Plant and Soil 105, 283–286 (1988)

PLSO 6872

Photosynthesis of salt-stressed maize as influenced by Ca:Na ratios in the nutrient solution

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Received 12 May 1986. Revised July 1987

Key words: maize, photosynthesis, salinity, water use efficiency, *Zea mays* L. Ca, Na, Mg

Abstract

The CO_2 fixation rate of salt-stressed maize leaves was influenced by the Ca:Na ratio in the solution cultures. At an osmotic potential of -0.4 MPa in the root media, both the photosynthetic rate and the water-use efficiency declined as substrate Ca increased. Blade-Ca concentration also increased, while blade-Na and -Mg decreased. Apparently photosynthetic activity was inhibited in part by internal Mg deficiency rather than by Na toxicity or by Na-induced Ca deficiency. Reduction of the Ca:Mg ratio in the culture stimulated the CO_2 fixation rate.

Introduction

Plants grown in saline solution cultures often exhibit symptoms of specific ion toxicities, deficiencies, and nutritional imbalances. These effects may depend, among other factors, upon the ratio of the salinating cations, commonly Na and Ca. Some graminaceous species, grown in nutrient cultures containing NaCl as the sole osmoticum, frequently display blade deformations and necrosis that are characteristic of severe Ca-deficiency (Kawasaki and Moritsugu, 1979). At the other extreme, high concentrations of substrate Ca usually result in increased leaf-Ca along with a marked reduction in leaf-Mg (Bernstein and Hayward, 1958). There is evidence that such a Ca-Mg imbalance could lead to disturbances in photosynthesis. Magnesium deficiency in maize leaves has been associated with reduced photosynthetic rates (Peaslee and Moss, 1966). High concentrations of leaf-Ca may interfere with CO_2 fixation by inhibition of stroma enzymes, especially those that are Mg^{2+} activated (Brand and Becker, 1984).

The objective of our study was to assess the influence of different Ca:Na and Ca:Mg ratios in isoosmotic solution cultures on both the nutritional status and the photosynthesis rates in attached maize leaves.

Materials and Methods

Maize seeds (*Zea mays* L. cvs Pioneer 3906 and DeKalb XL-75) were soaked for 30 hours in an aerated solution of 0.5 m*M* $CaSO_4$, then spread on moist germination paper. Three day-old seedlings were placed on cheesecloth supported between 2 plastic grids with 1.7 cm^2 openings and covered with moist vermiculite. The grid assemblies, each containing 40 seedlings were transferred to the glasshouse and supported over plastic pots containing 28 l of nutrient solution. The composition of the nutrient solution was: 2.5 m*M* $Ca(NO_3)_2$, 3 m*M* KNO_3, 1.5 m*M* $MgSO_4$, 0.17 m*M* KH_2PO_4, 50 μM Fe (as sodium ferric diethylenetriamine pentaacetate), 23 μM H_3BO_3, 5 μM $MnSO_4$, 0.4 μM $ZnSO_4$, 0.2 μM $CuSO_4$, and 0.1 μM H_2MoO_4. Seven days after germination the cultures were salinated with NaCl and $CaCl_2$ (concentrations given in Table 1) calculated to reduce the osmotic poten-

Table 1. Concentrations of Na, Ca and Mg (mol m^{-3}) and ratios of Ca:Na and Ca:Mg in the nutrient cultures for *Zea mays* cvs. Pioneer 3906 and DeKalb XL-75

Treatment	Solution composition				
	Na	Ca	Mg	Ca:Na	Ca:Mg
Control	0	2.5	1.5	–	1.7
S1[a]	86.5	2.5	1.5	0.03	1.7
S2	71.3	12.6	1.5	0.18	8.4
S3	43.1	34.0	1.5	0.79	22.7
S4	14.1	54.6	1.5	3.87	36.4
S5[b]	14.1	37.3	18.9	2.65	2.0

[a] S = isotonic salinity treatment at −0.4 MPa.
[b] Cv. DeKalb XL-75 was not subjected to this treatment.

tial of the solutions by 0.4 MPa. Salts were added at a rate equivalent to −0.1 MPa.day^{-1}. All solutions were changed 4 times during a 26-day growing period. The pH of the solution fluctuated between 5.2 and 6.2 between changes. Both cultivars were grown in January—February, 1985. The average daily maximum and minimum temperatures in the glasshouse were 30° and 18°, respectively. During June—July, 1985, the experiment was repeated using only Pioneer 3906; temperature extremes were 37.2° and 22.5°.

The photosynthetic capacities of the youngest, fully expanded leaf blades of 25-day-old maize seedlings were measured between 11 a.m. amd 2 p.m. at a radiant flux density of 1100—1200 mol $m^{-2}s^{-1}$ CO_2 concentration of 373 ± 28 ppm. The rate of photosynthesis was determined with a LiCor 6000[1] portable photosynthesis system equipped with the 6000-12 one-liter chamber (Li-Cor Inc., Lincoln, Nebraska). An 11.4 cm^2 leaf area was confined by inserts. Flow rate was 10 cm^3s^{-1}. The CO_2 analyzer was calibrated daily with a series of CO_2 air-mixtures. Leaf temperatures were measured with a chromel-constantan thermocouple, chamber temperature with a linearized thermistor and humidity with a Vaisala sensor. These parameters were used for the calculation of leaf water vapor conductance according to Jarvis (1981).

Ten consecutive measurements at 5 second intervals were taken for the rate of CO_2 depletion from the chamber and for leaf water vapor conductance. These measurements were replicated 6 times on different plants. In the June—July experiment with Pioneer 3906, fully expanded blades of leaf 6 (n = 12) were harvested for mineral analysis. The blades were dried at 65°, then gorund to a fine powder.

The Na, K, Ca and Mg concentrations in the blade tissue were determined by atomic absorption spectral analysis of nitric-perchloric acid digests. Phosphorus analyses were conducted with the molybdate-vanadate colorimetric method (Kitson and Mellon, 1944) and chloride analyses with the coulometric-amperometric titration procedure (Cotolove, 1963).

[1] Mention of company names of products is for the benefit of the reader and does not imply endorsement, guarantee, or preferential treatment by the USDA of its agents.

Results and discussion

A salt stress of −0.4 Mpa reduced the dry shoot yield of 25-day-old Pioneer 3906 and DeKalb XL-75 plants by 35 and 41%, respectively (data not presented). In neither cultivar did the variation in Ca:Na ratio in the nutrient cultures cause a significant difference in dry-matter production of the shoots. However, some ratios caused visible signs of nutrient imbalance. At the lowest Ca:Na ratio (S1) many of the shoots were injured. Blades were often deeply serrated with pronounced withering of the tip. In the most acute cases, leaves failed to unroll normally so that adjacent blades frequently adhered to each other. The sheaths of the affected shoots were enlarged and abnormally fleshy. This response pattern has been associated with severe Ca-deficiency in cereals and grasses (Kawasaki and Moritsugu, 1979; Loneragan *et al.*, 1968; Maas and Grieve, in preparation). Leaf element analyses confirmed the sub-optimal levels of Ca in Sl blades (Table 2). This injury was not observed in plants grown at any other Ca:Na ratio. DeKalb XL-75 appeared to be more sensitive than Pioneer 3906 to high substrate Na.

In response to the highest Ca:Na ratio (S4), both cultivars developed chlorosis. Often the lower 3 or 4 leaves were damaged and senescent, while the rest of the shoot appeared to be normal for 25-day-old plants developing under −0.4 MPa stress. Plants grown at higher Mg:Ca ratio (S5) remained green and uninjured.

At low external Ca:Na ratios, blade-Ca and Mg

Table 2. Element concentrations (mmol × kg^{-1} dry wt) in the blades (6th leaf) of Pioneer 3906. Values are the mean ± SD of 3 plants

Treatment	Ca	Mg	Na	K	P	Cl
Control	42 ± 2	88 ± 2	0.31 ± 1	696 ± 9	61 ± 4	37 ± 4
S1	22 ± 2	60 ± 1	448 ± 21	822 ± 32	106 ± 12	439 ± 9
S2	71 ± 5	59 ± 3	212 ± 18	895 ± 31	81 ± 8	519 ± 12
S3	84 ± 1	54 ± 1	44 ± 3	891 ± 47	77 ± 9	513 ± 9
S4	150 ± 24	52 ± 3	4 ± 1	936 ± 42	83 ± 10	500 ± 36
S5	124 ± 13	114 ± 5	4 ± .3	930 ± 21	78 ± 2	584 ± 18

in Pioneer 3906 were 53% and 69%, respectively, of that in non-salinated control blades, while K increased by 18% (Table 2). As Ca concentration in the cultures increased, Mg concentration in the blades decreased by up to 40% while that of K increased by a similar percentage. When Mg was substituted for part of the substrate Ca, blade-Mg increased, and Ca decreased, while K concentration was unaffected. The ratio of Ca:Na in blades of S1 through S3 was about 1.7–2.4 times higher than that in the nutrient solutions. This ratio was, however, increased tenfold or more in blades of S4 and S5 over the concentration in solutions, mainly due to a large decrease in Na accumulation.

Photosynthesis in maize was reduced by salinity (Table 3). The rate of CO_2 fixation at a salinity of −0.4 MPa was highest at the lowest Ca:Na ratio (S1) and was decreased when this ratio was increased. The decrease was only significant with blades of S4 in which the ratio of Ca:Na in blades became enormously high as compared with that in the solution. The rate of CO_2 fixation in blades of non-salinated DeKalb XL-75 shoots was 26.4 ± 2.7 μmole $CO_2 \cdot m^2 \cdot s^{-1}$, and decreased to 20.5 ± 2.7 and 13.6 ± 2.7 μmole $CO_2 m^{-2}/s^{-1}$ in response to external Ca:Na ratios of 0.03 and 3.85, respectively.

Data for Pioneer 3906 (Table 3) suggest that two distinct mechanisms may be responsible for the decrease in CO_2 fixation when the Ca:Na ratio in cultures increased. One is decreaed stomatal opening, and the second is inhibition of a non-stomatal component of photosynthesis. Hsiao (1976) has shown that increased Ca decreased stomatal opening. It seems that in this case, a non-stomatal mechanism of photosynthesis was markedly inhibited as indicated in the greater inhibition of CO_2 fixation relative to the rate of transpiration and the increased intercellular CO_2 concentration in S3 and S4. As a result, water-use efficiency was decreased when the Ca:Na ratio increased, similar to the decrease in CO_2 fixation.

Replacement of one-half of the Ca with Mg decreased, but did not reverse these effects. The inhibition of photosynthetic activity, however, was not entirely due to blade Mg insufficiency. Although Mg in the leaf blades was higher than in the unsalinated control blades (Table 2), the CO_2 fixation

Table 3. Effect of ionic composition of nutrient solution on photosynthetic activity in maize (cv. Pioneer 3906). Salinity of solutions was equivalent to −0.4 MPa. Data are the mean ± SD for n = 6

		Ca:Na and Ca:Mg ratios				
	Control	S1	S2	S3	S4	S5
Ca:Na Ratio	–	0.03	0.18	0.79	3.87	2.65
Ca:Mg Ratio	1.7	1.7	8.4	22.7	36.4	2.0
CO_2 Fixation rate (μmol $CO_2 m^{-2} s^{-1}$)	27.1 ± 4.2	22.1 ± 1.7	19.0 ± 2.2	18.2 ± 2.6	14.6 ± .72	19.3 ± 4.0
Intercellular CO_2 concentration (ppm)	165 ± 18	182 ± 26	165 ± 11	199 ± 22	208 ± 29	166 ± 38
Transpiration rate (mmole $H_2O m^{-2} s^{-1}$)	10.9 ± 1.4	11.0 ± 0.8	10.2 ± 1.2	10.5 ± 1.3	9.4 ± 0.5	10.7 ± 1.7
Water use efficiency (mmol $CO_2 mol^{-1} H_2O$)	2.49 ± .23	2.00 ± .19	1.87 ± .14	1.73 ± .20	1.55 ± .12	1.80 ± .24

[a] Refers to the ratios outlined in Table 1.

rate did not rise correspondingly. Since Na in the blades of S4 and S5 was as low as in the controls, it seems that the inhibition of photosynthesis at maximal Ca:Na was mainly due to high Ca accumulation.

Estimates of the intercellular distribution of Ca indicate that while the Ca content of the chloroplasts is high compared to the cytoplasm Yamagishi *et al.*, 1981), the concentration of free Ca in the stroma is very low (Miginiac-Maslow and Itoarau, 1977). High substrate Ca may thus lead to excessive Ca and an insufficient Mg concentration in the stroma that might subsequently inhibit CO_2 fixation rates due to repressed activity of some key enzymes of the Calvin cycle like FBPase and SDPase (Charles and Halliwell, 1980).

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