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ORIGINAL ARTICLE

Salt secretion in Rhodes grass (*Chloris gayana* Kunth) under conditions of excess magnesium

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Abstract

Rhodes grass (*Chloris gayana* Kunth) is known to be a salt-tolerant grass, and its tolerance is related to the presence of salt glands that secrete excess salts transported into the leaves. The salt glands of Rhodes grass reportedly have a high ability to secrete Na^+, but their ability to secrete Mg^{2+} remains unclear. In the present study, we examined salt secretion via the salt glands under conditions of excess Mg^{2+} using both whole plants and detached leaves of Rhodes grass. $MgCl_2$ treatment significantly increased Mg^{2+} secretion, but the extent of secretion remained relatively minor. $MgCl_2$ treatment significantly increased K^+ secretion, and the increase in K^+ secretion was more than 50-fold higher than the increase in Mg^{2+} secretion. The increase in K^+ secretion caused by $MgCl_2$ treatment was inhibited by the application of ion transport inhibitors. Inhibition of K^+ secretion amplified the increase in leaf sap osmolality caused by $MgCl_2$ treatment. These results indicate that: (1) salt glands of Rhodes grass have a low ability to secrete Mg^{2+}, (2) salt glands of Rhodes grass substitute K^+ secretion for Mg^{2+} secretion under conditions of excess Mg^{2+}, (3) substitutive K^+ secretion may play a role in the alleviation of osmotic changes caused by Mg^{2+} accumulation.

Key words: Chloridoideae, glandular trichome, magnesium, potassium, salt excretion.

INTRODUCTION

Rhodes grass (*Chloris gayana* Kunth), which belongs to the subfamily Chloridoideae, is a popular and widespread fodder and is used as a pasture plant and for hay production in many parts of the world. Rhodes grass is considered to be a particularly useful crop in saline areas because of its salt tolerance (Masters *et al.* 2001; Suttie 2000). The salt tolerance of Rhodes grass is related to a special organ called the "salt gland", which is located on the leaves and secretes excess salts transported into the leaves (Liphschitz *et al.* 1974; Liphschitz and Waisel 1982).

Salt glands are found in a variety of both monocotyledous and dicotyledonous plant species. Among the monocotyledons, active salt glands are mainly found in the subfamily Chloridoideae (Amarasinghe and Watson 1989; Liphschitz and Waisel 1982), and one of the features of salt secretion via the salt glands of the Chloridoideae is the phenomenon of cation selectivity. A preference for sodium over potassium secretion has been observed in many Chloridoideae plants, including Rhodes grass (Bhatti and Sarwar 1993; Kobayashi *et al.* 2007; Pollak and Waisel 1970; Rozema *et al.* 1981). Calcium secretion has also been examined in various Chloridoideae plants; these plants are less able to secrete Ca^{2+} than K^+ (Pollak and Waisel 1970; Rozema *et al.* 1981). However, the magnesium secreting ability of Chloridoideae plants remains unclear.

Magnesium, like potassium and calcium, is an important macronutrient for plants. It is also the second major cation in seawater (approximately 50 mmol L^{-1}), and its concentration in soils and groundwater is greatly increased by seawater intrusion. For example, seawater intrusion increases the concentration of Mg^{2+} in the saturation extracts of soils to 20 mmol L^{-1} and that in well water to 16 mmol L^{-1} (Ammal *et al.* 1999; Wu 1981). Our previous work has shown that concentrations of 25 mmol L^{-1} Mg^{2+} in culture solutions inhibited the growth of Rhodes grass by 50% (Kobayashi *et al.* 2004). Therefore, the concentration of Mg^{2+} in fields suffering seawater intrusion can become sufficiently high to affect the growth of Rhodes grass.

In the present study, we treated Rhodes grass with an excess of Mg^{2+} to quantify the ability of the salt glands

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to secrete Mg^{2+}. During the course of our experiments, we noted that excess Mg^{2+} treatment greatly increased K^+ secretion, so we also investigated this phenomenon in detail.

MATERIALS AND METHODS

Whole plant experiments

The cultivation of Rhodes grass (*Chloris gayana* Kunth cv. Asatsuyu) was conducted in a growth cabinet with an air temperature of 25°C during the day and 20°C at night and a 14 h day/10 h night cycle. Light was provided from high-pressure sodium vapor lamps and metal halide lamps at 480 μmol m^{-2} s^{-1} at plant height.

Seeds were germinated on 0.4% agar plates containing one-fifth strength Hoagland's solution (Hoagland and Arnon 1950). Fourteen days after sowing, four seedlings were transplanted into a pot (159 mm diameter, 190 mm depth) containing 3.6 L of one-third strength Hoagland's solution supplemented with 40 μmol L^{-1} Fe-ethylenediaminetetraacetic acid (EDTA) and 500 μmol L^{-1} Na_2SiO_3. The solution pH was measured daily and maintained at 5.4 by the addition of either 1 mol L^{-1} HCl or 1 mol L^{-1} NaOH. The solution was completely aerated and replaced at 8 days and 15 days after transplantation.

At 8 days after transplantation, the plants were thinned to two plants per pot and treatment commenced. The experiment consisted of a control and a $MgCl_2$ treatment (50 mmol L^{-1}), with three replicates of each.

Twenty days after transplantation the shoots were carefully excised and immediately placed in 50 mL of distilled water in a test tube and then shaken for 10 s. Subsequently, the shoots were removed, dried at 60°C for 72 h and weighed. The solution was frozen and stored for subsequent ion analysis.

Detached leaf experiments

For the detached leaf experiments, Rhodes grass was cultivated as above, but without the $MgCl_2$ treatment and the experiments were conducted at 14 days after transplantation. The youngest of the fully expanded leaves on the main stem was used in these experiments. Before commencing the experiment, the leaf surface was wiped with a cotton swab wetted with distilled water to remove any previously secreted salts. The leaf blades were detached and the cut ends were immersed in 12 mL of treatment solution in a glass test tube (15 mm diameter, 90 mm length). The test tube was sealed with Parafilm and the leaf blades were inserted through a slit that was cut in the film. Approximately 90% of each leaf blade was freely exposed to the atmosphere. Twenty-four hour incubation under constant light conditions (480 μmol m^{-2} s^{-1} at plant height) increased the dry weight of the leaf blades twofold compared with the weight before the incubation (data not shown). Therefore, the leaf blades were incubated under constant dark conditions for 24 h. Incubation was started approximately 1 h after transition to the night condition. The temperature was maintained at 25°C and the relative humidity at 60–70%.

We conducted four experiments using detached leaves: a dose–response experiment, an inhibitor application experiment, an Mg-salt comparison experiment and an osmolality experiment. In the dose–response experiment, the leaf blades were immersed in 0, 20, 40, 60 and 80 mmol L^{-1} $MgCl_2$ solution. In the inhibitor application experiment, the leaf blades were immersed in 40 mmol L^{-1} $MgCl_2$ solution containing the ion transport inhibitors. The ion transport inhibitors were: $BaCl_2$ (an inhibitor of various cation channels and transporters), ouabain (an inhibitor of Na^+-K^+-ATPase in animal cells), tetraethylammonium chloride (TEA, an inhibitor of the K^+ channel) and verapamil (an inhibitor of the K^+ channel and Ca^{2+} channel). All inhibitors were purchased from Wako Pure Chemical Industries, Osaka, Japan. The concentrations of the inhibitors were: $BaCl_2$ at 4 mmol L^{-1}, ouabain at 4 mmol L^{-1}, TEA at 18 mmol L^{-1} and verapamil at 3 mmol L^{-1}. In our previous report, all inhibitors at these concentrations significantly inhibited Na^+ secretion under NaCl treatment (Kobayashi *et al.* 2007). The application of inhibitors at higher concentrations caused damage to the leaf blades, such as necrosis and chlorosis. In the Mg-salt comparison experiment, the leaf blades were immersed in 40 mmol L^{-1} $MgCl_2$ or $Mg(NO_3)_2$ solution. In the osmolality experiment, the leaf blades were immersed in 0, 20 and 40 mmol L^{-1} $MgCl_2$ solutions with or without 3 mmol L^{-1} verapamil. In all experiments using detached leaves, a distilled water treatment (0 mmol L^{-1} Mg-salt) was used as a control.

After 24 h incubation, the part of the leaf blade that was freely exposed to the atmosphere was carefully excised and immediately placed in 10 mL of distilled water in a test tube and then shaken for 10 s. The solution was frozen and stored for subsequent ion analysis. In all experiments other than the osmolality experiment, the leaf blades were dried at 60°C for 72 h and weighed. In the osmolality experiment, the leaf blades were blotted dry and weighed and immediately placed in a microcentrifuge tube and frozen in liquid nitrogen. To obtain enough leaf sap to determine the osmolality, two leaves were treated as one replicate.

Ion analysis

To determine the cation concentrations in the plant tissue, dried and ground samples were ashed for 7 h at 450°C, dissolved in 4 mol L^{-1} HNO_3, and subsequently

diluted with distilled water. The cation concentrations in the secreted salts and plant tissue were determined with an atomic absorption flame emission spectrophotometer (AA-6200, Shimadzu Corporation, Kyoto, Japan). For the determination of Cl^- and NO_3^- concentrations in plant tissue, dried and ground samples were extracted with distilled water for 1 h at room temperature. The Cl^- and NO_3^- concentrations in the secreted salts and plant tissue were determined using ion chromatography as previously reported (Kobayashi *et al.* 2005).

Leaf sap osmolality analysis

Tubes containing the leaf blades were thawed and centrifuged at 1.3×10^4 *g* for 25 min at 4°C to extract the leaf sap. The osmolality of the leaf sap was measured using a Wescor vapor pressure osmometer 5500 (Wescor, Logan, UT, USA).

Statistical analysis

Statistical analysis was carried out using the statistical computer software package JMP (4.0.5 J, SAS Institute, Cary, NC, USA). Before making comparisons among treatments the homogeneity of variance was checked, and logarithmic transformations were carried out if required. Data were compared using *t*-test in the whole plant experiment, using Tukey's test in the dose–response experiment and Mg-salt comparison experiment, and using Dunnett's test in the inhibitor application experiment. In these experiments the significance was set at $P < 0.05$. In the osmolality experiment, a simple regression was used to assess the relationship between $MgCl_2$ concentration in the treatment solution and leaf sap osmolality. Differences in regression coefficients for the regression lines obtained from the data with and without (the control) the application of verapamil were determined by testing the *t*-value.

RESULTS

In the whole plant experiments, $MgCl_2$ treatment for 12 days significantly increased the amounts of secreted Mg^{2+} and Cl^-, but the increase in secreted Mg^{2+} was minor (Table 1). The amount of secreted Mg^{2+} increased by 6 μmol g^{-1} dry weight (DW) in the $MgCl_2$ treatment, whereas the amount of retained Mg^{2+} in the shoots (the Mg^{2+} concentration in the shoots) increased by 367 μmol g^{-1} DW. In addition, the increase in the amount of secreted Mg^{2+} was only 2% of that of secreted Cl^-.

The $MgCl_2$ treatment had significant effects on the amount of other ions secreted and retained (Table 1). The $MgCl_2$ treatment significantly increased the amount of secreted K^+; the increase in the amount of secreted K^+ was 58-fold greater than that of secreted Mg^{2+}. The $MgCl_2$ treatment significantly decreased the amount of retained K^+ in the shoots, and there was no significant difference in the sum of secreted and retained K^+ between the treatments. The $MgCl_2$ treatment significantly decreased the amount of retained Na^+ and Ca^{2+} in the shoots, but had no significant effect on the amount of secreted Na^+ and Ca^{2+}. The $MgCl_2$ treatment decreased shoot dry weight to 45% of that in the control.

Table 1 Amount of ions secreted from and retained in the shoots of Rhodes grass, and the shoot dry weight after 12 days of treatment in the whole plant experiments

		Control	Mg 50 mmol L^{-1}
		(μmol g^{-1} DW)	
Mg^{2+}	Secreted	0.6 ± 0.1	6.6 ± 0.8*
	Retained	73 ± 3	440 ± 9*
	Secreted + retained	73 ± 3	446 ± 10*
Cl^-	Secreted	36 ± 2	332 ± 27*
	Retained	244 ± 30	483 ± 45*
	Secreted + retained	280 ± 31	815 ± 18*
K^+	Secreted	265 ± 54	613 ± 46*
	Retained	1,388 ± 62	929 ± 43*
	Secreted + retained	1,653 ± 112	1,541 ± 8
Na^+	Secreted	106 ± 3	88 ± 6
	Retained	114 ± 8	34 ± 3*
Ca^{2+}	Secreted	1.5 ± 0.1	1.1 ± 0.1
	Retained	77 ± 1	25 ± 1*
		(g pot^{-1})	
Shoot dry weight		2.6 ± 0.2	1.2 ± 0.1*

Data are mean ± standard error of three samples. *$P < 0.05$ (significantly different from the control using a *t*-test). DW, dry weight.

To examine in detail ion secretion under conditions of excess $MgCl_2$, detached leaves were treated with $MgCl_2$ solution (Fig. 1). The secretion of Mg^{2+} significantly increased with increasing concentrations of $MgCl_2$ in the treatment solution, but it was still lower than that of Na^+ and K^+, even at the highest $MgCl_2$ concentration examined (Fig. 1A). In contrast, Mg^{2+} concentration in the leaves increased markedly with increasing concentration of $MgCl_2$ in the treatment solution, and ultimately became higher than Na^+ and K^+ concentrations in the leaves (Fig. 1B).

In the same way as for the whole plant experiments, $MgCl_2$ treatment significantly increased the secretion of K^+ from the detached leaves (Fig. 1A). The secretion of K^+ increased until a concentration of 40 mmol L^{-1} of $MgCl_2$ was reached in the treatment solution, and it then leveled off above 40 mmol L^{-1}. The increase in K^+ secretion elicited by the $MgCl_2$ treatment was far greater than the increase in Mg^{2+} secretion; for example, the increase in K^+ secretion elicited by the 80 mmol L^{-1} $MgCl_2$ treatment was approximately 85-fold greater

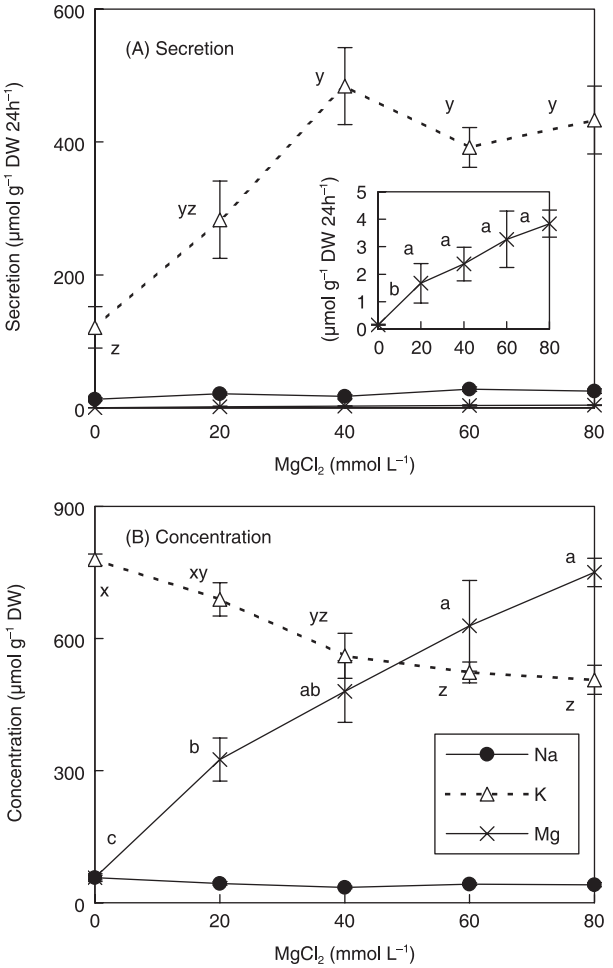

Figure 1 (A) Secretion and (B) concentration of Na^+, K^+ and Mg^{2+} in response to $MgCl_2$ treatment of detached leaves. The inset details the Mg^{2+} secretion. Data are mean ± standard error of four samples. Data followed by the same letters are not significantly different ($P < 0.05$) according to Tukey's test. DW, dry weight.

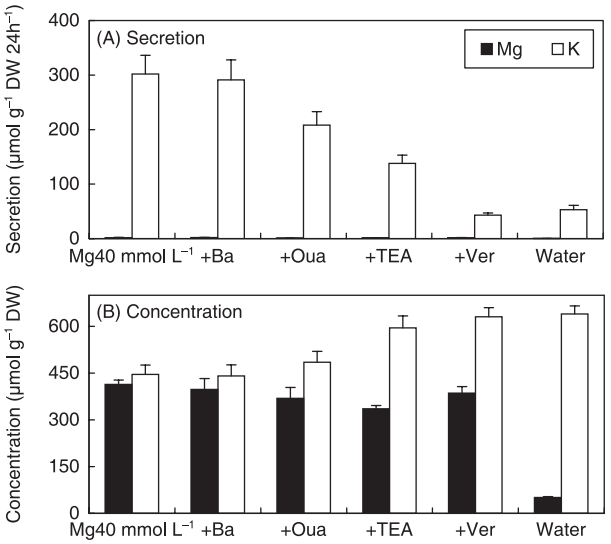

Figure 2 Effects of the inhibitors on the (A) secretion and (B) concentration of K^+ and Mg^{2+} in the $MgCl_2$ treatment with detached leaves. Data are mean ± standard error of eight samples. DW, dry weight; Oua, ouabain; TEA, tetraetylammonium chloride; Ver, verapamil; Water, distilled water treatment ($MgCl_2$ 0 mmol L^{-1}).

Table 2 Statistical comparison in the inhibitor application experiment

	Mg^{2+}		K^+	
	Secr.	Conc.	Secr.	Conc.
Control: $MgCl_2$ 40 mmol L^{-1}				
+$BaCl_2$	ns	ns	ns	ns
+Ouabain	ns	ns	*	ns
+TEA	ns	ns	*	*
+Verapamil	ns	ns	*	*
Control: Water ($MgCl_2$ 0 mmol L^{-1})				
+$BaCl_2$	*	*	*	*
+Ouabain	*	*	*	*
+TEA	*	*	*	ns
+Verapamil	*	*	ns	ns

*$P < 0.05$ (significantly different from the control [$MgCl_2$ 40 mmol L^{-1} or water treatment] using a Dunnett's test). ns, not significant; TEA, tetraethylammonium chloride.

than the increase in Mg^{2+} secretion. The concentration of K^+ in the leaves decreased with increasing concentrations of $MgCl_2$ in the treatment solution (Fig. 1B). The secretion and concentration of Na^+ were not significantly different among the treatments.

To examine whether the increase in K^+ secretion in the $MgCl_2$ treatment was the result of K^+ leakage from damaged cells, we applied various inhibitors of the proteins that transport ions across the plasma membrane (Fig. 2). $MgCl_2$ treatment without any inhibitors significantly increased Mg^{2+} concentration and the secretion of Mg^{2+} and K^+ ions, and significantly decreased the K^+ concentration when compared with the water treatment ($P < 0.001$, *t*-test). Although the application of $BaCl_2$ to the $MgCl_2$ solution did not have significant effects on K^+ secretion, the application of ouabain, TEA and verapamil significantly decreased K^+ secretion (Fig. 2, Table 2). In particular, the inhibition of K^+ secretion by verapamil was so severe that the levels of K^+ secretion and K^+ concentration were similar to those in the water treatment. None of the inhibitors examined had significant effects on the secretion and concentration of Mg^{2+} in the $MgCl_2$ treatment, and these parameters were, therefore, significantly greater than those in the water treatment (Fig. 2, Table 2).

To examine the effects of coexisting anions on the secretion of Mg^{2+} and K^+, we compared the ion secretion

Table 3 Secretion and concentration of ions in the Mg-salt comparison experiment

	Water	$MgCl_2$	$Mg(NO_3)_2$
Secretion (μmol g^{-1} DW 24 h^{-1})			
Mg^{2+}	0.2 ± 0.1 b	2.7 ± 0.7 a	2.7 ± 0.9 a
K^+	79 ± 13 b	244 ± 37 a	220 ± 20 a
Cl^-	7 ± 1 c	205 ± 28 a	16 ± 2 b
NO_3^-	n.d.	n.d.	100 ± 25
Concentration (μmol g^{-1} DW)			
Mg^{2+}	67 ± 4 b	433 ± 23 a	453 ± 21 a
K^+	546 ± 12 a	421 ± 23 b	423 ± 24 b
Cl^-	161 ± 18 b	826 ± 44 a	170 ± 14 b
NO_3^-	228 ± 29 b	186 ± 36 b	1,050 ± 86 a

Salts were applied at 40 mmol L^{-1}. Data are mean ± standard error of five samples. Data followed by the same letters within rows are not significantly different according to Tukey's test ($P < 0.05$). n.d., not detected (less than 5 μmol g^{-1} dry weight [DW] 24 h^{-1}).

between the $MgCl_2$ and $Mg(NO_3)_2$ treatments (Table 3). The $MgCl_2$ treatment increased the secretion and concentration of Cl^-, which became far greater than those of NO_3^-. The $Mg(NO_3)_2$ treatment increased the secretion and concentration of NO_3^-, which became far greater than those of Cl^-. Both Mg-salt treatments significantly increased both the Mg^{2+} concentration in the leaves and the secretion of Mg^{2+} and K^+. These treatments also both significantly decreased K^+ concentration. However, the secretion and concentration of Mg^{2+} and K^+ did not differ between the $MgCl_2$ and $Mg(NO_3)_2$ treatments.

To examine the effects of K^+ secretion under conditions of excess Mg^{2+} on the leaf osmolality, we measured leaf sap osmolality when K^+ secretion was inhibited (Fig. 3). As expected, the application of verapamil almost completely inhibited the increase in K^+ secretion in the $MgCl_2$ treatment (Fig. 3A). Strong positive correlations were found between the $MgCl_2$ concentrations in the treatment solution and leaf sap osmolality (Fig. 3B). The regression lines using leaf sap osmolality as the response variable (y) and $MgCl_2$ concentration in the treatment solution as the independent variable (x) were $y = 6.615x + 519.4$ ($R^2 = 0.858$, $P < 0.001$) and $y = 3.985x + 474.1$ ($R^2 = 0.829$, $P < 0.001$) for the treatments with and without the application of verapamil, respectively. The regression coefficient for the regression line with the application of verapamil was significantly higher than that without the application of verapamil ($t = 2.92$, $P < 0.01$).

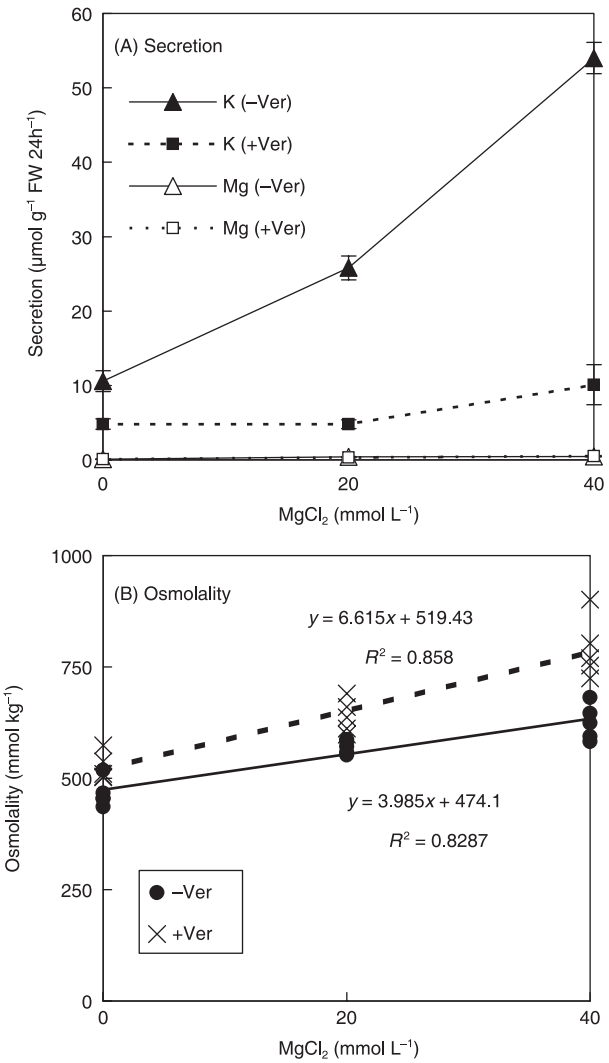

Figure 3 (A) Secretion of K^+ and Mg^{2+} and (B) leaf sap osmolality in the $MgCl_2$ treatment with (+Ver) or without verapamil (–Ver). For the secretion results (A) the data points are mean ± standard error of five samples. For the osmolality results (B) each dot represents one sample. Each sample contains two leaves. "Secretion" in this experiment is expressed on a fresh weight (FW) basis.

DISCUSSION

In both the whole plant experiments and the detached leaf experiments, the extent of Mg^{2+} secretion via the salt glands of Rhodes grass was relatively minor, even in the $MgCl_2$ treatments (Table 1, Fig. 1). When the ratio of secreted to retained Mg^{2+} in the whole plant experiments was calculated, the ratio was 0.015 in the 50 mmol L^{-1} $MgCl_2$ treatment. This ratio was much smaller than the equivalent ratio for Na^+ in the 50 mmol L^{-1} NaCl treatment (0.873) and for K^+ in the 50 mmol L^{-1} KCl treatment (0.360) in our previous work (Kobayashi *et al.* 2007). These results indicate that the salt glands in Rhodes grass have only a limited ability to secrete Mg^{2+}.

Interestingly, the $MgCl_2$ treatment significantly increased K^+ secretion, and the increase in K^+ secretion

was far greater than that for Mg^{2+} secretion (Table 1, Fig. 1A). As the $MgCl_2$ treatment also significantly decreased K^+ concentration in the leaves (Table 1, Fig. 1B), the increase in K^+ secretion must have been caused by changes in the secretion process, and not by changes in the uptake or translocation processes.

It could be argued that the increase in K^+ secretion by the $MgCl_2$ treatment observed in the present study was not a physiological reaction, but rather was the result of ion leakage from damaged cells. To examine this possibility, we applied inhibitors of ion transport proteins to detached leaves. The increase in K^+ secretion in the $MgCl_2$ treatment was inhibited by ouabain, TEA and verapamil, but not by $BaCl_2$ (Fig. 2). These results are in agreement with the results for K^+ secretion in the KCl treatment (Kobayashi *et al*. 2007). In addition, none of the inhibitors examined had significant effects on the secretion and concentration of Mg^{2+} (Fig. 2, Table 2). These results indicate that the ion transport inhibitors inhibited K^+ secretion, but not Mg^{2+} uptake. Therefore, the increase in K^+ secretion with $MgCl_2$ treatment does appear to represent a physiological reaction via the ion transport proteins, and is not simply the result of ion leakage from damaged cells.

The phenomenon whereby treatment with a particular ion greatly increases the secretion of other ions has not, to our knowledge, been reported before in any plant species. Boon and Allaway (1986) examined the effect of treating detached leaves of *Avicennia marina*, a dicotyledonous plant, with 1 mol L^{-1} $MgCl_2$; they observed an increase in Mg^{2+} secretion and a decrease in Na^+ and K^+ secretion. In the Chloridoideae plants, *Aeluropus litoralis* and *Leptochloa fusca*, a slight increase in Na^+ and K^+ secretion following $CaCl_2$ treatment has been reported, but the increases were too small to affect Na^+ and K^+ concentrations in the leaves (Pollak and Waisel 1970; Wieneke *et al*. 1987). Further research will be needed to examine whether the large increase in K^+ secretion observed in the present study is a unique phenomenon arising under excess Mg^{2+} conditions, and whether it is a common phenomenon among Chloridoideae plants.

The phenomenon whereby $MgCl_2$ treatment greatly increases K^+ secretion can be explained by differences in the ability to secrete Mg^{2+} and K^+ in Rhodes grass. As previously indicated, the ability of Rhodes grass to secrete Mg^{2+} is far lower than for Na^+ or K^+. In addition, there is plenty of K^+ in the leaves of Rhodes grass (Table 1, Fig. 1B). Therefore, when Rhodes grass grows under conditions of excess $MgCl_2$, it may substitute K^+ secretion for Mg^{2+} secretion because K^+ is preferentially secreted and is abundant in the leaves.

It remains unclear why K^+ is secreted in place of Mg^{2+} under conditions of excess $MgCl_2$. One possible reason is the avoidance of Cl^- accumulation in the leaves. Hill and Hill (1973) have suggested that transport of Cl^- is the active process and that cations are transported as counter ions for Cl^- secretion in the salt glands of *Limonium*, a dicotyledonous plant. However, in our experiment, an increase in K^+ secretion was observed under the $Mg(NO_3)_2$ treatment as well as under the $MgCl_2$ treatment (Table 3). Therefore, substitutive K^+ secretion under excess Mg^{2+} conditions does not appear to be a response to increasing Cl^- secretion in Rhodes grass.

A further possibility is that K^+ secretion alleviates the osmotic changes caused by excess Mg^{2+} treatment. Marcum (2006) has indicated that leaf sap osmolality under saline conditions is negatively correlated with salt tolerance within the subfamily Chloridoideae, and osmotic adjustment under salinity stress is minimized in salt-tolerant grasses. In the present study, the response of leaf sap osmolality to $MgCl_2$ concentration in the treatment solution was significantly greater in the presence of verapamil, an inhibitor that almost completely inhibited K^+ secretion (Fig. 3). These results indicate that the increase in osmolality caused by the $MgCl_2$ treatment becomes more pronounced in the absence of K^+ secretion. Therefore, K^+ secretion appears to play a role in the alleviation of osmotic changes caused by Mg^{2+} accumulation in the leaves.

In conclusion, our results show that the ability of salt glands in Rhodes grass to secrete Mg^{2+} is relatively minor. When Rhodes grass grows in conditions of excess Mg^{2+}, K^+ is secreted in place of Mg^{2+} because of a physiological preference towards K^+, and because of the abundance of K^+ in the leaves. The substitutive K^+ secretion under conditions of excess Mg^{2+} may play a role in the alleviation of osmotic changes caused by Mg^{2+} accumulation.

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