Regulation of Gas Exchange by Rapid Signals between Roots and Shoot

C. Koziolek [1], T. E. E. Grams [1], R. Matyssek [1], J. Fromm [2]

[1] Lehrstuhl fuer Forstbotanik, TU Muenchen, Am Hochanger 13, 85354 Freising
[2] Institut fuer Holzforschung, TU Muenchen, Winzererstr. 45, 80797 Muenchen

Introduction

There has been growing evidence that a broad array of environmental stimuli may affect the gas exchange of plants. In experiments submitting plants to drought, non-hydraulic signals were observed, which may serve as a sensitive link between changes in soil water relations and responses of the shoot [1]. Fromm and Fei [2] showed that, in maize, a decrease in soil water content did not only reduce the rates of CO_2 uptake and transpiration of leaves but also induced a decline in the electric potential, as measured on the leaf surface. Immediately after irrigation an action potential followed by a hyperpolarisation was recorded, and after 12-15 min CO_2 uptake and transpiration began to increase. Using stained water the authors proved that this increase was not triggered by the ascent of water in the xylem. In parallel to electric potentials, also hydraulic changes that were found in xylem vessels of maize roots to be light-induced [3], may provide a rapid signal to the shoot. In the present study we compare electric and hydraulic pulses as induced by sudden irrigation of drought-stressed maize plants in order to distinguish the signal that primarily controls the rapid response of leaf gas exchange to changing water supply.

Material and methods

Plant Material: Maize plants (*Zea mays* L. var. *frivol*) were grown in pots (3 l) filled with garden-mould (Fruhstorfer Erde, Typ P; Archut, Germany) under greenhouse conditions (PAR of 200 µmol m^{-2} s^{-1}, provided by mercury halide lamps; 14/10 h light/dark period; constant temperature of 22 °C).

Experimental Setup: Plants of 80-100 cm height were placed into a fully climate-controlled growth chamber (constant temperature of 22 °C; relative humidity of 60 %; 14/10 h light/dark period). Irrigation was suspended until

the stomatal conductance had decreased to 50-60 % of the initial level displayed under non-limiting soil water supply.

Gas Exchange Measurements: Gas exchange was measured with a minicuvette system (Walz, Effeltrich, Germany). Cuvette conditions during the experiments were maintained at a CO_2 concentration of 350 µl l^{-1}, a relative humidity of 60 % and an irridance of 425 µmol m^{-2} s^{-1}.

Assessment of the Membrane Potential: For measuring the membrane potential of the epidermis of a mature leaf a microelectrode filled with 100 mmol degased KCl solution was punctured into the upper surface while the reference electrode (grounded) was attached at a distance of 15-30 cm to the shoot surface (the latter being moistened with 100 mmol KCl agar). Both electrodes consisted of AgCl and were connected to a differential amplifier (WPI-Instruments, model 750, USA). The recordings were displayed on a chart recorder. Prior to starting an experiment, both electrodes were calibrated (0 mV) in 100 mmol KCl agar.

Measurement of Cell Turgor: The turgor of epidermal leaf cells was measured at the lower side of mature leaves at 5-10 cm distance from the leaf tip using a cell pressure probe [4]. Recordings were displayed on a chart recorder.

Results

Gas Exchange: Well-watered plants showed an CO_2 uptake rate (A) in the range of 16 to 19 µmol m^{-2} s^{-1} and a stomatal conductance (g_{H2O}) of about 120 to 140 mmol m^{-2} s^{-1}. After three to five days without irrigation A and g_{H2O} decreased in a distinct way. Prior to resuming irrigation drought-stressed plants showed an CO_2 uptake rate of 13.6 ± 1.6 µmol m^{-2} s^{-1} and a stomatal conductance of 75 ± 15 mmol m^{-2} s^{-1}. At 4.6 ± 3.2 min after irrigation both, A and g_{H2O} decreased by 1.3 ± 1.0 µmol m^{-2} s^{-1} and by 15 ± 5 mmol m^{-2} s^{-1}, respectively (all values as means ± SD). Fig. 1 shows a typical response of A and g_{H2O} to an irrigation pulse.

Electric Potential: The membrane potential measured in the leaf epidermis showed a great variability between -250 and -75 mV which might depend on the water status of the plant. Immediately after irrigation an action potential was generated in the roots and recorded in the leaf epidermis. The response velocity (RV) as averaged across five plants was 28 ± 13 cm s^{-1} at an amplitude (Δ) of ± 17 ± 6 mV (values as means ± SD). Fig.2 shows a typical action potential after an irrigation pulse with RV of 24 cm s^{-1} and a Δ of 12 mV.

Cell Turgor in a Leaf Epidermic Cell: The turgor of epidermal cells decreased in parallel with the soil water content. The pressure in epidermal leaf cells of maximum turgidity was in the range of 3 to 5 bar. In drought-stressed plants, the turgor was found to be reduced to 0.8 to 2.0 bar. Mean values of seven plants showed a response velocity of 4 ± 3 cm s^{-1} with an average am-

plitude of -0.16 ± 0.06 bar (means ± SD). Fig. 2 gives a typical turgor signal as measured in an epidermal cell after an irrigation pulse. The turgor response was accompanied by RV of 8.30 cm s^{-1} and an amplitude of -0.25 bar.

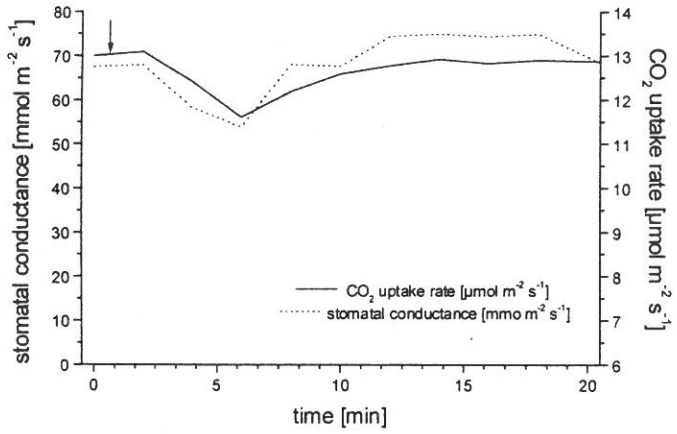

Fig. 1. Response of the CO_2 uptake rate (A; —) and the stomatal conductance (g_{H2O} ; ---) of a drought-stressed maize plant to irrigation. The arrow denotes the instant of irrigation.

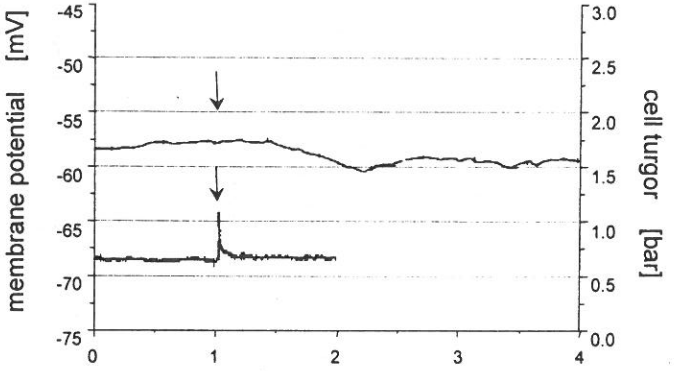

Fig. 2. Epidermic leaf cell turgor (line above) and membrane potential (line below) after irrigation of a drought-stressed maize plant. The arrow denotes the instant of irrigation.

Discussion

Results of the present study clearly showed that the electric signal had a higher response velocity than the hydraulic signal. Malone and Stancovic [5] also measured hydraulic signals and surface potentials in wheat seedlings in parallel to each other. These authors found that the turgor increased immediately after burning the leaf while the depolarisation of the electric surface potential occurred with some delay, indicating that the response of the turgor depends on the type of stimulus. Injury to the plants caused rapid hydraulic signals, whereas non-damaging stimuli like irrigation generated slow hydraulic signals and rapid electric signals.

The membrane potential which had a mean velocity of 28 cm s^{-1} was faster than the surface potential measured by Fromm and Fei [2]. If the electric signal affects the stomata primarily it is expected to reach the leaf before the arrival of the hydraulic signal. The time interval between the electric signal and the stomatal response was smaller as compared with the findings by Fromm and Fei [2], however, but this does not entirely explain the initiation of the stomatal movement. The hydraulic signal, which was not as fast as the electric one, might be mainly involved in the stomatal response. After the irrigation pulse, the turgor in epidermal cells showed a mean decrease of 0.16 bar, which was followed after a few seconds by an increase of the turgor towards its initial level. As shown in Fig. 1 the assimilation rate and the stomatal conductance also decreased after irrigation rather than were built up again. This might be caused first by a decrease, second by an increase in the turgor of the guard cells.

For achieving final conclusions about the signal which governs the rapid response of stomata to irrigation, further experiments are planned to either filter out the electric signal by cooling the stem tissue with ice, or by counterbalancing the hydraulic signal through pressurising the root system in a root pressure chamber.

Acknowledgement

This work was supported by DFG funding FR 955/4-1,2. Part of the funding was supported by SFB 607.

References

[1] W. J. Davies, J. Zhang (1991): Root signals and the regulation of growth and development of plants in drying soil. Annu. Rev. Plant Physiol. Plant Mol. Biol. 42, 55-76.

[2] J. Fromm, H. Fei (1998): Electrical signaling and gas exchange in maize plants of drying soil. Plant Science 132, 203-213.

[3] L. H. Wegener, U. Zimmermann (1998): Simultaneous reading of xylem pressure and trans-root potential in roots of intact glycophytes using a novel xylem pressure probe technique.Plant, Cell and Environment 21, 849-856.

[4] E. Steudle (1993): Pressure probe technique: basic principles and application to studies of water and solute relations at the cell, tissue and organ level. *InWater Deficits: Plant Responses From Cell to Community* (eds. J. A. C. Smith & H. Griffith), pp. 5-36. BIOS Scientific Publishers, Oxford.

[5] M. Malone, B. Stankovic (1991): Surface potentials and hydraulic signals in wheat leaves following localized wounding. Plant, Cell and Environment 14, 431-436.