 1970 and others). It has been found that the illumination of plant cells induces transient changes of electric potential differences across the plasmalemma or, in higher plants, between illuminated and shadowed areas of the leaves (Gradmann 1976, Prins et al. 1980, Stolarek et al. 1984, Trębacz and Zawadzki 1985, Tazawa et al. 1986).

In spite of the abundant literature concerning photoelectric reactions in plants, only a few papers deal with a mathematical description of these phenomena in giant algal cells (Hansen 1978, 1985, Martens et al. 1979, Thiel et al. 1984, Fisahn et al. 1985) and in higher plants (Pasichnyj et al. 1977).

According to the model proposed for internodal cells of *Nitella*, light triggers a photoelectric response by acting on membrane transport via two metabolic pathways, one of them (path A) hyperpolarizes the membrane potential difference across the plasmalemma when light is switched on, while the other (path B) depolarizes it (Hansen 1985).

The aim of the present paper was the analysis of the bioelectric reaction to light of a higher plant (*Cucurbita pepo* L.) by means of mathematical modelling using a second order linear differential equation.

MATERIAL AND METHOD

The experiments were carried out with 14-16 day old pumpkin plants (*Cucurbita pepo* L.) grown in Hoagland's medium under incandescent and luminescent light. The duration of the light period was 16 hours daily. The measurements of electrical potential differences were done with the use of a conventional microelectrode technique (Stolarek and Karcz 1987). In some measurements, contact-surface calomel electrodes were also employed (Stolarek and Pazurkiewicz-Kocot 1980). The microelectrodes, consisting of Pyrex micropipettes filled with 3M KCl, were joined to calomel electrodes and inserted into the midpoint of the main rib of the leaf. The surface electrodes were also in contact with the main rib of the leaf. The reference electrode was placed in the pot containing the root system and filled with Hoagland's

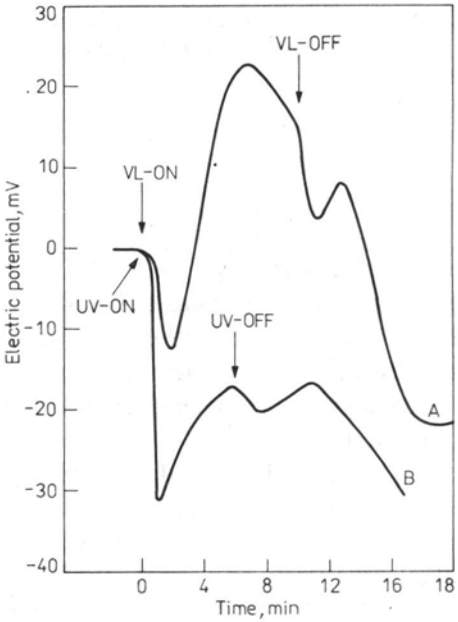

Fig. 1. Electric reactions of the leaf of *Cucurbita pepo* L. induced by visible light (VL, curve A) and UV-C (UV, curve B) measured by the use of a conventional method using extracellular contacts

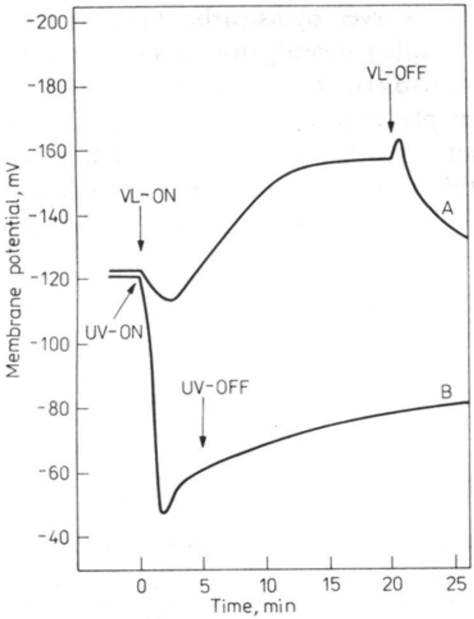

Fig. 2. Electric reactions induced by VL (curve A) and UV-C radiation (curve B) in giant algae (*Nitellopsis obtusa*) measured with the use of intracellular microelectrodes

solution. Electrical potential differences were recorded with a high-speed multichannel chart recorder (type: Rikadenki KB-66, Japan).

The plants were maintained in the dark for 3h prior to the electrophysiological measurements. The bioelectric reactions were induced by visible and UV-C light. The source of UV-C light was a Philips TUV-30W lamp having peak emission at 253.7 nm. The irradiance at leaf-level measured with a Kipp and Zonen compensating thermopile equalld to 4.5 Wm^{-2} and 70 Wm^{-2} of UV-C and visible light, respectively. The measurements were done at room temperature (23-25°C). The duration of light illumination or UV-C irradiation was 600 and 300 sec, respectively (as shown in the Figures). The number of the measurements was 20 and 25 in the case of *Cucurbita pepo* L. and *Nitellopsis obtusa,* respectively. Each experiment was carried out with a separate plant or cells. Typical examples of photoelectric reactions of plants are shown in Fig. 1 and 2.

RESULTS

The electrical reaction of the leaves of pumpkin plants to the action of visible light observed in our experiments exhibited a two phase transient character as exemplified by Fig. 1A (independent of the type of the electrode employed in the measurement). Such behaviour of the photoelectric response of green plants has been observed by us earlier (Stolarek et al. 1984, Karcz et al. 1986) as well as by other investigators (Brinckmann and Lüttge 1974, Adygezalov and Grodzinsky 1976). In view of the fact that the electrical responses of different plants possess common features, it seemed possible to attempt to work out a mathematical model of this phenomenon.

Let us consider the linear differential equation with constant coefficients for the harmonic oscillator with external force $f(t)$ and dumping:

$$ay'' + by' + cy = f(t), \tag{1}$$

where a, b, c are real, $a \neq 0$ and $f(t) \subset \{C^{\circ}\}$. When $f(t)$ equals zero, equation (1) becomes a homogenous one. Then the characteristic equation is given by a quadratic one:

$$ar^2 + br + c = 0 \tag{2}$$

and has three possible solutions which depend on the sign of $\Delta = b^2 - 4ac$. In the method described here we have chosen the most simple case when $\Delta = 0$. Taking into account the work by Pasichnyj et al. (1977) this equation carries the information concerning the involvement of cations and anions in the particular phases of the bioelectrical reaction of green plants to the action of visible light.

In the method based on mean-quadratic approximation lets consider the function:

$$F(T, x_1, x_2, \ldots, x_N) = \int_0^T [W_N(t) - k(t)]^2 \, dt, \tag{3}$$

where T is the time of exposure of the leaf to the light. In order to minimize the function described by the above formula, the condition $\partial F = 0$ has to be fulfilled. In other words, the Jacobian over the given parameters $\{x_i\}$ of equation (1) has to become 0:

$$\partial F / \partial x_i = 0. \tag{4}$$

This gives us a set of nonlinear algebraic equations for parameters $\{x_i\}$. This set of equations can be solved with the help of numerical methods. For the sake of brevity we will not present their explicit form here. The $W_N(t)$ expresses a polynomial of n-th power i.e.:

$$\mathrm{W}_N(t) = \sum^{N} a_i t^i, \tag{5}$$

where coefficients $\{a_i\}$ are known on the base of the Newton-Lagrange interpolation for experimental points (potential changes in the course of time) (Fig. 3). In the special case of $N = 5$ the correlation function between experimental and theoretical data is nearly equal to one. The other function stands for the sum:

$$k(t) = i(t) + j(t), \tag{6}$$

where functions

$$\begin{aligned} i(t) &= (x_1 + tx_2)exp(-tx_3) \\ j(t) &= -(x_4 + tx_5)exp(-tx_6) \end{aligned} \tag{7}$$

are the solution of the homogenus equation (1) (Fig. 4). The parameters $\{x_i\}$ are positively defined.

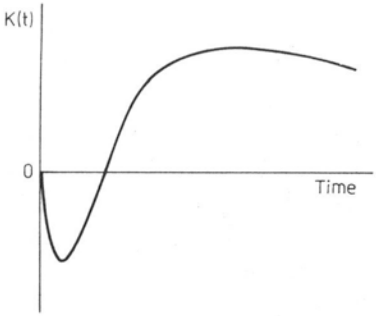

Fig. 3. Interpolation curve (Newton-Lagrange approximation) based on experimental data

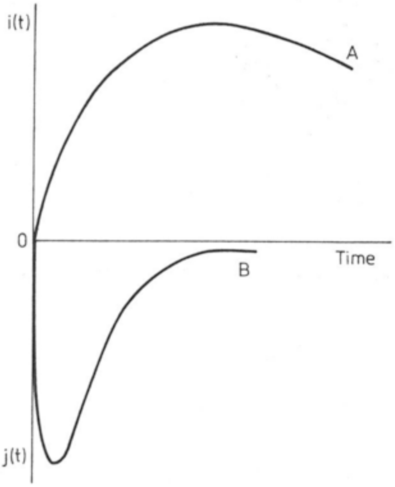

Fig. 4. Ingredient functions (positive, A, negative, B) gained with the help of a minimization procedure of the F function

DISCUSSION

Having accepted some of the elements of the approach made by Pasichnyj et. al. (1977), we have introduced the second order differential equation, which describes in a sufficient way the behaviour of light-induced electrical potential of the leaves. The numerical treatment of the shape of electric impulses induced by the light can be described with the use of the 5-th order polynomial (5). We have shown that this polynomial can be subdivided into two component functions, namely positive and negative ones (7). It can be assumed that in this case the positive function mainly expresses the activity of the proton extruding pump, which according to the generally accepted view is involved in the changes of light-driven electrical phenomena in giant algal cells (Hope and Walker 1975). Spanswick (1972) has shown that light-induced hyperpolarization of membrane potential in *Nitella translucens*, also observed by us in *Nitellopsis obtusa* (Fig. 2, curve A), can be accounted for by rapid stimulation of the proton electrogenic pump, extruding H^+ out of the cell.

In the case of light-induced changes of the electric potential in higher plants (*Cucurbita pepo* L.) investigated by us (Fig. 1, curve A), it can be assumed that proton pump, driven by light is mainly responsible for the rising phase of the photoelectric response. To a certain extent this positive function might also be connected with the photosynthesis-dependent Cl^- influx which can, however, be neglected due to the fact that this influx is substantially smaller in comparison with the H^+ efflux in the light. On the other hand, the negative function can reflect the participation of the Cl^- efflux responsible for the depolarization phase (in the case of algal cells, Fig. 2., curve A) of the light-induced reaction. The involvement of this negative function in photoelectric response is probably more pronounced in higher plants where it can be responsible for the first negative light-induced transient change of the electric potential, which is substantially higher in *Cucurbita pepo* L. in comparison with *Nitella*. In contrast to visible light, UV-C induces an electric response of a different shape (Fig. 1.B and 2.B). It is known that UV inhibits the proton pump and significantly stimulates Cl^- efflux (Doughty and Hope 1973, 1976a-c; Stolarek and Karcz 1987). The difference between the response of the leaves to UV-exposure in comparison with the VL-induced electrical impulse can result from the greater participation of the negative function in the former case.

APPENDIX

While solving equation (3) several integrals of the type $\int t^n exp(at)dt$ are encountered. These are solved with the help of the recursive formula:

$$\int t^n exp(at)dt = (1/a)t^n exp(at) - (n/a)\int t^{n-1} exp(at)dt.$$

REFERENCES

Adygezalov V. F., Grodzinsky D. M., 1976. Studies in metabolic nature of the leaf photoinduced biopotentials. Fiziol. Biokhim. Kult. Rast. 8: 601-606.

Brinckmann E., Lüttge U., 1974. Lichtabhängige Membranpotentialschwankungen und deren interzellulare Weiterleitung bei panaschierten Fotosynthese-Mutanten von *Oenothera*. Planta 119: 47-57.

Doughty C. J., Hope A. B., 1973. Effects of ultraviolet radiation on the membranes of *Chara corallina*. J. Membr. Biol. 13: 185-198.

Doughty C. J., Hope A. B., 1976a. Effects of ultraviolet radiation on the membranes of *Chara corallina*. I. The hyperpolarized state. Aust. J. Plant Physiol. 3: 677-685.

Doughty C. J., Hope, A. B., 1976b. Effects of ultraviolet radiation on the membranes of *Chara corallina*. II. The action potential. Aust. J. Plant Physiol. 3: 687-692.

Doughty C. J., Hope A. B., 1976c. Effects of ultraviolet radiation on the membranes of *Chara corallina*. III. Action spectra. Aust. J. Plant Physiol. 3: 693-699.

Fisahn J., Wittmaack W., Hammer M., Hansen U. P., 1985. Quasi und nicht-lineare Ansätze: Die Intensitatsabhängigkeit der Zeitkonstanten in der Lichtwirkung auf den Transport am Plasmalemma von *Nitella*. Ber. Deutsch. Bot. Ges. Bd. 98: 131-141.

Gradmann D., 1976. "Metabolic" action potentials in *Acetabularia*. J. Membr. Biol. 29: 23-45.

Hansen U.-P., 1978. Do light-induced changes in the membrane potential of *Nitella* reflect the feed-back regulation of a cytoplasmic parameter? J. Membr. Biol. 41: 197-224.

Hansen U.-P., 1985. Messung und Interpretation der Kinetik der Lichtwirkung auf den elektrophoretishen Transport über die Plasmamembran der Alge *Nitella*. Ber. Deutsch. Bot. Ges. Biol. 98. 105-118.

Hope A. B., Walker N. A., 1975. The physiology of giant algal cells. Cambridge University Press, London.

Karcz W., Stolarek J., Michalczuk B., 1986. Electric responses of higher plants to the action of UV-C and visible light. 5th Congress of the Federation of European Societies of Plant Physiology. Hamburg, Session 8, Abstract 12.

Martens J., Hansen U.-P., Wrancke J., 1979. Further evidence for the parallel pathway model of the metabolic control of the electrogenic pump in *Nitella* as obtained from the high frequency slope of the action of light. J. Membr. Biol. 48: 115-139.

Pallaghy C. K., Lüttge U., 1970. Light-induced H^+-ion fluxes and bioelectric phenomena in mesophyll cells of *Atriplex spongiosa*. Z. Pflanzenphysiol. 62: 417-425.

Pasichnyj A. P., Ponomareva I. D., Tsepkov G. V., 1977. Analysis of leaf bioelectric reaction to change in light conditions by the method of mathematic modelling. Physiol. Biochem. Cultiv. Plants 9: 322-327.

Prins H. B. A., Harper J. R., Higinbotham N., 1980. Membrane potentials of *Vallisneria* leaf cells and their relation to photosynthesis. Plant Physiol. 65: 1-5.

Spanswick R. M., 1972. Evidence for electrogenic ion pump in *Nitella translucens*. I. The effect of pH, K^+, Na^+, light, and temperature on the membrane potential and resistance. Biochim. Biophys. Acta 288: 73-89.

Stolarek J., Jabłońska B., Karcz W., 1984. Comparative investigations of action potentials induced by electric, thermal and light stimuli in *Cucurbita pepo* L. Folia Soc. Sci. Lublinensis, vol. 26, Biol. 2: 135-138.

Stolarek J., Karcz W., 1987. Effects of UV-C radiation on membrane potential and electric conductance in internodal cells of *Nitellopsis obtusa*. Physiol. Plant. 70: 473-478.

Stolarek J., Pazurkiewicz-Kocot K., 1980. Light induced action potentials in *Phaseolus vulgaris* L. Acta Biol., Katowice 9: 9-17.

Tazawa M., Shimmen T., Mimura T., 1986. Action spectrum of light-induced membrane hyperpolarization in *Egeria densa*. Plant Cell Physiol. 27: 163-168.

Thiel M., Keunecke P., Hansen U.-P., 1984. The effects of light on the proton pump and on a leak in *Nitella.* In: Membrane transport in plants. Akademie, Prague. pp. 60-61.

Trębacz K., Zawadzki T., 1985. Light-triggered action potentials in the liverwort *Concephalum conicum.* Physiol. Plant. 64: 482-486.

Waller J. C., 1929. Plant electricity. II. Towards an interpretation of the photo-electric currents of leaves. New Phytologist, 28: 291-302.

Zurzycki J., 1968. Changes of the transmembrane potential of the leaf cell of *Funaria hygrometrica* under influence of light. Acta Soc. Bot. Pol. 37: 519-531.

Matematyczne modelowanie reakcji elektrycznej liści Cucurbita pepo L. indukowanej światłem

Streszczenie

Badano elektrofizjologiczną reakcję 14-16 dniowych roślin dyni (*Cucurbita pepo* L.) i pojedynczych komórek glonu *Nitellopsis obtusa*, indukowaną przez światło widzialne i promieniowanie ultrafioletowe (UV-C). Na podstawie uzyskanych wyników, rozważono możliwość matematycznej analizy fotoelektrycznej reakcji dyni, wykorzystując jednorodne równanie różniczkowe liniowe drugiego rzędu. Rozwiązanie tego równania (funkcje: dodatnia i ujemna) może, w przybliżeniu, odzwierciedlać udział jonów H^+ i Cl^- w powstawaniu fotoelektrycznej odpowiedzi komórek roślin zielonych.