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JOURNAL OF PLANT NUTRITION, 19(3&4), 469–480 (1996)

INFLUENCE OF POTASSIUM:RUBIDIUM RATIOS ON THE XYLEMATIC TRANSPORT OF SOLUTES IN CUCUMBER PLANTS GROWN WITH NITRATE PLUS AMMONIUM

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***ABSTRACT*:** The influence of three potassium:rubidium (K:Rb) ratios (6:0, 5:1, and 4:2) on the xylematic transport of solutes in cucumber plants cv. Medusa supplied with both nitrate (NO_3^-) (60%) and ammonium (NH_4^+) (40%) was studied in greenhouse conditions. In the xylem sap of plants grown with a K:Rb ratio of 4:2, there was an increase in the transport of NO_3^-, phosphate ($H_2PO_4^-$), calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^+), manganese (Mn) and boron (B) while that of organic-N, organic-P, K^+, zinc (Zn), organic acids, and carbohydrates decreased, if compared with the sap of the plants supplied with K alone. The translocation of NO_3^-, $H_2PO_4^-$, Ca^{2+}, Mg^{2+}, and Mn was enhanced and that of K^+ and organic acids decreased when the plants were supplied with a K:Rb ratio of 5:1. The K:Rb ratio detected in the xylem sap was the same K:Rb ratio as in the solutions. However, in the cucumber plant substituting 33% of total K by Rb resulted in an alteration in the transport of solutes, probably due to a competition between Rb and K rather than between the latter two and NH_4^+.

INTRODUCTION

One of the most interesting challenges of plant nutrition nowadays is the research into ionic interactions that occur when the plants are supplied with both

NO_3^- and NH_4^+ as N sources. Plants grown with NH_4^+ are often lower in Ca, Mg, and K than those grown on NO_3^- (1,2,3). This is attributed to the competitive interaction between NH_4^+ and the cationic nutrients in the absorption process (4). The decrease, however, in the accumulation of divalent cations by NH_4^+ is greater than that of K (1). Some researchers (2,5,6,7) have reported that the NH_4^+ supply depresses K accumulation in plants, whereas others found that adding NH_4^+ had little or no effect on K accumulation (8,9). As regards the uptake of K, the response or lack of response to NH_4^+ supply has been used as an indicator for NH_4^+ tolerance by the crop (4,8).

Ion competition occurs between ions with similar physico-chemical properties (valency and ion diameter). The sizes of Rb^+, K^+, and NH_4^+ ions are almost the same when hydrated (10). Therefore, Rb^+ has been used as a tool for the study of K^+ uptake, transport, and accumulation (11). The competition between K^+ and NH_4^+ is difficult to explain with the competition alone for binding sites at the plasma membrane. Ammonium is quite effective in competing with K, while the opposite was not observed (12).

The cucumber plant has been classified as a typical plant preferring NO_3^-(6). However, the growth of this crop was enhanced by using solutions containing more or less similar amounts of NH_4^+ and NO_3^- (13,14). The aim of this study was to examine the influence of three K:Rb ratios on the xylematic transport of solutes in cucumber plants grown with both NO_3^- and NH_4^+ in order to learn more about the competition between NH_4/K, NH_4/Rb and K/Rb.

MATERIALS AND METHODS

Seeds of cucumber (*Cucumis sativus* L. cv. Medusa) were germinated on washed sand for 25 days. Afterwards, the seedlings were transferred to plastic pots containing 10 kg of white quartz sand. The plants were grown in a greenhouse equipped with an artificial lighting system. The internal temperature ranged from 20 to 28°C in daytime and from 10 to 15°C at night. Relative humidity was kept at between 65 and 80%. Daily irradiance was 250 W m^{-2}.

Three nutrient solutions were prepared with an NO_3^-:NH_4^+ ratio of 60:40 and different K:Rb ratios (6:0, 5:1, and 4:2). The composition of the 6:0 solution was as follows (meq mL^{-1}): 9 $Ca(NO_3)_2$; 6 NH_4HCO_3; 2 KH_4PO_4; 2 KCl; 2 K_2SO_4; 2.5 $MgSO_4$; 2 $CaCl_2$ and 0.2 NaCl. The 5:1 solution had the following composition: 9 $Ca(NO_3)_2$; 6 NH_4HCO_3; 2 KH_2PO_4; 2.5 $MgSO_4$; 2 K_2O_4; 1 KCl; 2 $CaCl_2$; 1 RbCl and 0.2 NaCl. The 4:2 solution consisted of 9 $Ca(NO_3)_2$; 6 NH_4HCO_3; 2 KH_2PO_4; 2.5 $MgSO_4$; 2 K_2SO_4; 2 $CaCl_2$; 2 RbCl and 0.2 NaCl. The micronutrients were supplied as (µg element mL^{-1}): 2.5 EDDHA; 0.1 $ZnSO_4 .7H_2O$; 0.1 $CuSO_4 .5H_2O$; 0.5 $MnSO_4 .H_2O$; 0.5 H_3BO_3 and 0.05 $(NH_4)_6Mo_7O_{24} .4H_2O$. The pH was adjusted to 6.0. The nutrient solutions were changed completely twice a week. Distilled water was added to maintain the initial volume between changes.

The experimental design was a completely randomized system with three replications per K:Rb ratio (6:0; 5:1 and 4:2). The tops of the 77-day-old plants were removed four hours after the beginning of the light period. Bleeding sap was collected for two hours after discarding the first drops. The samples were stored in ice until they could be transferred to a freezer (-18°C) for storage. The bleeding sap was analyzed as follows: NO_3^--N, NH_4^+-N, $H_2PO_4^-$-P, organic-P, organic-N and B by means of a Technicon AutoAnalyzer; K, Na, and Rb by flame emission spectrophotometry; Ca, Mg, Fe, Mn, Cu, and Zn by atomic absorption spectrophotometry; Cl^- with a chloride electrode and $SO_4^=$-S turbidimetrically.

The sugars in the xylem sap were analysed by HPLC with a system that consisted of a Beckman 110 pump with a Beckman refractive index detector. A Beckman µ-Spherogel carbohydrate column was used, heated to 90°C with milli-Q water delivered at 0.5 mL min^{-1}. The sample size was 20 µL and sugars were identified by comparison to retention times of standards. A computer provided with Beckman System Gold (7.0) software was used for quantitation. Organic acids were analysed by HPLC (a Beckman intelligent pump equipped with photodiode array detector) with a Beckman ODS Ultrasphere column using formic acid 0.02% (v/v) as the mobile phase. Elution was performed at a flow rate of 0.3 mL min^{-1}. Detection was achieved at 210 nm. The UV spectra of the different acids in the samples and standards were recorded with a photodiode detector, quantitation was carried out the same as for sugars. In the xylem sap all determinations were done in duplicate.

Mean separation was done by variance analysis followed by a test for the least significant difference (LSD) with a probability of 0.05.

RESULTS AND DISCUSSION

The concentrations of N fractions in the xylem sap of cucumber plants influenced by the K:Rb ratio are given in Table 1. Irrespective of the K:Rb ratio assayed, no significant changes in NH_4^+-N and total N levels were detected. The xylem sap of plants grown with the 5:1 ratio transported more NO_3^--N (21%) and inorganic-N (18%) than those grown with K alone. By contrast, the supply of a K:Rb ratio of 4:2 produced a decrease of organic-N (12%), and although an increase of inorganic-N translocation (11%) was observed, the total N transport remained equal to that of the control treatment (6:0). This decrease in the transport of organic-N and the growing tendency towards of free NH_4^+ translocation indicates that the root of plants grown with 4:2 K:Rb ratio has a lower capacity for NH_4^+ detoxification or for NO_3^- reduction than the others. High levels of Rb affect root growth (15), and this may be responsible for the lower metabolic activity of this organ, since lower sugar translocation was detected in plants supplied with Rb (16).

Organic-N was clearly the predominant N fraction detected in the xylem sap of the cucumber plant. It reached about 61%, 63%, and 55% of the total transported N in the 6:0, 5:1 and 4:2 treatments, respectively. Several researchers (1,3) have reported that the presence of both NO_3^- and NH_4^+ in the nutrient medium stimulated glutamic acid formation in the root. This acid plays a key role in the synthesis of other amino acids and amino compounds. The high levels of organic-N transported by the xylem sap of this cultivar, in the first place, indicate high NR activity of its root and, secondly, a high capacity for NH_4^+ detoxification. Both facts are responsible for the NH_4^+ tolerance shown by this cultivar. In a previous study (17), it was found

TABLE 1. Concentrations of N-fractions (meq L^{-1}) in the xylem sap influenced by the K:Rb ratio.

	K:Rb ratios			
N-fractions	**6:0**	**5:1**	**4:2**	**$LSD_{p=0.05}$**
NO_3^--N	11.2	13.5	12.3	0.9
NH_4^+-N	2.2	2.3	2.8	n.s.
Inorganic-N	13.4	15.8	15.1	1.4
Organic-N	21.4	21.7	18.8	2.4
Total-N	35.0	37.5	33.9	n.s.

that 'Hyclos' cucumber plants transported only 35% of the total N in its organic form, which points to a lower genetic ability for N assimilation by the root of this cultivar.

The phosphorus fractions, Cl^-, and $SO_4^=$-S concentrations in the xylem sap of the cucumber plant influenced by the K:Rb ratio are given in Table 2. Phosphate translocation was enhanced as K supply decreased. It was 41% in the 5:1 ratio and 88% in the 4:2 ratio in comparison with the 6:0 treatment. On the other hand, organic-P tended to decrease. This, however, was significant only in the 4:2 treatment. Irrespective of the K:Rb ratio assayed, there were no differences in the total P transported through the xylem sap. As a result, the amount of phosphate increased at the expense of the organic fraction (18).

The contribution of organic-P, however, to total P was 65%, 55% and 44% in the 6:0, 5:1 and 4:2 treatments, respectively. The Hyclos cultivar grown with NO_3^-:NH_4^+ of 60:40 (17) produced a similar percentage. The different K:Rb ratios did not vary in Cl^- concentrations, whereas the $SO_4^=$-S levels were lower in plants grown with both K and Rb than in those grown with K alone.

The cation results in the xylem sap of cucumber plants grown with different K:Rb ratios are summarized in Table 3. Potassium translocation was reduced in the

TABLE 2. Concentrations of P-fractions, Cl^- and $SO_4^=$-S (meq L^{-1}) in the xylem sap influenced by the K:Rb ratio.

	K:Rb ratios			
N-fractions	**6:0**	**5:1**	**4:2**	**$LSD_{p=0.05}$**
$H_2PO_4^-$-P	1.7	2.4	3.2	0.5
Organic-P	3.2	2.9	2.5	0.6
Total-P	4.9	5.3	5.7	n.s.
Cl^-	4.4	3.9	3.9	n.s.
$SO_4^=$-S	2.9	1.3	1.3	0.5

TABLE 3. Concentrations of cations (meq L^{-1}) in the xylem sap influenced by the K:Rb ratio.

	K:Rb ratios			
Cations	**6:0**	**5:1**	**4:2**	**$LSD_{p=0.05}$**
K^+	11.1	4.9	4.3	1.4
Ca^{2+}	8.7	14.4	14.8	2.2
Mg^{2+}	2.4	3.8	3.4	0.8
Na^+	1.2	1.4	2.0	0.5
Rb^+	---	0.8	2.3	0.8

plants supplied with K plus Rb, the reduction being 50% higher than that transported by the plants grown with K alone. The presence of Rb can depress the K^+ uptake by the plant roots (19). On the other hand, the translocation of Ca^{2+}(70%), Mg^{2+}(42%) and Na^+(67%) was enhanced in the plants grown with a 4:2 K:Rb ratio if compared with those of the 6:0 treatment. The xylem sap of plants supplied with a K:Rb ratio of 5:1 presented a behavior similar to that of the 4:2 treatment, although, in this case, the Na^+ translocation was unaffected. The increase of K supply often reduces the absorption of Ca and Mg. High levels of monovalent cations promote low transpiration rates, therefore Ca absorption is depressed (20).

Rubidium concentrations in the xylem sap were similar to those placed in the nutrient solutions and their levels clearly reflect the different amounts of Rb^+ supplied. The sum of the concentrations of K^+ and Rb^+ translocated by the xylem sap of plants grown with K plus Rb was nearly 6 meq L^{-1}, whereas the transport in plants grown with K alone reached 11 meq L^{-1}, which shows that the Rb supply affected the K uptake regardless of the level of Rb supplied.

Details of the ionic balance are given in Table 4. The xylem sap of plants grown with 4:2 K:Rb ratio transported more total cations than those supplied with K alone (6:0). Inorganic anion translocation was unaffected by the K:Rb ratio, whereas organic acid levels decreased as the Rb supply was increased, amounting to 21% in the 5:1 ratio and 34% in the 4:2 ratio in comparison with that grown without Rb. Organic acid anions were detected in the xylem exudate when there is an excess of cation uptake, such as a lot of K and little $SO_4^{=}$ (20). Malate originating in the roots is translocated to the leaves with K as counter cation.

Malate and other carboxylates are lower in NH_4^+ fed plants than those fed with NO_3^- alone (21). But in conditions of mixed N nutrition, NO_3^- reduction promotes an alkaline shift of the pH, producing an increase of malate by the stimulation of phosphoenolpyruvate carboxylase activity (22).

The translocation of total anions remained unchanged in plants grown with a 5:1 K:Rb ratio, whereas it was reduced in the other K:Rb. Irrespective of the K:Rb ratio, the cations exceeded the mineral anions and were superior to the total anions released into the xylematic stream. Thus Anion/Cation (A/C) ratios are lower than 1, but show a significant decrease in plants grown with high levels of Rb. The pH values were similar in all treatments. By contrast, the exudate volume was significantly reduced in plants grown with 4:2 K:Rb ratio.

The data in Table 5 show the changes in the concentrations of organic acids. Plants grown with a 5:1 K:Rb ratio presented lower transports of glutamate (23%)

TABLE 4. Concentrations of total cations, inorganic, organic and total anions (meq L^{-1}), pH and exudate volume in the xylem sap influenced by the K:Rb ratio.

	K:Rb ratios			
Cations	**6:0**	**5:1**	**4:2**	**$LSD_{p=0.05}$**
Total cations	25.6	26.8	27.3	1.6.
Inorganic anions	20.2	21.1	20.7	n.s.
Organic anions	4.7	3.7	3.1	0.6
Total anions	24.9	24.8	23.8	0.8
A/C ratio	0.97	0.93	0.87	0.1
pH	5.7	5.5	5.6	n.s.
mL h^{-1}	6.8	6.3	5.8	0.9

TABLE 5. Concentrations of organic acids (mM) in the xylem sap influenced by the K:Rb ratio.

	K:Rb ratios			
Organic acid	**6:0**	**5:1**	**4:2**	**$LSD_{p=0.05}$**
Glutamate	1.14	0.88	0.61	0.15
Oxalate	0.23	0.20	0.17	0.04
L-malate	3.27	2.65	2.35	0.44
Citrate	0.03	----	----	----

and L-malate (19%) than those fed with K alone. The 4:2 K:Rb ratio produced reductions of glutamate (46%), oxalate (26%) and L-malate (28%). L-malate was used as the C skeleton for NH_4^+ detoxification (23). The decrease of glutamate levels after the supply of both K and Rb point to an alteration of the N metabolism in their roots, probably due to reduced root respiration caused by Rb presence and by the inadequate translocation of amido and amino acids caused by low K availability. Malate is the most frequent organic acid found in the xylem sap of the cucumber plant, amounting to 70% of the total. Glutamate and oxalate represented about 20% and 5%, respectively, and citrate only occurred in small amounts in the sap of plants grown with K alone. It is interesting to note that although the concentrations of each organic acid varied with the K:Rb ratio, the contribution percentages as regards the total also remained unchanged in the different treatments.

The concentrations of micronutrients in the xylem sap influenced by the K:Rb ratio are shown in Table 6. Different K:Rb ratios did not create variations in Fe and Cu levels. Manganese and B transports were enhanced in plants grown in 4:2 K:Rb ratio, while the opposite happened with Zn. Copper and Zn levels in the xylem sap of cucumber plants were higher than those put in the nutrient solutions, whereas Fe and Mn concentrations were reduced and B remained the same. Iron is a nutrient that tends to be accumulated in the roots and is least released to the xylematic stream.

Table 7 gives the sugar concentrations in the xylem sap influenced by the K:Rb ratio. In plants grown with the 4:2 ratio, the total sugars decreased (35%) in comparison with the 6:0 ratio. This improved the reductions in the transport of hexoses-P (41%), glucose (90%) and fructose (84%). The xylem sap of plants grown with the 5:1 ratio transported similar amounts of hexoses-P and stachyose, lower amounts of glucose and fructose and higher amounts of dulcitol. As a result the total concentration remained unchanged.

The soluble carbohydrates in the roots of NH_4^+-fed plants were lower than those grown with NO_3^- alone (24,25), since the carbohydrates are used as NH_4^+ acceptors, which reduce their concentration in the root and are exported to the shoot through the xylematic stream to a lesser extent. In addition, adequate levels of K favor the translocation of amino acids and carbohydrates in plants (26).

Irrespective of the K:Rb ratio, the main monosaccharide detected in the xylem sap of the Medusa cultivar was hexoses-P, which surpassed 70% of the total. Dulcitol amounted to 10% although the contribution percentages to the total increased as the K supply decreased. Glucose, fructose and stachyose are translocated in small amounts.

TABLE 6. Concentrations of micronutrients (mg L^{-1}) in the xylem sap influenced by the K:Rb ratio.

	K:Rb ratios			
Micronutrient	**6:0**	**5:1**	**4:2**	**$LSD_{p=0.05}$**
Fe	0.46	0.57	0.33	n.s.
Mn	0.27	0.67	0.43	0.09
B	0.60	0.55	0.86	0.08
Cu	0.23	0.21	0.13	n.s.
Zn	0.69	0.65	0.55	0.06

TABLE 7. Concentrations of sugars (μM) in the xylem sap influenced by the K:Rb ratio.

	K:Rb ratios			
Sugar	**6:0**	**5:1**	**4:2**	**$LSD_{p=0.05}$**
Hexose-P	3830.1	4045.3	2254.0	595.5
Stachyose	104.1	111.9	125.4	n.s.
Glucose	216.4	38.3	22.2	40.6
Fructose	342.9	19.4	53.3	19.1
Dulcitol	516.5	777.4	785.9	257.2
Total	5010.0	4992.3	3240.8	565.4

Finally, the reduction of K supply from 6 to 4 meq L^{1-} resulted in a lower fixation of NH_4^+ to the C skeletons, thus diminishing the organic-N released to the xylem vessels. This may be due to several factors, on the one hand, a direct effect of Rb reducing K uptake as well as the growth of the root and its primary metabolism, and on the other, the low availability of K causing a low transport of photosynthates towards the root and of organic-N and organic acids to the shoot. The decrease of K supply from 6 to 5 meq L^{-1} did not vary the translocation of organic-N and carbohydrates, and although the organic acid transport decreased, the total anions transported by the xylem sap remained similar to those of the control treatment (6 meq L^{-} of K). It is also interesting to note that, although the K:Rb ratio detected in the xylem sap was the same as that in the nutrient solutions, the replacement of 2 meq L^{-1} of K by Rb resulted in an alteration in the xylematic transports of carboxylates and carbohydrates.

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JOURNAL OF PLANT NUTRITION, 19(3&4), 481-491 (1996)

EFFECT OF PHOSPHORUS, COPPER, AND ZINC ADDITION ON THE PHOSPHORUS/COPPER AND PHOSPHORUS/ZINC INTERACTION IN LETTUCE

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ABSTRACT: The effect of phosphorus (P), copper (Cu), and zinc (Zn) addition on the P-Cu and P-Zn interaction in lettuce (*Lactuca sativa* L.) was analyzed following a factorial design. The experiment was conducted in a greenhouse. Two levels of P (62 and 224 ppm), three levels of Zn (0, 0.17, and 0.34 ppm), and three levels of Cu (0, 0.03, and 0.06 ppm) were applied in all combinations to lettuce grown in perlite. The influence of the different treatments on the leaf P concentration suggests that the P-Cu interaction was positive, whereas P-Zn was negative. An increase in root absorption and retention and a decrease in translocation to leaves were observed for Zn and Cu when the nutrient solution was supplied at a luxurious consumption level of P.

INTRODUCTION

The use of fertilizers as a form of soil management has helped to improve the yields of crops, but has also brought about nutritional unbalance. Maximum yields should be the result of an optimal specific combination of nutrient concentrations.

An element can affect not only another element concentration but also its critical concentration. Thus, it has been observed that the addition of different amounts of P affects various elements, such as Cu and Zn. The study of these interactions has led to contradictory results, although the experiments carried out were themselves quite different. For example in citrus, highly concentrated long-term applications of P fertilizers have resulted in and intensified Cu deficiencies (Olsen, 1972).