



Effect of simultaneously induced environmental stimuli on electrical signalling and gas exchange in maize plants

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ABSTRACT

Electrical signalling in response to environmental stimuli is a well-known phenomenon in higher plants. For example, in maize, different stimuli, such as wounding or re-irrigation after drought, incite characteristic electrical signals which have quite particular effects on gas exchange. What is less well understood is how plants (specifically maize) respond when two different environmental stimuli are applied simultaneously. To explore this, a three-stage experiment was designed. In the first stage, drought conditions were simulated by decreasing the soil water content to 30–40 % of field capacity. In these conditions, and in contrast to well-watered plants, the maize exhibited only 60–70% of the original level of stomatal conductance and 50–60 % of the original photosynthesis rate. In the second stage of the experiment the plants were re-irrigated and heat stimulated separately. Re-irrigation led to specific electrical signals followed by a gradual increase of gas exchange. In contrast, after heat stimulation of a leaf an electrical signal was evoked that reduced the net CO₂-uptake rate as well as stomatal conductance. In the third stage, to elucidate how plants process simultaneous re-irrigation and heat stimulation, the drought-stressed maize plants were re-watered and heat-stimulated at the same time. Results showed a two phase response. In the first phase there was a rapid decrease in both the CO₂ uptake rate and the stomatal conductance, while in the second phase each of these parameters increased gradually. Thus, the results strongly support the view that the responses from both stimuli were combined, indicating that maize plants can process simultaneously applied stimuli.

1. Introduction

A range of plant physiological processes have been shown to depend on plant cells' ability to evoke and transmit electrical signals; including photosynthesis and respiration (Lautner et al., 2013; Gallé et al., 2015; Vodenev et al., 2016), intercellular communication (Davies, 2004) and the capture of insects in carnivorous plants like the Venus flytrap (Scherzer et al., 2017). Indeed, electrical signals are ubiquitous in the plant kingdom and occur at various evolutionary levels from algal to bryophytes (Favre et al., 1999) to higher plants (Pickard, 1973; Fromm and Lautner, 2007; Hedrich et al., 2016). Although plants possess most of the biochemistry of the neural motoric system in animals, such as neurotransmitters, ion channels and cellular messengers (Volkov, 2012), electrical signalling in plants is not as complex as in animal nerves. The phloem can be considered to be a simple neural network, however – like a signalling pathway (Fromm and Eschrich, 1988; Salvador-Recatalà et al., 2014; Hedrich et al., 2016), enabling plants to communicate over long distances. Most likely the presence of long-distance electrical signalling in plants is due to the need to respond

rapidly to external stimuli and both abiotic and biotic stress. Stimuli such as wounding, cold and re-irrigation after a drought period evoke characteristic electric responses in excitable plant cells that then transmit these signals via plasmodesmata to the phloem, from where they propagate to distant responding regions (Van Bel et al., 2011). In general, plants make use of two types of electrical signal: rapid action potentials (with a velocity of 0.5–20 cm s⁻¹) and slower variation potentials with a speed in the range of 0.1–1.0 cm s⁻¹ (Fromm and Lautner, 2007; Stahlberg and Cosgrove, 1997). Action potentials are generally triggered by non-invasive stimuli (Trebacz et al., 2006), while variation potentials are mostly triggered when the plant is wounded in some way, for example when it is cut or burnt (Stankovic et al., 1998; Gallé et al., 2013). In addition, serious damage to the plant can provoke composite signals, which include both action and variation potentials (Hlavackova et al., 2006; Davies and Stankovic, 2006).

In the present study two strong external stimuli were applied simultaneously in order to study how two different types of information are transmitted to a responding leaf region and how these affect gas exchange. A variation potential was evoked by burning a leaf tip while

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a transient depolarization was induced by re-watering the roots of drought-stressed plants. The latter signal presumably causes an increase in gas exchange while burning causes a transient decrease in CO₂-uptake rate (Grams et al., 2009). It is particularly interesting, therefore, to explore the sequence of events in respect to gas exchange after applying these two, contradictory, stimuli.

2. Materials and methods

2.1. Plant materials

Maize plants (*Zea mays* L.) were grown for four weeks in the greenhouse. The plants were grown at between 18 and 22 °C and 60–80 % relative humidity, using a 14 h light/10 h dark period and a light intensity of 400 μmol m⁻² s⁻¹. The light was provided by mercury halide lamps. The uniform soil 73 was composed of 60–80 % white peat, 20–40 % clay, 1 kg/m² nutrients and 2 kg/m² of long term fertilizer (pH 5.8). After this initial four-week period the plants were placed in bigger pots and irrigated. They were then subjected to a period of drought lasting from three to four weeks. The plant-soil-system was weighed both at the beginning and the end of the drought period. Measurements were performed on mature leaves of plants that were 100–120 cm in height.

2.2. Detection of electrical signals

Drought-stressed maize plants were re-watered with 2.5 L H₂O and they were heat-stimulated by heating the tip of a leaf for 3 s (ca.1000 °C). Initially, these stimuli were applied separately but then simultaneously. In each case, gas exchange and electrical potentials were measured using a porometer and a two-electrode technique in a Faraday cage (Fig. 1A and B). For intracellular detection of the membrane potential, the two microelectrodes were filled with 500 mM KCl and inserted into mesophyll cells of a mature leaf. The reference electrode was immersed together with the cut end of a neighbouring leaf into artificial pond water (APW, composed of 1.0 mM NaCl, 0.1 mM KCl, 0.1 mM CaCl₂ and 1.0 mM MES, adjusted with Tris to pH 6.0). The electrodes were connected to a dual channel amplifier (World Precision Instruments, Model Duo 773, Sarasota, FL, USA).

After the experiment the shoot was cut off from the irrigated plants and the soil was dried in an oven for three days at 100 °C. The dry weight of this soil was added to the shoot weight. The sum of the dry soil and shoot weight was then subtracted from the weight of the plant-soil system taken at the end of the drought period to determine the

weight (%) of the soil water.

2.3. Surface electrode technique

Within the Faraday cage the measuring electrode was attached to the upper surface of a mature leaf (the third leaf from the top) at a distance of between 10 and 20 cm from the leaf tip. The reference electrode was attached to the surface between the measured leaf and the shoot. The electrodes comprised 0.25 mm diameter Ag/AgCl wire and were embedded in 10% agar immersed in artificial pond water (composed of 1.0 mM NaCl, 0.1 mM KCl, 0.1 mM CaCl₂ and 1.0 mM MES adjusted with Tris to pH 6.0). Signals were detected using an amplifier (WPI, Model 750 B) to which a 173 A Keithley multimeter was attached.

2.4. Leaf gas exchange measurements

The gas exchange was measured on the same leaf in which the measuring electrodes were inserted. The distance of the porometer to the first electrode near the leaf tip was 27 cm ± 2 cm and to the soil/root system 85 cm ± 6 cm (Fig. 1A). Changes in CO₂ concentration and stomatal conductance were measured with the porometer (Li-Cor Li 6400, Lincoln, NE). The measurements were started 5 min before stimulation and were performed at a CO₂ concentration of 400 ppm, a relative humidity of 40% and a light intensity of 1000 μmol photons m⁻² s⁻¹.

2.5. Temperature measurements

The temperature sensor from a polygraph (PolyGraphBio, version 2.1, Zug, Switzerland) was attached on the leaf surface at a distance of 9 cm to the leaf tip. The measurements were started 10 min before heat stimulation of the leaf tip. Simultaneously the temperature of artificial pond water, which included the reference electrodes, was measured with a thermometer.

3. Results

Although the plants showed no typical drought-stressed phenomena such as leaf curling, when the root/soil system was touched no humidity could be sensed. Measurements of the plant-soil-system over the whole period of the experiment showed that, in the beginning, the weight of the soil-root including water was 4.114 ± 0.058 kg (Table 1). Transpiration reduced the water content consistently by

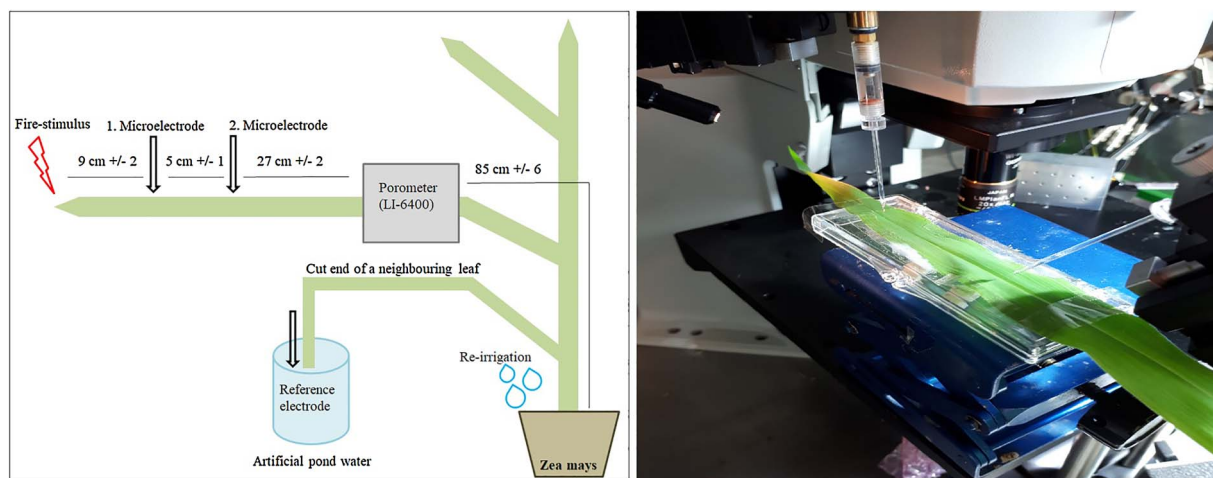


Fig. 1. (A) Schematic overview of the set up with two microelectrodes and the reference electrode as well as a porometer (LI-6400). (B) The measuring electrodes were inserted into mesophyll cells of the leaf at a distance of 9 cm ± 2 cm to the leaf tip. The distance between both microelectrodes was 5 cm ± 1 cm, while the distance between the heated leaf tip and the porometer was 27 ± 2 cm.

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