Available online at www.sciencedirect.com
SCIENCE DIRECT®
Electrochimica Acta 50 (2005) 4241–4247
ELECTROCHIMICA Acta
www.elsevier.com/locate/electacta

Phototropism and electrified interfaces in green plants

Alexander G. Volkov*,[1], Tanya C. Dunkley, Anthony J. Labady, Courtney L. Brown

Department of Chemistry, Oakwood College, Huntsville, AL 35896, USA

Received 30 June 2004; received in revised form 7 February 2005; accepted 10 February 2005

Abstract

Living organisms generate electrical fields. The conduction of electrochemical excitation is a fundamental property of living organisms. Cells, tissues, and organs transmit electrochemical signals over short and long distances. Excitation waves in higher plants are possible mechanisms for intercellular and intracellular communication in the presence of environmental changes. Ionic channels, as natural nanodevices, control the plasma membrane potential and the movement of ions across membranes; thereby, regulating various biological functions. Some voltage-gated ion channels work as plasma membrane nanopotentiostats. Tetraethylammonium chloride and $ZnCl_2$ block K^+ and Ca^{2+} ionic channels. These blockers inhibit the propagation of action potentials induced by blue light, and inhibit phototropism in soybean plants. The irradiation of soybean plants at 450 ± 50 nm induces action potentials with duration times of about 0.3 ms and amplitudes around 60 mV. The role of the electrified nanointerface of the plasma membrane in signal transduction is discussed.

Keywords: Signal transduction; Action potential; Phototropism; Ion channels; Nanodevices

1. Introduction

Plants continually gather information about their environment. This conglomerate of information supports the maintenance of homeostasis. Environmental changes elicit various biological responses. Plants synchronize their normal biological functions with their responses to the environment. The synchronization of internal functions, based on external events, is linked with the phenomenon of excitability in plant cells. The cells, tissues, and organs of plants possess the ability to become excited under the influence of environmental factors, referred to as irritants. The extreme sensitivity of the protoplasm to chemical stimuli is the basis for excitability; these signals can be monitored [1–8].

Nerve cells in animals and phloem cells in plants share one fundamental property: they possess excitable membranes through which electrical excitations, in the form of action potentials, can propagate [9]. Plants generate bioelectrochemical signals that resemble nerve impulses, and are present in plants at all evolutionary levels [10]. Prior to the morphological differentiation of nervous tissues, the inducement of nonexcitability after excitation and the summation of subthreshold irritations were developed in the vegetative and animal kingdoms in protoplasmatic structures [10].

The cells, tissues, and organs of plants transmit electrochemical impulses over short and long distances via the plasma membrane. It is conceivable that action potentials are the mechanisms for intercellular and intracellular communication in response to environmental irritants.

Initially, plants respond to irritants at the site of stimulation; however, excitation waves can be distributed across the membranes throughout the entire plant. Bioelectrical impulses travel from the stem to the root and vice versa. Chemical treatment, intensity of the irritation, mechanical wounding, previous excitations, temperature, and other irritants influence the speed of propagation [11–18].

Conductive bundles of vegetative organisms sustain the flow of material and trigger the conduction of bioelectrical impulses. This feature supports the harmonization of

* Corresponding author. Tel.: +1 256 726 7113; fax: +1 256 726 7113.
E-mail addresses: gvolkov@oakwood.edu, agvolkov@yahoo.com (A.G. Volkov).
[1] ISE member.

0013-4686/$ – see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.electacta.2005.02.094

biological processes involved in the fundamental activity of vegetative organisms.

The conduction of bioelectrochemical excitation is a rapid method of long distance signal transmission between plant tissues and organs. Plants quickly respond to changes in luminous intensity; osmotic pressure; temperature; cutting; mechanical stimulation; water availability; wounding; chemical compounds, such as herbicides, plant growth stimulants, salts, and water [18]. Once initiated, electrical impulses can propagate to adjacent excitable cells. The change in transmembrane potential creates a wave of depolarization or action potential, which affects the adjoining resting membrane.

The phloem is a sophisticated tissue in the vascular system of higher plants. Representing a continuum of plasma membranes, the phloem is a potential pathway for transmission of electrical signals [19]. It consists of two types of conducting cells: the characteristic sieve-tube elements, and the companion cells. Sieve-tube elements are elongated cells that have end walls perforated by numerous minute pores through which dissolved materials can pass. Sieve-tube elements are connected in a vertical series known as sieve tubes. Sieve-tube elements are alive at maturity; however, before the element begins its conductive function, their nuclei dissipate. The smaller companion cells have nuclei at maturity and are living. They are adjacent to the sieve-tube elements. It is hypothesized that they control the process of conduction in the sieve tubes. Thus, when the phloem is stimulated at any point, the action potential is propagated over the entire length of the cell membrane and along the phloem with a constant voltage [13].

Electrical potentials have been measured at the tissue and whole plant level [3,7]. At the cellular level, electrical potentials exist across membranes, and thus between cellular and specific compartments. Electrolytic species, such as K^+, Ca^{2+}, H^+, and Cl^- are actively involved in the establishment and modulation of electrical potentials [3]. The highly selective ion channels serve as natural nanodevices. Voltage-gated ion channels, as nanopotentiostats, regulate the flow of electrolytic species, and determine the membrane potential.

Light is an essential source of energy on which many of the biological functions of plants depend. The sun's radiant energy optimizes germination, photosynthesis, flowering, and other processes needed to maintain homeostasis. Plants contain specific photoreceptors that perceive light ranging from ultraviolet to far-red light. Natural radiation concurrently excites multiple photoreceptors in higher plants. Specific receptors initiate distinct signaling pathways leading to wavelength-specific light responses. Photoreceptors, phototropins, cryptochromes, and phytochromes have been identified at the molecular level [20–24].

Phototropins, such as PHOT1 and PHOT2, are the flavoprotein photoreceptor that responds to light with a wavelength of 360–500 nm (blue light) [20–24]. It regulates phototropism and intracellular chloroplast movements. PHOT1 contains two 12 kDa flavin mononucleotide binding domains. LOV1 (light, oxygen, and voltage) and LOV2 are located within its N-terminal region and a C-terminal serine/threonine protein kinase domain. Phototropin, when activated by light, undergoes a conformational change. PHOT1 and PHOT2 bind FMN and undergo light-dependent autophosphorylation. PHOT2 is localized in the plasma membrane. Cryptochromes and phototropin have different transduction pathways, but similar traits [20].

The main goals of this work are the detection of bioelectrochemical responses induced by blue photosensory system in soybean plants and to check the role of ionic channels in propagation of photoinduced action potentials along electrified interfaces in green plants.

2. Materials and methods

2.1. Interfacing

A diagram is given, in Fig. 1, depicting the experimental setup. Measurements were taken inside a Faraday cage mounted on a vibration-stabilized table. An *IBM*-compatible microcomputer with multi I/O plug-in data acquisition board NI 6052E DAQ (*National Instruments*) was interfaced through a NI SC-2040 Simultaneous Sample and Hold (*National Instruments*). The multifunction NI 6052E data acquisition board provides high resolution and a wide gain range and supports continuous, high-speed data acquisition. Single channels can be sampled at any gain up to 333 ksamples/s. The digitized data includes negligible time skew (less than 50 ns) between channels. Measuring signals were recorded as ASCII files using *LabView* (*National Instruments*) software.

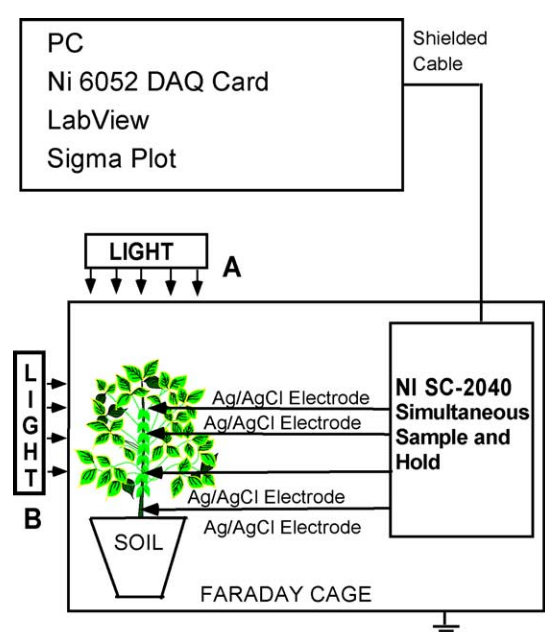

Fig. 1. Experimental set-up for measuring electrical signals in green plants.