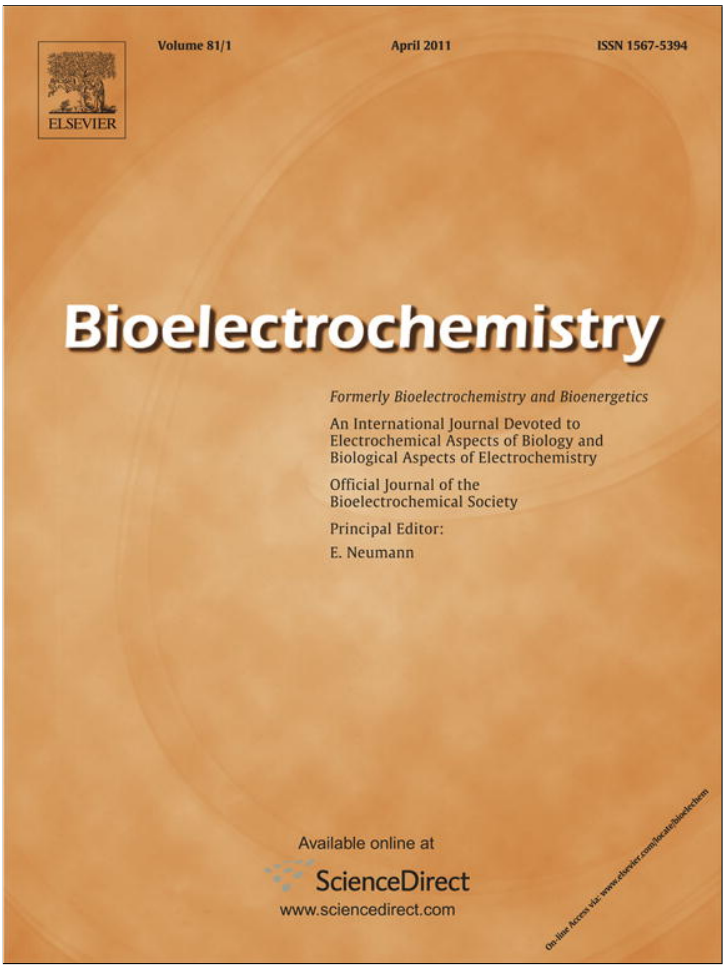

Bioelectrochemistry 81 (2011) 39–45

Contents lists available at ScienceDirect

Bioelectrochemistry

journal homepage: www.elsevier.com/locate/bioelechem

Circadian variations in biologically closed electrochemical circuits in *Aloe vera* and *Mimosa pudica*

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ARTICLE INFO

Article history:
Received 17 November 2010
Received in revised form 16 January 2011
Accepted 23 January 2011
Available online 4 February 2011

Keywords:
Mimosa pudica
Aloe vera
Circadian clock
Electrostimulation
Charge stimulation method

ABSTRACT

The circadian clock regulates a wide range of electrophysiological and developmental processes in plants. This paper presents, for the first time, the direct influence of a circadian clock on biologically closed electrochemical circuits *in vivo*. Here we show circadian variation of the plant responses to electrical stimulation. The biologically closed electrochemical circuits in the leaves of *Aloe vera* and *Mimosa pudica*, which regulate their physiology, were analyzed using the charge stimulation method. The electrostimulation was provided with different timing and different voltages. Resistance between Ag/AgCl electrodes in the leaf of *Aloe vera* was higher during the day than at night. Discharge of the capacitor in *Aloe vera* at night was faster than during the day. Discharge of the capacitor in a pulvinus of *Mimosa pudica* was faster during the day. The biologically closed electrical circuits with voltage gated ion channels in *Mimosa pudica* are also activated the next day, even in the darkness. These results show that the circadian clock can be maintained endogenously and has electrochemical oscillators, which can activate ion channels in biologically closed electrochemical circuits. We present the equivalent electrical circuits in both plants and their circadian variation to explain the experimental data.

1. Introduction

The circadian clock is an endogenous oscillator with a period of approximately 24 h; its rhythm is linked to the light–dark cycle. The circadian clock in plants is sensitive to light, which resets the phase of the rhythm [1–5]. *Mimosa pudica* is a model for the study of plant nyctinastic movements and circadian rhythms. The circadian clock was discovered in 1729 by De Mairan in his first attempt to resolve experimentally the origin of rhythm in the leaf movements of *Mimosa pudica* [6]. This rhythm continued even when *Mimosa pudica* was maintained under continuous darkness.

Mimosa pudica is a nyctinastic plant that closes its leaves in the evening; the pinnules fold together and the whole leaf droops downward temporarily until sunrise. The leaves open in the morning due to a circadian rhythm, which is regulated by a biological clock with a cycle of about 24 h.

During photonastic movement in *Mimosa pudica*, leaves recover their daytime position. During a scotonastic period, the primary pulvini straighten up and pairs of pinnules fold together about the tertiary pulvini. The closing of pinnae depends upon the presence of phytochrome in the far-red absorbing form [7].

Isolated pulvinar protoplasts are responsive to light signals *in vitro* [2,8,9]. In the dark period, the closed inward-directed K^+ channels of extensor cells are opened within 3 min by blue light. Conversely, the inward-directed K^+ channels of flexor cells, which are open in the darkness, are closed by blue light. In the light period, however, the situation is more complex. Premature darkness alone is sufficient to close the open channels of extensor protoplasts, but both darkness and a preceding pulse of red light are required to open the closed channels in the flexor protoplasts [8,9].

Aloe vera (L.) is a member of the Asphodelaceae (Liliaceae) family with crassulacean acid metabolism (CAM). In *Aloe vera*, stomata are open at night and closed during the day [10]. CO_2 acquired by *Aloe vera* at night is temporarily stored as malic and other organic acids, and is decarboxylated the following day to provide CO_2 for fixation in the Benson–Calvin cycle behind closed stomata. *Aloe vera* is a model for the study of plant electrophysiology with crassulacean acid metabolism.

Electrical phenomena in plants have attracted researchers since the eighteenth century [11–17]. The cells of many biological organs

Abbreviations: *C*, capacitance; CAM, crassulacean acid metabolism; DPDT, double pole double throw switch; *E*, DC power supply voltage; PXI, PCI eXtensions for Instrumentation; *R*, resistance; τ, the circuit time constant; *t*, time; *Q*, charge; *U*, voltage; U_0, the initial voltage of a capacitor..

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doi:10.1016/j.bioelechem.2011.01.004

generate electric potentials that result in the flow of electrical currents [15,17]. Electrical impulses may also arise as a result of stimulation. Once initiated, these impulses can propagate to adjacent excitable cells. The change in transmembrane potential creates a wave of depolarization which affects the adjoining, resting membrane [15]. Electrical signals can propagate along the plasma membrane on short distances in plasmodesmata [18] and on long distances in conductive bundles [14,19]. Light-sensitive movements of the leaflets of *Mimosa pudica* depend on ion fluxes across the plasma membrane of extensor and flexor cells in the pulvinus, which create changes in turgor [1,5].

The Charge Stimulation Method (CSM) [20–25] was used to evaluate the electrical equivalent schemes of biological tissue in plants and to estimate the amount of electrical energy necessary to induce a plant response. This DC method permits direct *in vivo* evaluation of the simplest electrical circuits in a cluster of cells or in a single cell. Equivalent electrical schemes of biologically closed electrical circuits were then evaluated inside the pulvinus of *Mimosa pudica* and the leaf of *Aloe vera* during the day, night and darkness period during next day.

2. Materials and Methods

2.1. Electrodes

Ag/AgCl electrodes were prepared in the dark from Teflon coated silver wires (A-M Systems, Inc., Sequim, WA, USA) by electrolysis in 0.05 M KCl aqueous solution [25]. The resistance between two Ag/AgCl electrodes that are 2 cm apart in 0.1 M KCl solution was found to be 10 kΩ. The response time of Ag/AgCl electrodes was less than 0.1 μs.

2.2. Plant Electrostimulation

All measurements were conducted in the laboratory at 21 °C inside a Faraday cage mounted on a vibration-stabilized table. Plants were allowed to rest after electrode insertion. The electrode with the positive and negative potential are always considered as the measuring and the reference electrode, respectively.

We used PXI (PCI eXtensions for Instrumentation), a rugged PC-based platform, as a high-performance measurement and automation system. A NI-PXI-4071 digital multimeter (National Instruments, Austin, TX, USA), connected to 0.2 mm thick nonpolarizable reversible Ag/AgCl electrodes, was used to record the digital data. A NI PXI-4110 DC Power Supply (National Instruments) was also used to provide a voltage source for capacitor charging. A 47 μF and a 1 μF charged capacitors were used in all experiments for electrostimulation of *Aloe vera* and *Mimosa pudica*, respectively.

We designed and implemented the plant stimulator to allow multiple stimulations with precise timing, voltage, and charge during stimulations. The plant stimulator is a battery powered portable device controlled by a low-power microcontroller MSP430F1611 (Texas Instruments, Texas, USA). A specialized PC program allows flexible configuration of the controller and communicates with the controller through optically isolated USB interface [25]. During each stimulation cycle, the controller charges a capacitor with a predefined voltage using an integrated digital to analog (DA) converter of the microcontroller. Each pulse can be controlled with microsecond resolution. A dual integrated SPDT analog switch is controlled by the microcontroller and connects the capacitor to the DA converter during charging and to the plant during stimulation.

2.3. Plants

Aloe vera L. was grown in clay pots. Fifty plants were exposed to a 12:12 h light/dark photoperiod at 21 °C. Volume of soil was 2.0 L. *Aloe vera* plants had 25–35 cm leaves.

The seeds of *Mimosa pudica* L. were soaked in warm water (30 °C) for 48 h. They were then grown in well drained peat moss at 21 °C with a 12:12 h light:dark photoperiod (*Environmental Corporation, USA*). After growing for two weeks, the seedlings were transplanted into pots and placed in a plant growing chamber.

The average humidity was 40%. Irradiance was 700–800 μmol photons m^{-2} s^{-1}. All experiments were performed on healthy adult specimens.

3. Results

The main goal of our experiments was to investigate circadian variation of the plant responses to electrical stimulation. We investigated the response of *Aloe vera* and *Mimosa pudica* during the day, then at night, and the following day in darkness.

3.1. Electrostimulation of a Leaf of Aloe vera by a Charged Capacitor

If a capacitor of capacitance C with initial voltage U_0 is discharged during time t through a resistor R (Fig. 1a), the voltage at time t is

$$U(t) = U_0 \cdot e^{-t/\tau} \quad (1)$$

where

$$\tau = RC \quad (2)$$

denotes the time constant. Eq. (1) in logarithmic form reads:

$$lnU(t) = lnU_0 - t/\tau \quad (3)$$

The time constant τ can be determined from the slope of this linear function.

Time dependence of electrical discharge at night in the *Aloe vera* leaf between two Ag/AgCl electrodes connected to a charged capacitor located along the leaf, parallel to the conductive bundles, is shown in Figs. 2a and 3a. The difference between the two experiments is the polarity of the electrodes: the positive pole is closer to the base of a leaf in Fig. 2 and the positive pole is closer to the apex in Fig. 3. In both cases there is a strong deviation in logarithmic coordinates from the linear predictions in Eq. (3) (Figs. 2b and 3b) meaning that the conductance between two electrodes cannot be presented by a single constant resistance. This deviation can be described by the more complex equivalent electrical circuits shown in Fig. 1b and c. If the capacitor discharge has a two-exponential character and does not depend on the polarity of electrodes in the plant tissue, the deviation from linear dependence can be successfully modeled by the circuit in Fig. 1b, as was shown theoretically earlier with the extraction of values of capacitance and resistance between electrodes in plants [23].

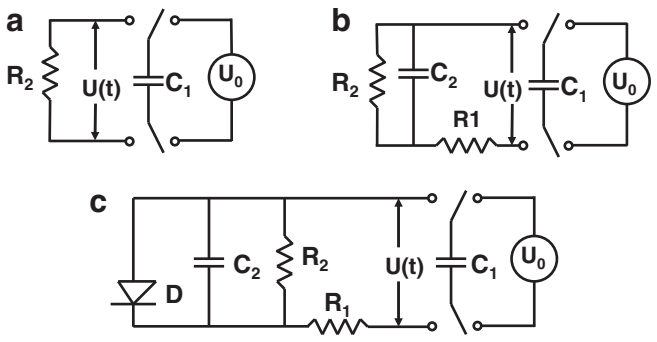

Fig. 1. Electrical equivalent schemes of a capacitor discharge in plant tissue. Abbreviations: C_1 — charged capacitor from voltage source U_0; C_2 — capacitance of plant tissue; R — resistance, D — a diode as a model of voltage gated ion channels.

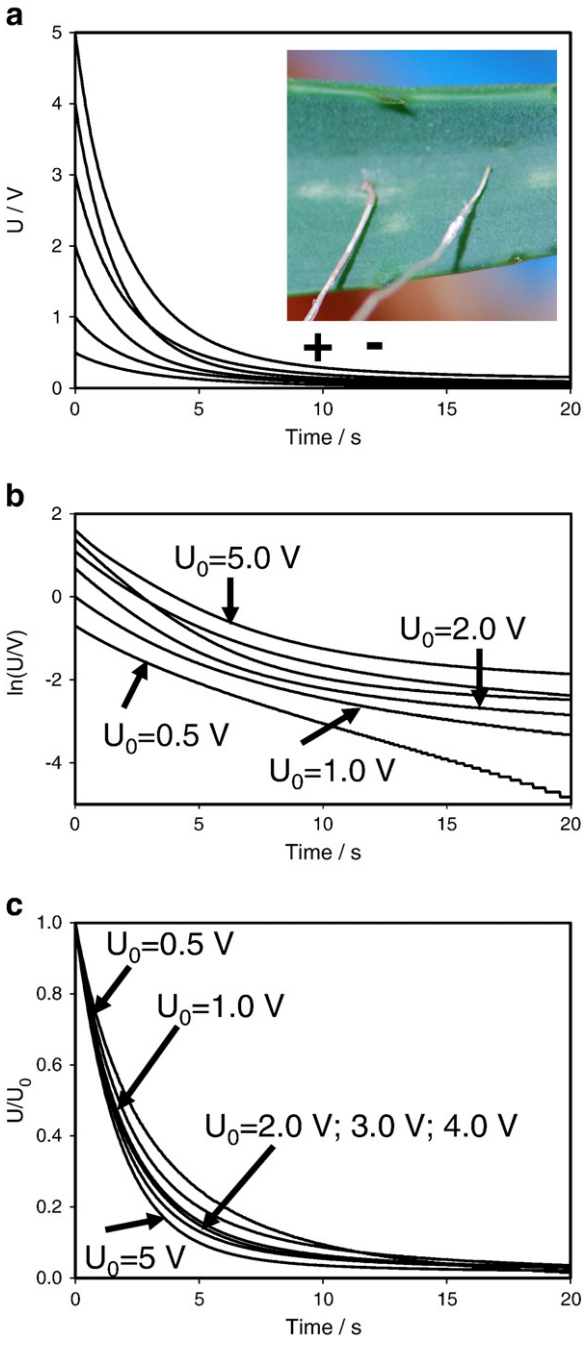

Fig. 2. (a): Time dependencies of electrical discharge in the *Aloe vera* leaf between two Ag/AgCl electrodes connected to a charged capacitor during a night. (b): Time dependencies of electrical discharge in the *Aloe vera* leaf between two Ag/AgCl electrodes connected to a charged capacitor in logarithmic coordinates. (c): Normalized presentation of time dependencies of electrical discharge in the *Aloe vera* leaf between two Ag/AgCl electrodes connected to a charged capacitor. *U* is the capacitor voltage and U_0 is the initial voltage in volts. Polarity and location of electrodes along leaf are shown. Distance between electrodes was 1.2 cm.

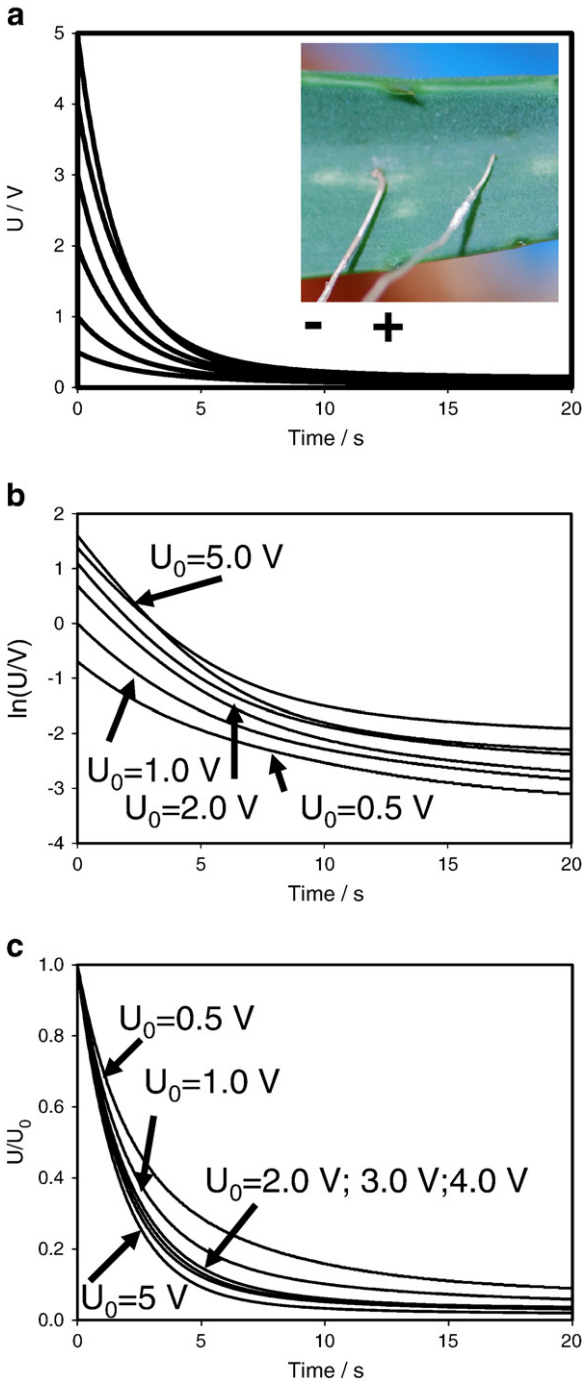

Fig. 3. (a): Time dependencies of electrical discharge in the *Aloe vera* leaf between two Ag/AgCl electrodes connected to the charged capacitor at night. (b): Time dependencies of electrical discharge in the *Aloe vera* leaf between two Ag/AgCl electrodes connected to the charged capacitor in logarithmic coordinates. (c): Normalized presentation of time dependencies of electrical discharge in the *Aloe vera* leaf between two Ag/AgCl electrodes connected to a charged capacitor. *U* is the capacitor voltage and U_0 is the initial voltage in volts. Polarity and location of electrodes along leaf are shown. The distance between electrodes was 1.2 cm.

Time dependence of a capacitor discharge in the *Aloe vera* leaf between two Ag/AgCl electrodes during the day is shown in Fig. 4a. Kinetics of a capacitor discharge in the *Aloe vera* leaf during the day (Fig. 4a) is slower than at night (Fig. 3a). Fig. 4b shows the kinetics of a capacitor discharge in the *Aloe vera* leaf between two Ag/AgCl electrodes during the day time, but in the dark.

Though the data presented in Figs. 2 and 3 are qualitatively similar, there are important quantitative differences in the kinetics of a capacitor discharge for different amplitudes of stimulation. This can be clearly seen in Fig. 5 where data in Fig. 3a are subtracted from Fig. 2a.

Consequently, the kinetics of a capacitor discharge depends on the polarity of electrodes indicating the electrical rectification in the *Aloe vera* leaf. This dependence can be explained by a change in resistivity with applied potential due to opening of voltage gated ion channels, which can be modeled as diodes in Fig. 1c. Opening of voltage gated channels induce the effect of electrical rectification

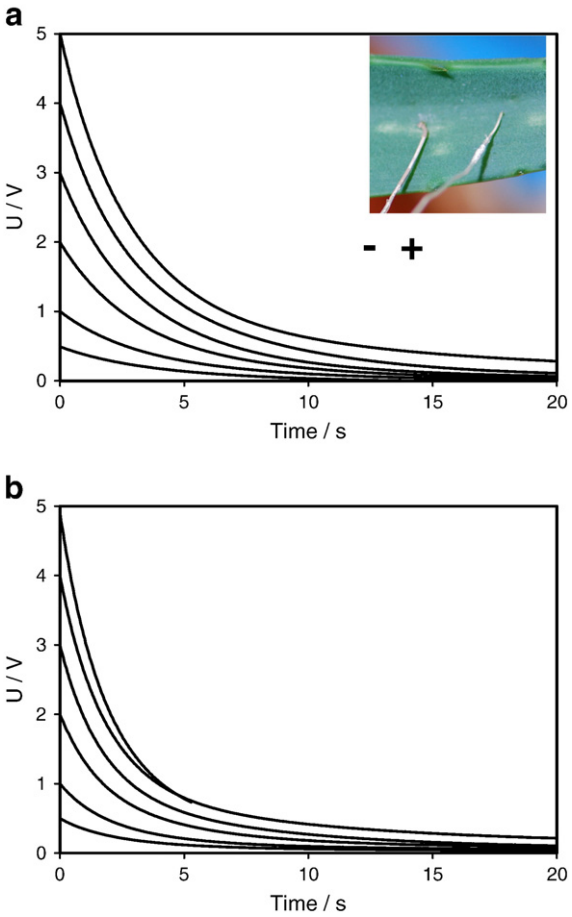

Fig. 4. Time dependencies of electrical discharge in the *Aloe vera* leaf between two Ag/AgCl electrodes connected to the charged capacitor at day time light (a) and darkness during next day (b). *U* is the capacitor voltage and U_0 is the initial voltage in volts. Polarity and location of electrodes along leaf are shown. Distance between electrodes was 1.2 cm.

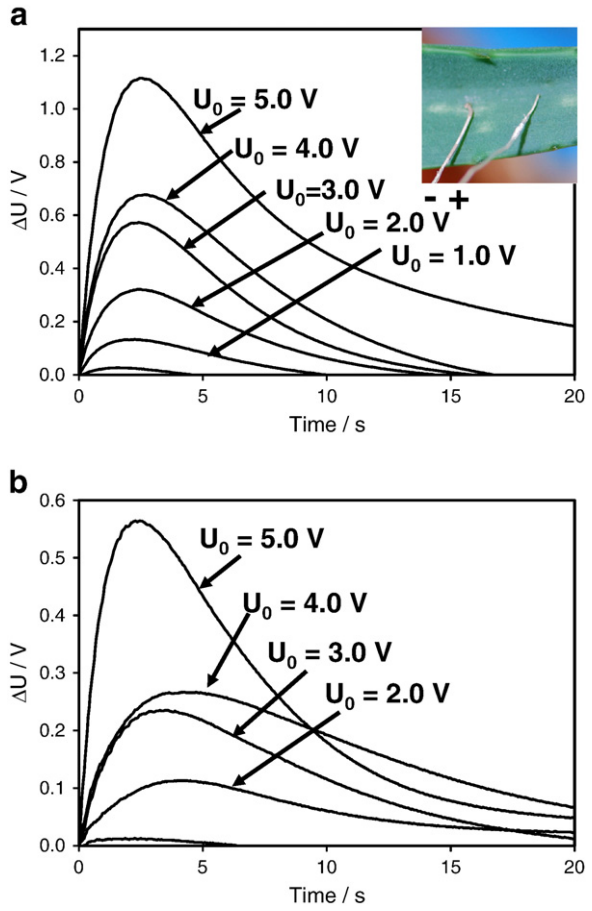

Fig. 6. (a): Difference in time dependencies of electrical discharge in the *Aloe vera* leaf at night and at day time (response during the night (Fig. 3a) subtracted from the response during the day (Fig. 4a)). (b): Difference in time dependencies of electrical discharge in the *Aloe vera* leaf at night and darkness during next day (response during the darkness (Fig. 4b) subtracted from the response during the darkness).

shown in Fig. 5. Similar rectification effects were found in *Aloe vera* [25] (see Fig. 5), the Venus flytrap [17,22] and *Mimosa pudica* [26,27] during the day. We used a silicon rectifier Schotky diode NTE583 as a model of a voltage gated channel and reproduced experimental dependencies of a capacitor discharge in plant tissue [22].

The difference in kinetics of discharge between night and day in the *Aloe vera* leaf, when the response during the night is subtracted from response during the day, is shown in Fig. 6a. Discharge of the capacitor at night was faster than during the day. This means that leaf resistance decreases at night. The difference in discharge kinetics between day light and the next day in the darkness is shown in Fig. 6b. The difference in kinetic discharge during the day and during the following day in the darkness is about two times less than the difference in kinetics of discharge between the day and night. The biological clock in *Aloe vera* recognizes the day time, even in darkness, but in the absence of light voltage gated ion channels have some electrical responses about two times less than at night.

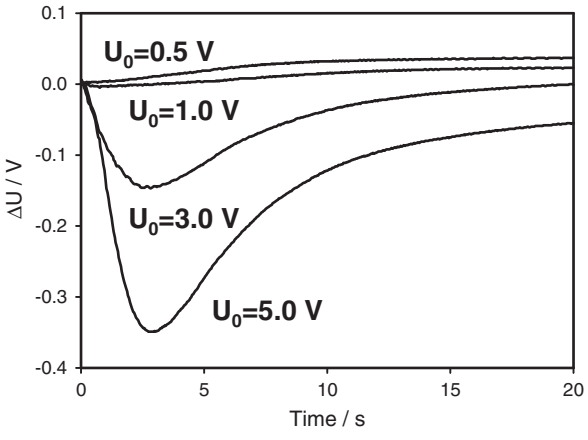

Fig. 5. Time dependencies of difference in kinetics of the capacitor discharge in the *Aloe vera* leaf on polarity of electrodes (Figs. 2a–3a) during a night.

3.2. Electrostimulation of a Pulvinus of Mimosa pudica by a Charged Capacitor

Fig. 7a shows the kinetics of a capacitor discharge in a pulvinus of *Mimosa pudica* during the day. We selected 1 μF capacitor instead of 47 μF capacitor to avoid closing of pinnules and dropping of the petiole, because we found earlier that high electrical charge $Q = 1.5\ \text{V} \times 47\ \mu\text{F} = 70.5\ \mu\text{C}$ can stimulate mechanical movements of a petiole, pinnules and morphing of a pulvinus in *Mimosa pudica* [16,24,26]. Fig. 7b shows the kinetics of a capacitor discharge in logarithmic coordinates. There is a strong deviation from linearity predicted by Eq. (3) for a simple resistance. The non-linear effect in Fig. 7b can be caused by low resistance of the gated ion channels opened by the stimulation voltage during the day.

Fig. 8 shows the kinetics of a capacitor discharge in a pulvinus of *Mimosa pudica* at night. Kinetics of a capacitor discharge at night is slower than during the day (Fig. 8a), linear in logarithmic coordinates (Fig. 8b)

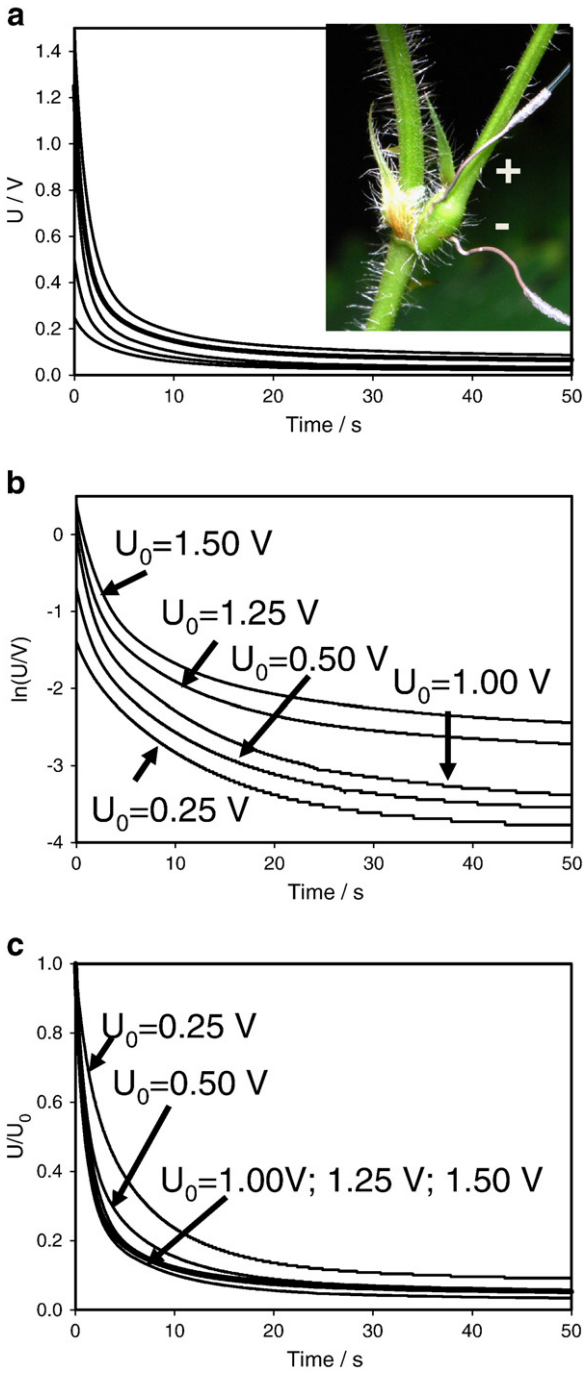

Fig. 7. (a): Time dependencies of electrical discharge in a pulvinus of *Mimosa pudica* during day time. (b): Time dependencies of electrical discharge in a pulvinus of *Mimosa pudica* in logarithmic coordinates. (c): Normalized presentation of time dependencies of electrical discharge; U is the capacitor voltage and U_0 is the initial voltage in volts; Polarity and location of electrodes are shown.

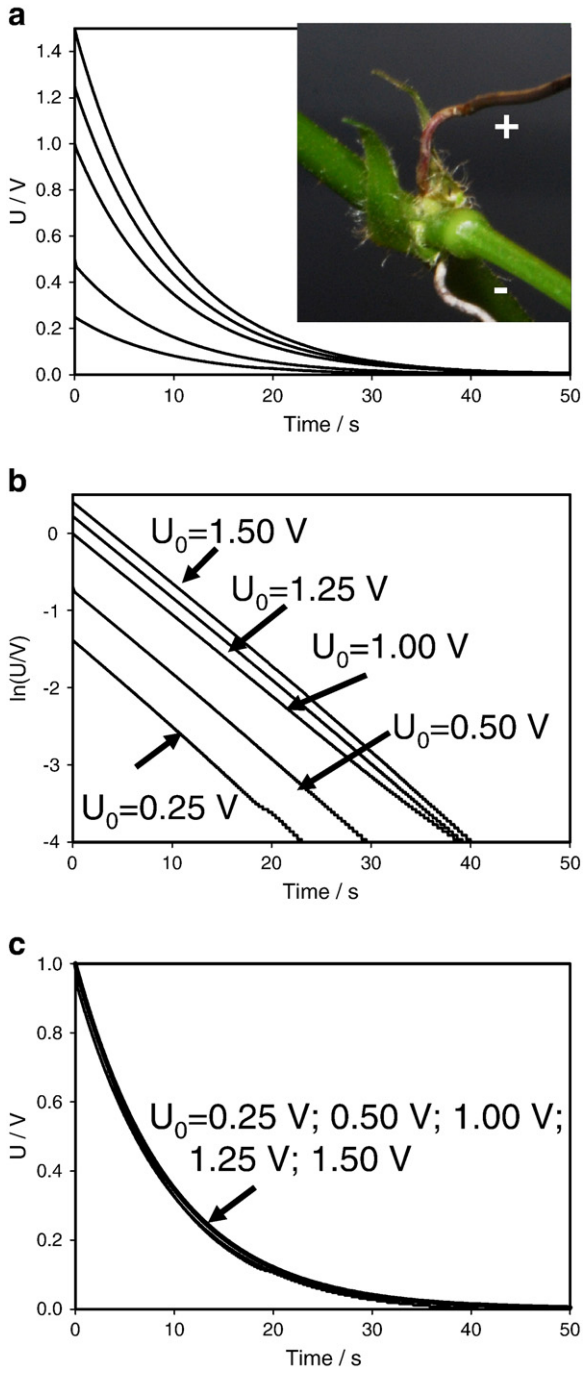

Fig. 8. (a): Time dependencies of electrical discharge in a pulvinus of *Mimosa pudica* during a night time. (b): Time dependencies of electrical discharge in a pulvinus of *Mimosa pudica* in logarithmic coordinates. (c): Normalized presentation of time dependence of electrical discharge in a pulvinus of *Mimosa pudica*. U is the capacitor voltage and U_0 is the initial voltage in volts. Polarity and location of electrodes are shown.

and can be described by Eq. 3. In normalized coordinates all curves coincide independent of the initial voltage (Fig. 8c). As it follows from Fig. 8c, the time constant $\tau = RC$ does not depend on applied voltage and is equal to 9.4 s (mean 9.4 s, median 9.4 s, std. dev 0.1414 s, std. err. 0.0632 s, n = 5). According to Eq. (2), the resistance in the pulvinus of *Mimosa pudica* between electrodes is R = 9.4 s/47 μF = 200 kμ·Ω. Biologically closed electrical circuits with voltage gated ion channels in *Mimosa pudica* are deactivated at night (Fig. 8b and c).

Recently, we analyzed kinetics of a capacitor discharge during a day in *Mimosa pudica* and found the input resistance between electrodes inserted across the pulvinus [16,23,24,26]. The difference in the discharge kinetics between day and night time is shown in Fig. 9. Initial difference in the speed of the response (faster during the day), can be explained by activation of ion channels, equivalent to the high rectification effect. This effect depends on the applied stimulation voltage.

Fig. 10 shows the effects of changing the polarity of electrodes presented in Figs. 7 and 8. The difference in response during the day (Fig. 10a) and night (Fig. 10b) can be clearly seen. Fig. 10c shows relative difference in kinetics of a capacitor discharge during the day and at night (night–day).

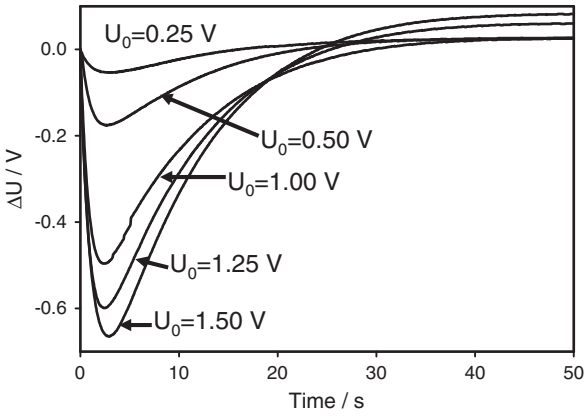

Fig. 9. Difference in time dependencies of electrical discharge in a pulvinus of *Mimosa pudica* at night and at day time (night–day response).

Fig. 11a shows the kinetics of a capacitor discharge in a pulvinus during the day time, but in the dark. *Mimosa pudica* was exposed to a 12:12 h light/dark photoperiod during a 2 month period, but in the morning of the experiment, the light source was not switched on for the day. Fig. 11b shows the difference in time dependence of electrical discharge in the dark in the day time (difference of responses from Figs. 11a and 8a). The biologically closed electrical circuits with voltage gated ion channels in *Mimosa pudica* are activated the next day even in the darkness. This phenomenon can be caused by biological clock in *Mimosa pudica*. The nonlinear effect of activation of electrical circuits during the day time is stronger (Fig. 9) than during the next day in the darkness (Fig. 11b).

4. Discussion

Circadian oscillators are components of the biological clock that regulate the activities of plants in relation to environmental cycles and provide an internal temporal framework. The circadian clock regulates a wide range of electrophysiological and developmental processes in plants. Plant tissues have biologically closed electrochemical circuits that are involved in these regulations. We found periodic activation and deactivation of these circuits in the leaves of *Aloe vera* and *Mimosa pudica* controlled by internal clock, rather than environmental clues. We tested electrical characteristics of biologically closed electrical circuits in *Aloe vera* and *Mimosa pudica*. Response of circuits in *Aloe vera* at night was faster than during the day (Fig. 6a) and these variations steadily repeat day after day. However, the internal clock alone cannot generate the same values of day and night conductance. Fig. 6b shows effect of circadian rhythms in *Aloe vera* without environmental clues (light). There is a significant difference in electrical responses between day time in the presence of light as compared to darkness. To maintain the same values of conductance, the circadian clock mechanism needs additional activation by environmental light. This plant response is probably related to crassulacean acid metabolism in *Aloe vera* with stomata closed during the day and open at night.

The pulvinus of *Mimosa pudica* has mechanical and electrical anisotropy and we found that movements of the petiole are accompanied by a change of the pulvinus shape [26]. As the petiole falls at evening, the volume of the lower part of the pulvinus decreases and the volume of the upper part increases due to the redistribution of water between the upper and lower parts of the pulvinus. This hydroelastic process is reversible. During the relaxation of the petiole in the morning, the volume of the lower part of the pulvinus increases and the volume of the upper part decreases. Changing the polarity of electrodes leads to a strong rectification effect in a pulvinus and to different kinetics of a capacitor discharge if the applied initial voltage is 0.5 V or higher [26].

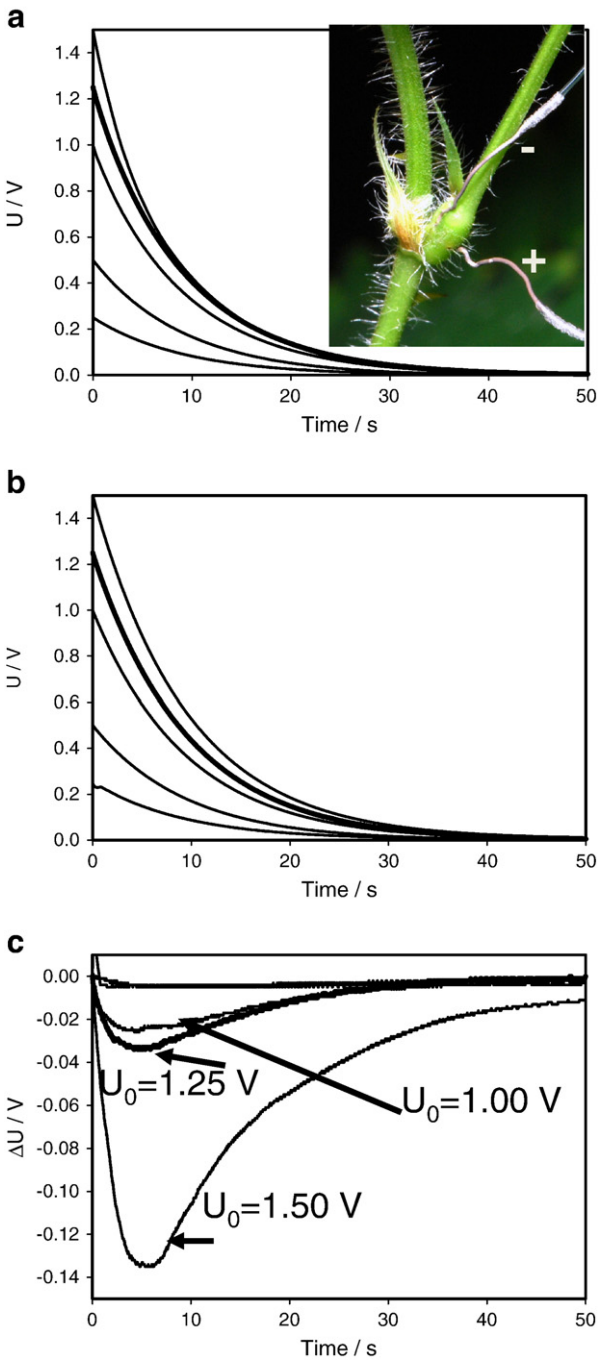

Fig. 10. Time dependencies of electrical discharge in a pulvinus of *Mimosa pudica* with negative voltage on flexor of pulvinus during day time (a) and at night (b). (c): Difference in time dependencies of electrical discharge at night and at day time. *U* is the capacitor voltage and U_0 is the initial voltage in volts. Polarity and location of electrodes are shown.

The circadian clock was discovered in 1729 by De Mairan in his first attempt to resolve experimentally the origin of rhythm in the leaf movements of *Mimosa pudica* [6]. This rhythm continued even when *Mimosa pudica* was maintained under continuous darkness. De Mairan [6] hypothesized that the *Mimosa pudica* leaf movement is controlled by a biological clock. We also investigated the electrical activity of *Mimosa pudica* in the day light (Fig. 7), at night (Fig. 8), and in the darkness the following day (Fig. 11). Fig. 11 shows for the first time the direct influence of a circadian clock on biologically closed electrochemical circuits in a pulvinus *in vivo* and the biological clock memory in *Mimosa pudica*. The response is similar to a typical daily response, although the plant is in the darkness.

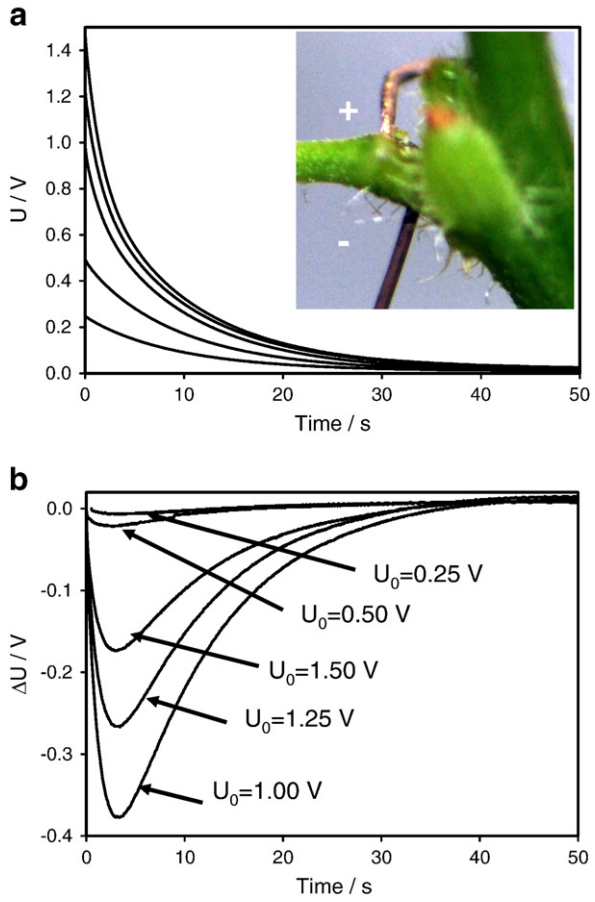

Fig. 11. (a): Time dependence of electrical discharge in a pulvinus of *Mimosa pudica* in the dark during day time with positive stimulation on the flexor side of the pulvinus; (b): Difference in time dependencies of electrical discharge at night and in the dark at day time as a difference between Fig. 11(a) and Fig. 8a. *U* is the capacitor voltage and U_0 is the initial voltage in volts.

This circadian rhythm can be related to the difference in the membrane potentials during the day and night time, which was found in pulvini of different plants [8,9,27–29]. During the day in darkness, there is still a rectification effect in the pulvinus (Fig. 11b), however, in the presence of light during the daytime, this rectification effect and the resistance decrease in the pulvinus are two times higher. These results demonstrate that the circadian clock can be maintained endogenously, probably involving electrochemical oscillators, which can activate or deactivate ion channels in biologically closed electrochemical circuits.

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