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Effect of Zn^{2+} on water and K^+ fluxes in detopped maize plants

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Abstract

Water and K^+ fluxes were examined in detopped plants of *Zea mays* L. (cv. White Horse Tooth), which were grown and exuded on half-strength Long Ashton nutrient solution containing the appropriate concentration of Zn^{2+} at 20 °C. In light-grown plants, 100 and 500 μM Zn^{2+} increased both water and K^+ fluxes in detopped maize plants whereas 1 000 μM Zn^{2+} inhibited both fluxes. In the dark-pretreated plants, 1 000 μM Zn^{2+} in the medium stimulated K^+ flux. The fluxes of K^+, Zn^{2+}, Ca^{2+} and Mg^{2+} were usually higher in detopped plants than in intact ones. At 1 000 μM Zn^{2+} in the exudation medium, Zn^{2+} concentration was higher in the xylem exudate of dark-pretreated plants than in roots of plants maintained in light. The results are discussed in relation to the influence of Zn^{2+} on the membrane permeability and transport in plants.

Introduction

It is still not clear whether the uptake of zinc is active or passive. Schmid *et al.* (1965) and Chaudhry and Loneragan (1972) found that uptake of Zn^{2+} was reduced at low temperatures and by the respiratory inhibitor dinitrophenol (DNP) and azide. In many studies, it has been reported, that Zn^{2+} inhibited the uptake of ions as Ca^{2+}, K^+, Mg^{2+} and Na^+ (Chaudhry and Loneragan 1972, Wyn Jones and Sutcliffe 1972, Abbas 1986).

It has also been shown, that Zn^{2+} alters the membrane permeability and this is one of the primary mechanisms of Zn^{2+} toxicity (Woolhouse 1983). Wyn Jones and Sutcliffe (1972) found that 10 μM Zn^{2+} in the medium enhanced K^+ leakage from maize roots, whereas De Filippis (1979) found that Zn^{2+} levels above 100 μM induced K^+ leakage from *Chlorella*. Also, Abbas (1992) found that Zn^{2+} levels above 10 μM in the sea water increased the membrane permeability of *Ulva lactuca* cells which resulted in an increase in Na^+ and decrease in K^+ concentrations in the algal cells.

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On the other hand, Wainwright and Woolhouse (1977) using a zinc-tolerant clone of *Agrostis tenuis* found that Zn^{2+} was without effect upon K^+ release from the roots.

The aim of the present work is to examine the influence of Zn^{2+} on water and ion fluxes, in particular K^+, in detopped maize plants. A comparison between fluxes in intact and detopped plants was taken into considerations.

Materials and methods

Seedlings of *Zea mays* L. cv. White Horse Tooth were grown on nylon mesh suspended on half-strength Long Ashton nutrient solution (Hewitt 1952) to which Zn^{2+} was added at the appropriate concentration, as shown in the results, in a controlled environment growth chamber. The growth chamber was maintained under continuous irradiance of 600 μmol(photon) m^{-2} s^{-1} at the surface of the nutrient solution, 20 °C and relative humidity 90 ± 3 %.

Measurements of rate of exudation: The whole root systems of 12-d old plants were excised leaving about 0.8 cm of the stem. The cut portion of the stem was sealed with wax into suitable plastic tubing. A glass tube was similarly sealed into the other end of the plastic tubing. The exudation medium was aerated and kept at 20 °C in a water bath. Roots excised from plants directly brought from the growth chamber are called light roots while those from plants kept in darkness for 24 h before detopping are called dark roots.

The exudate on the cut end inside the glass tube was removed at regular intervals after root excission with a microsyringe. The exudation rate on root fresh mass basis is expressed as water flux [μl kg^{-1}(root fresh mass) s^{-1}].

The concentration of K^+ was measured by the flame emission spectrophotometry, and Zn^{2+}, Ca^{2+} and Mg^{2+} were measured by atomic absorption spectrophotometry.

K^+ flux through the root was calculated from the water flux and K^+ concentration in the xylem exudate as follow:

$$J_K = J_{H_2O} \cdot C_K$$

where J_{H_2O} is water flux, C_K is K^+ concentration in the exudate [μmol μl^{-1}(exudate)], thus J_K is K flux [μmol kg^{-1}(root fresh mass) s^{-1}].

Results

Zn^{2+} concentration in the medium was without effect on K^+ concentration in the xylem exudate and K^+ concentration was almost unaffected with time after detopping of the plants at all Zn^{2+} concentrations in the medium (Table 1). Zn^{2+} concentration in the exudate was not proportional to its increase in the medium. Also, there was a slight increase in Ca^{2+} and Mg^{2+} concentrations in the exudate with increasing Zn^{2+} in the medium.

Table 1. Ions concentrations [mM] in the xylem exudate of 12-d old detopped maize plants grown and exuded on half-strength Long Ashton nutrient solution containing the appropriate Zn concentration at 20 °C. Each value is the mean of 8 samples (each from one root) ± standard error.

Zn^{2+} conc. in medium [μM]	Time after excision [h]	$[K^+]$	$[Zn^{2+}]$	$[Ca^{2+}]$	$[Mg^{2+}]$
5	0 - 2	32.5 ± 2.6	0.081 ± 0.002	2.10 ± 0.17	1.11 ± 0.09
	2 - 6	28.9 ± 1.2	0.093 ± 0.002	2.02 ± 0.11	1.17 ± 0.05
	6 - 12	29.6 ± 1.2	0.086 ± 0.003	2.03 ± 0.16	1.13 ± 0.06
	12 - 18	33.2 ± 1.2	0.091 ± 0.002	1.99 ± 0.14	1.18 ± 0.06
	18 - 24	34.2 ± 1.4	0.087 ± 0.002	2.06 ± 0.13	1.02 ± 0.04
100	0 - 2	31.9 ± 2.4	0.201 ± 0.011	2.10 ± 0.18	1.21 ± 0.08
	2 - 6	30.5 ± 2.1	0.210 ± 0.012	2.29 ± 0.19	1.19 ± 0.06
	6 - 12	28.9 ± 1.8	0.219 ± 0.011	2.32 ± 0.19	1.26 ± 0.06
	12 - 18	30.2 ± 2.0	0.226 ± 0.010	2.41 ± 0.13	1.30 ± 0.04
	18 - 24	31.3 ± 2.1	0.221 ± 0.013	2.40 ± 0.15	1.32 ± 0.06
500	0 - 2	30.8 ± 1.8	0.361 ± 0.017	2.41 ± 0.16	1.43 ± 0.09
	2 - 6	28.7 ± 1.2	0.426 ± 0.021	2.56 ± 0.19	1.21 ± 0.09
	6 - 12	29.9 ± 1.7	0.389 ± 0.016	2.31 ± 0.19	1.24 ± 0.08
	12 - 18	32.6 ± 1.7	0.411 ± 0.019	2.06 ± 0.11	1.15 ± 0.06
	18 - 24	32.8 ± 2.1	0.398 ± 0.018	2.46 ± 0.13	1.23 ± 0.03
1 000	0 - 2	33.1 ± 2.1	0.584 ± 0.036	2.84 ± 0.14	1.72 ± 0.07
	2 - 6	29.3 ± 1.3	0.526 ± 0.031	2.68 ± 0.14	1.47 ± 0.08
	6 - 12	30.2 ± 1.3	0.468 ± 0.026	2.55 ± 0.17	1.38 ± 0.05
	12 - 18	33.1 ± 2.1	0.472 ± 0.012	2.67 ± 0.16	1.25 ± 0.05
	18 - 24	30.9 ± 2.1	0.429 ± 0.019	2.46 ± 0.19	1.15 ± 0.06

Zn^{2+} at 100 and 500 μM in the medium increased both water and K^+ fluxes whereas 1 000 μM Zn^{2+} inhibited water flux and in turn caused a decrease in K^+ flux (Fig. 1a, b).

In another experiment, the 11-d old maize plants were kept in the dark for 24 h before detopping in order to examine the influence of depletion of energy derived from photosynthesis on the transport of K^+, Ca^{2+} and Mg^{2+} in the detopped plants.

In this experiment, K^+ concentration in the exudate increased at higher Zn^{2+} concentrations (500 and 1 000 μM) in the medium (Table 2). Simultaneously, K^+ concentration decreased in the exudate with time after detopping. Generally, K^+ concentrations in the exudate, in this experiment, were usually less than 50 % of their respective values in the roots of plants without dark pretreatment. The effect of Zn^{2+} on Ca^{2+} concentration in the exudate was almost similar to that on K^+. On the other hand, the concentrations of Zn^{2+} and Mg^{2+} were slightly higher. But whereas Zn^{2+} concentration in the exudate was little increased, Mg^{2+} concentration was slightly decreased with time after detopping.

In dark pretreated roots, water fluxes at higher Zn^{2+} concentrations were lower or similar to that of control roots (Fig. 2a), whereas K^+ fluxes were higher or similar to that of control roots (Fig. 2b).

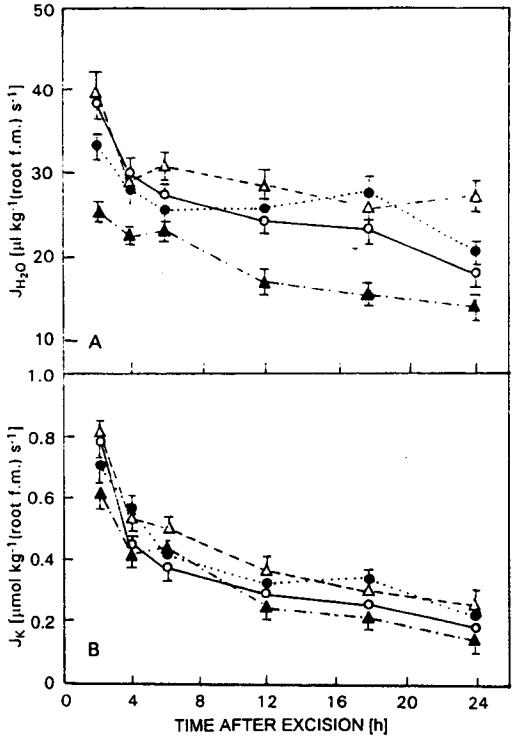

Fig. 1. Changes in water (*A*) and K^+ (*B*) fluxes in maize plants detopped immediately after light period at 20 °C on half strength Long Ashton nutrient solution containing Zn^{2+} at concentrations: 5 (*open circles*), 100 (*closed circles*), 500 (*open triangles*) and 1 000 (*closed triangles*) μM. Each value is the mean of 8 samples. Bars represent standard errors.

K^+ and Ca^{2+} concentrations in the roots before and after exudation and in the cut shoots were decreased whereas that of Zn^{2+} was increased with increasing Zn^{2+} concentration in the medium (Table 3). It seems that the influence of Zn^{2+} on ion transport was different in detopped and intact plants. The fluxes of all ions measured were greater in the roots of detopped plants than that in the roots of intact plants, though the difference was greater at higher Zn^{2+} concentration in the medium (Table 4).

Discussion

Increasing Zn^{2+} concentration in the medium differently influenced the water and K^+ transport in intact and detopped roots of *Zea mays* seedlings. Generally, the exudation volume flux (J_{H_2O}) and K^+ flux (J_K) were decreased with time after detopping and the rate of decrease in both fluxes was almost similar, since the decrease in K^+ flux was mainly due to the decrease in water flux (see Fig. 1 and 2). This decline in water and K^+ fluxes could be attributed to a change in the supply of energy to the root system (Brouwer 1965, Abbas 1981). Pretreatment the seedlings in darkness for 24 h caused about 70 % reduction in J_{H_2O} and J_K. It appears that the effect of darkness on water and K^+ transport was similar to the effect of removing the shoot system (detopping the plants). Similar results were found also in mustard (Abbas 1981).

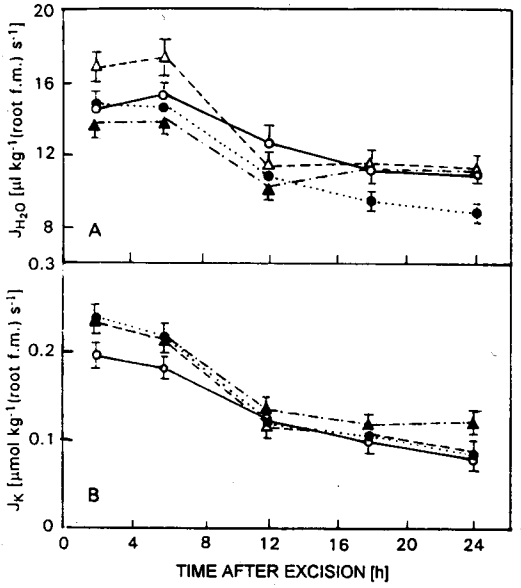

Fig. 2. Changes in water (*A*) and K^+ fluxes (*B*) in maize plants detopped after 24 h period of darkness at 20 °C on half strength Long Ashton nutrient solution containing Zn^{2+} at concentrations 5 (*open circles*), 100 (*closed circles*), 500 (*open triangles*) and 1 000 (*closed triangles*) µM. Each value is the mean of 8 samples. Bars represent standard errors.

Accumulation and transport of Zn^{2+} in roots of detopped plants were greater than in roots of intact ones (see Tables 1, 3 and 4). In consistence with these results, Chaudhry and Loneragan (1972) found that uptake and transport rates of Zn^{2+} were very different in the roots of intact and excised wheat seedlings. The decrease in K^+ and increase in Zn^{2+} concentration in the xylem exudate of dark pretreated roots suggests that Zn^{2+} transport in detopped seedlings is mainly passive.

Table 2. Ions concentrations [mM] in the xylem exudate of 12-d old detopped maize plants which were grown and exuded on half strength Long Ashton nutrient solution containing the appropriate Zn concentration at 20 °C. Plants were pretreated in dark for 24 h before detopping. Each value is the mean of 8 samples (each from one root) ± standard error.

Zn^{2+} conc. in medium [μM]	Time after excision [h]	$[K^+]$	$[Zn^{2+}]$	$[Ca^{2+}]$	$[Mg^{2+}]$
5	0 - 2	13.7 ± 0.9	0.096 ± 0.003	1.98 ± 0.07	1.30 ± 0.00
	2 - 6	12.5 ± 0.9	0.091± 0.003	1.82 ± 0.08	1.23 ± 0.09
	6 - 12	10.6 ± 0.6	0.112 ± 0.005	1.68 ± 0.03	1.18 ± 0.06
	12 - 18	9.9 ± 0.6	0.098 ± 0.002	1.72 ± 0.04	1.16 ± 0.07
	18 - 24	8.6 ± 0.5	0.092 ± 0.003	1.64 ± 0.06	1.19 ± 0.04
100	0 - 2	13.6 ± 0.9	0.198 ± 0.005	2.07 ± 0.09	1.66 ± 0.12
	2 - 6	12.2 ± 0.9	0.214 ± 0.005	2.08 ± 0.04	1.47 ± 0.08
	6 - 12	10.2 ± 0.5	0.247 ± 0.003	1.86 ± 0.07	1.21 ± 0.09
	12 - 18	8.9 ± 0.5	0.258 ± 0.005	1.84 ± 0.04	1.21 ± 0.09
	18 - 24	8.3 ± 0.4	0.237 ± 0.005	1.81 ± 0.04	1.23 ± 0.09
500	0 - 2	15.3 ± 1.2	0.422 ± 0.012	2.01 ± 0.012	1.68 ± 0.10
	2 - 6	13.7 ± 0.8	0.439 ± 0.010	2.00 ± 0.11	1.57 ± 0.09
	6 - 12	11.8 ± 0.6	0.522 ± 0.013	2.08 ± 0.07	1.43 ± 0.10
	12 - 18	10.8 ± 0.8	0.543 ± 0.011	2.08 ± 0.09	1.39 ± 0.08
	18 - 24	9.8 ± 0.6	0.525 ± 0.011	2.07 ± 0.09	1.41 ± 0.08
1 000	0 - 2	16.1 ± 1.2	0.618 ± 0.016	2.32 ± 0.19	1.61 ± 0.12
	2 - 6	15.0 ± 1.3	0.761 ± 0.029	2.40 ± 0.11	1.55 ± 0.07
	6 - 12	12.4 ± 0.5	0.750 ± 0.023	2.15 ± 0.12	1.47 ± 0.09
	12 - 18	10.8 ± 0.7	0.705 ± 0.019	1.92 ± 0.11	1.46 ± 0.09
	18 - 24	10.2 ± 0.4	0.720 ± 0.077	1.82 ± 0.08	1.34 ± 0.07

Table 3. Concentrations of K^+, Zn^{2+} and Ca^{2+} [mmol kg^{-1}(fresh mass)] in exuding roots before and after exudation and in the cut shoots. Each value is the mean of 8 samples. Standard error was usually less than 8 %.

Zn conc. in medium [μM]	Roots before exudation			Roots after exudation			Cut shoots		
	$[K^+]$	$[Zn^{2+}]$	$[Ca^{2+}]$	$[K^+]$	$[Zn^{2+}]$	$[Ca^{2+}]$	$[K^+]$	$[Zn^{2+}]$	$[Ca^{2+}]$
5	121.6	0.28	12.2	114.6	0.24	12.6	199.8	0.16	11.7
100	118.3	0.93	12.9	112.2	0.90	11.9	180.2	0.54	11.4
500	114.8	2.31	9.8	103.8	3.41	8.9	156.6	1.34	11.2
1 000	102.6	3.52	9.6	95.0	4.18	8.4	148.2	1.79	10.6

The decrease in K^+ and Ca^{2+} transport at higher Zn^{2+} concentration in the medium could be attributed to the effect of Zn^{2+} on the cell membranes. Zn^{2+} was found to increase the membrane permeability. Most studies of this type have been concerned

Table 4. Comparison between ion fluxes [mmol kg^{-1}(root fresh mass) s^{-1}] in roots of intact and detopped maize plants. Standard error was usually less than 9 %.

Zn conc. in medium [μM]	J_K detopped	intact	J_{Zn} detopped	intact	J_{Ca} detopped	intact	J_{Mg} detopped	intact
5	3.89	3.82	0.014	0.005	0.24	0.18	0.13	0.13
100	4.02	3.68	0.028	0.011	0.25	0.17	0.15	0.13
500	3.71	1.96	0.063	0.014	0.32	0.13	0.18	0.12
1 000	2.82	1.32	0.065	0.020	0.32	0.11	0.15	0.09

with leakage of K^+ from the root cells. It was observed that the effect on Zn^{2+} upon the leakage of K^+ from cells was greater in non-tolerant than in tolerant plants (Wyn Jones and Sutcliffe 1972, Wainwright and Woolhouse 1977). It could be concluded here that this cultivar of *Zea mays* can tolerate relatively high concentrations of Zn (up to 500 μM) without harmful effect on the growth and ion fluxes.

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