Effect of Potassium/Rubidium Ratio on the Uptake of Potassium by Jerusalem Artichoke Roots

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ABSTRACT

A common belief is that plant roots absorb cations from soil solution experiments with corn (*Zea mays* L.) using K/Rb ratio to evaluate the source of K and Rb absorbed indicated that the plant roots absorbed these ions in the ratio of exchangeable K and Rb. The objective of this research was to study the source of K and Rb absorbed from soil by Jerusalem artichoke (*Helianthus tuberosus* L.) roots since they do not have root hairs and this may influence the uptake mechanism. Jerusalem artichoke absorbed K/Rb with a ratio which was intermediate between the ratio of exchangeable K and Rb and the ratio of these cations in solutions. In comparison with corn, Jerusalem artichoke absorbed K at one-third the rate, but absorbed water three times faster so that mass flow contributed a greater proportion of K absorbed by Jerusalem artichoke than that by corn. This, rather than differences in root hairs may be the reason for the observed differences in K uptake between corn and Jerusalem artichoke.

***Key words*: Selectivity coefficient, diffusion coefficient, exchange cations, solution cations, ion influx kinetics, *Helianthus tuberosus* L.**

INTRODUCTION

Plant species differ in characteristics of ion uptake from soil. Species having root hairs may have greater depletion of nutrients concentrations in the soil solution than of that in species lacking root hairs (Barley and Rovira, 1970; Bhat and Nye, 1974a, 1974b). The previous experiments were conducted on K/Rb uptake (Baligar and Barber, 1978b) by corn (*Zea mays* L.), having root hairs. The current study is about Jerusalem artichoke (*Helianthus tuberosus* L.), having few if any roots hairs.

Most soil cations reaching the plant root are usually present in the soil solution and balanced with soluble anions and exchangeable forms. The mechanism of cation flux to the root is commonly believed to be uptake of ions solution by the root, diffusion of solutions ions through solution to the root. (Nye, 1966) and Jenny (1966) has also postulated direct absorption of exchangeable cations by the plant root. Baligar and Barber (1978b) used the K/Rb ratio of uptake of these ions by corn roots from soil to determine the source of cations directly supplied to the root. Corn absorbed K and Rb from solution culture in the same ratio as they were present in solution so that the K/Rb ratio of uptake could be used to indicate the source of ions being absorbed. Soil absorbed Rb more strongly than K so that the K/Rb in solution was larger (about three times) than the ratio on the exchange phase. Corn absorbed K and Rb from soil in the ratio similar to that on the exchange phase indicating that the commonly accepted mechanism for flux to the root may not apply in all situations.

The flux of ions to the plant root is dependent upon both soil and plant factors. The soil factors are ion concentration in the soil solution, effective diffusion coefficient of the ion in the soil and buffering capacity of the ions on the solid phase for ions in the solution phase. The plant factors include, ion flux vs ion concentration, root radius, rate of water uptake, initial root length, and rate of root growth. The soil and plant factors have been combined in a mathematical model simulating uptake (Claassen and Barber, 1976).

The objective of this research was to determine if K and Rb uptake by Jerusalem artichoke was influenced by the ions in the solution or by those on the exchange sites. In preparation, experiments using K/Rb ratio to measure uptake were conducted to determine of Jerusalem artichoke absorbed K and Rb from solution on a nonselective basis. The soils used were those used in similar experiments with corn as the test species (El-Sayed, 2013 ;Baligar and Barber,1978b).

MATERIALS AND METHODS

Solution Culture Studies

Jerusalem artichoke (Helianthus tuberosus L.) seeds were germinated in moistened paper towels immersed in aerated nutrient solution containing the levels of K and Rb used for Jerusalem artichoke growth. After 8 days, 10 seedlings were transferred to each 2-liter pot. The pots contained nutrient solution having the following composition: 2.5 mM Ca, 1 m M Mg, 3 m M N, 0.5 m M P, 2.0 m M S, 46 µ M B, 0.8 µ M Zn, 0.3 m M Cu, 0.5 µ M Mo, and 7.5 µ M Fe as Fe-DTPA (diethylene-triamine penta acetic acid). Solution pH was maintained at 5.5.

Three levels of K and Rb (290 K + 10 Rb, 150 + 150, and 240 +60 µ M) were maintained throughout the growth period. The plants were grown in a controlled

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climatic chamber with day temperature of 28°C for 16 hours with 20 Klux of light. The dark period was 8 hours at 22°C. The seedlings (at 8 days) and plants (harvested after different periods of growth) were separated into roots and shoots, and fresh and dry weights recorded. Newman's (1966) line intercept procedure was used to determine root length. The K and Rb in solution and in the wet-ashed (dried plant samples digested in H_2SO_4 and H_2O_2 and diluted to 100 ml) plant samples and seed were determined by flame emission.

Average influx (IN) was determined using Eq. [1] (Williams, 1948):

$$IN = [(\mu_2 - \mu_1)/(I_2 - I_1)]\,[(\ln L_2 - \ln L_1)/(L2 - L1)] \quad [1]$$

where μ_2 and μ_1 are the K and Rb content (moles/pot) of the plant at time T_2 and T_1 (sec), and L the root length (cm/pot).

Soil Culture Experiments

Two soils Zanesville (Typic Fragiudolf) and Raub (Aquic Arguidoell) were used from Kafr EL-Dawar City ; EL-Behera Governorate. Some of the physical and chemical properties are given in Table (1). Two K treatments, 0and 0.25 meq/100 g were used. Rubidium as Rb Cl_2 was added to all soils at 0.15 meq/100 g . Nitrate was added as either Ca or K nitrate to give 0.13 meq/100 g to Zanesville soil and 0.25 meq/100g to Raub soil . The lower rate was used on Zanesvile soil because its nitrate level before fertilization was higher. Phosphate was added as Ca $(H_2PO_4)_2$ on soils receiving no K and in addition to KH_2PO_4 on Zanesville soil to give 0.65 meq/100 g. All the nutrients were sprayed on the soil with an atomizer while soils were rotated in a mixer. After mixing, 2 kg of soil was placed into each 2-liter plastic pot and enough water added to bring the soil moisture to field capacity (0.3 bar), the soil was equilibrated for 5 days, then air dried, remoistened, and incubated at 25°C for an addition 21 days before planting.

Fifteen Jerusalem artichoke seeds were planted per pot, and after germination thinned to 10 plants/pot. The soil surface was covered with washed silica sand to minimize evaporation loss and pots without plants were included to measure evaporative loss. Plants were grown in a controlled environment chamber having the growth conditions as shown for solution culture. During growth, soil moisture was maintained at (F.C) by adding water daily. All treatments were replicated three times. Plants were harvested 10, 20 and 30 days after planting. Measurements made on the plants were: shoot dry weight, root fresh weight and dry weight, root length, mean root radius, and K and Rb content. Calculation procedures for these parameters were given by Baligar and Barber (1978b).

At planting and after each harvest soil samples were collected for determination of exchangeable ions, C, initial soil solution concentration, Cl and effective diffusion coefficients, $\overline{D}_e$, displaced soil solution was obtained from the soil for measurement of C_I by the procedure of Adams (1974). Total exchangeable cations were obtained by extracting with 1*N* NH_4OAC at pH 7. Mean effective diffusion coefficient, $\overline{D}_e$ for each soil system was calculated by the method of Nye (1968) using Eq. [2].

$$\overline{D}_e = \theta_1 f_1 D_1 (dC_1/dC) \quad [2]$$

Where; θ_1 refers to volumetric moisture content, f_I is the tortuosity factor for the diffusion path, D_I is the diffusion coefficient for the ions in water, and dC_I/dC is the inverse of the buffering power. The values of θ_1 were 0.30 and 0.32 and for f_I (taken from Warncke and Barber, 1972) were 0.37 and 0.18 for Zanesville and Raub soils, respectively. Diffusion in free liquid, D_I, as given by Parsons (1959) for K is 1.98 x 10^{-5} cm^2 Sec^{-1} and for Rb 2.07x10^{-5} cm^2 Sec^{-1}. In these calculations, *C1* (µ moles/ml) and *C* (µ moles/cm^3) were expressed per unit volume basis as it was necessary for obtained $\overline{D}_e$ and buffer power, *6,* which is dC/dC_I. The values can be converted to concentration per unit weight by dividing by 1.3; the bulk density (g / cm^3) to which soils were packed for crop growth and before measuring $\overline{D}_e$ and C_1.

Table 1. Chemical and physical properties of soils used

Characteristic	Soils*	
	Zanesville soil	Raub soil
pH (1:1 H_2O)	6.81	6.21
Organic C, %	1.61	1.55
Clay, %	11.51	27.81
Exchangeable Ca, meq/100 g	8.70	9.67
Exchangeable K, meq/100 g	0.50	0.20
Cation exchangeable capacity, meq/100 g	12.10	20.10
Field Capacity (F.C)	22.71	24.41

*{Soil Survey Staff (1998) and U .S. D. A.(2011)}.

RESULTS AND DISCUSSION

Uptake from Solution

The K/Rb ratio of uptake as compared to the K/Rb concentration of the solution culture is shown in Table (2). In the first experiment ratios of 290:10 and 150:150 of K/Rb were used and the plants harvested after 26 days. The K/Rb ratio was greater than the ratio in solution indicating some selectivity of K over Rb. In the second experiment a ratio of 240: 60 was used and plants harvested after 21 and 31 days. Again the K / Rb ratio of uptake of these ions exceeded the K/Rb ratio in solution. The average K/Rb ratio of uptake in these experiments was 1.9 ± 0.2 of that in solution. While, it would be preferable to have the ratio of uptake equal to the ratio in solution, the consistency of the difference indicates that K/Rb ratio can be used to measure source of K and Rb observed but one needs to correct for the greater uptake of K than Rb.

K and Rb Selectivity and Diffusion

Potassium and Rb distribution on exchange, solution and non-exchange phase, selectivity coefficient, and effective diffusion coefficients in four K-soil systems are given in Table (3). In both soils addition of K enhanced K concentration in solution and on the exchange phase and at the same time reduced the concentration of adsorbed Rb. Some adsorbed Rb moved to the non-exchangeable position and some to the solution phase. Baligar and Barber (1978a) have reported similar effects of K addition on Rb movement. The selectivity coefficient for the K-Rb system, $\mathbf{K_{Rb/K}}$, which describes the distribution of K and Rb between the solution and exchange phases was determined by Eq. [3].

$$K_{Rb/K} = \frac{[Rb - Soil]\ (K^+)}{[K - Soil]\ (Rb^+)}, \qquad [3]$$

where brackets indicate equivalent fractions of K and Rb on exchange sites and parenthesis equivalent fractions of K and Rb in solution.

Potassium and Rb distribution between solution, exchange sites and non- exchange sites (of added) given in Table (3) show that Rb was adsorbed into non-exchange sites on both soils while K was adsorbed as non-exchangeable K only on the Raub soil. Zanesville soil had a higher soluble salt content, hence higher levels of K and Rb in solution. In both soils Rb was adsorbed on the exchange sites preferentially to K so $\mathbf{k_{Rb/K}}$ exceeded 1.0. The $\mathbf{K_{Rb/K}}$ of 2.50 to 3.19 indicates that the K/Rb ratio in solution was 2.50 to 3.19 times larger than the K/Rb ratio on the exchange sites.

The effective diffusion coefficients given in Table (3) were larger for Zanesville soil than Raub because of the greater proportion of K and Rb in solution, and hence lower buffering. Adding K increased $\overline{D}_e$ for both K and Rb because of an increase in their levels in solution. Since the $\overline{D}_e$ values were calculated using $\Delta C/\Delta C_1$ obtained from the data in Table(3), the $\overline{D}_e$ values for K were 2.51 to 3.21 larger than those for Rb.

Uptake from soil

Jerusalem artichoke were grown on the four soil-K treatments and harvested after 11, 21, and 31 days of growth. The plant weight and root data from these harvests are shown in Table(4). Plant weight was greatest at 31 days on the Raub soil, however, root parameters were similar for all treatments. The rates of root growth, K and Rb uptake, water flux, and K and Rb flux are given in Table(5). Root growth k was calculated from the relation $k = (Ln\ L - L0)/t$. The value of k increased with growth on three of the four comparisons. Water flux also increased. However, k and Rb average flux into the root remained approximately constant during the two 11-day periods.

The K/Rb ratio of uptake of K and Rb by Jerusalem artichoke is given in Table 6.

Table 2. Uptake of K and Rb by Jerusalem artichoke as related to K and Rb concentrations in solution

Solution concentration (μM) K	Solution concentration (μM) Rb	Harvest age (days)	Influx *p* moles (cm^{-1} $Sec.^{-1}$) K	Influx *p* moles (cm^{-1} $Sec.^{-1}$) Rb	Ratio of influx (K/Rb)	K/Rb uptake (K/Rb) in solution
290	10	26	1.95	0.04	64.8	2.3
150	150	26	1.20	0.60	2.1	2.1
240	60	21	4.94	0.71	7.1	1.76
240	60	31	3.52	0.51	7.1	1.76

Table 3. Distribution of K and Rb between solution, exchangeable, non-exchangeable, selectivity coefficient, and effective diffusion coefficient as affected by soil type and K addition

Soil treatment	Displaced solution (μ moles ml^{-1})		Exchangeable (μ moles cm^{-3})		Nonexchangeable+ (μ moles cm^{-3})		$k_{Rb/K}$ selectivity	$\overline{D}_e$ (cm^2 Sec^{-1} x 10^7)	
	K	Rb	K	Rb	K	Rb		K	Rb
Zanesville	0.98 b*	0.035 b	6.48 b	0.73 b	-	1.21 (62)‡	3.19 a	3.31a	1.10 b
Zanesville + K	1.44 a	0.045 a	9.18 a	0.71 b	0 (0)	1.22 (64)	2.50 c	3.43 a	1.45 a
Raub	0.17 d	0.019 d	2.53 d	0.77 a	-	1.19 (70)	2.52 c	0.74 c	0.29 d
Raub + K	0.45 c	0.020 c	4.65 c	0.59 c	0.66 (21)	1.36 (71)	2.82 b	1.10 b	0.40 c

* Number in each column not followed by the same letter are significantly different as judged by Duncan's multiple range test at 0.05 probability.
+ Amounts of K and Rb original and added that were not measured as exchangeable or in solution.
‡ Average percent of applied K or Rb present in nonexchangeable form.

Table 4. Jerusalem artichoke plant weight and root growth as influenced by plant age and levels of K on two soils

Soil treatment	Plant age at harvest (days)	Plant weight (g/pot)	Root length (m/pot)	Mean root density (cm/cm^3)	Mean distance between roots (cm)	Mean root radius r_o (mm)
Zanesville	11	0.05 fg*	0.91 c	0.08 c	2.29 b	0.23 c
	21	0.14 efg	4.04 b	0.30 b	1.08 c	0.25 bc
	31	0.41 c	11.42 a	0.83 a	0.63 e	0.28 ab
Zanesville + K	11	0.04 fg	0.96 c	0.08 c	2.16 b	0.25 bc
	21	0.15 efg	4.81 b	0.36 b	0.97 cd	0.25 bc
	31	0.32 cd	10.68 a	0.78 a	0.66 de	0.26 bc
Raub	11	0.04 fg	0.64 c	0.06 c	2.65 a	0.24 c
	21	0.21 def	3.71 b	0.28 b	1.10 c	0.24 c
	31	0.73 b	12.26 a	0.90 a	0.62 e	0.28 ab
Raub + K	11	0.04 fg	0.63 c	0.06 c	2.74 a	0.25 bc
	21	0.18 defg	2.78 b	0.21 b	1.28 c	0.26 bc
	31	0.93 a	11.43 a	0.87 a	0.64 de	0.31 a

* Numbers in each column not followed by the same letter are significantly different as judged by Duncan's multiple range test at 0.05 probability.

Table 5. Influence of soil K and Rb levels on the root growth rate, water flux, and the uptake and influx of K and Rb into Jerusalem artichoke roots

Soil treatment	Harvest (days)	Root growth rate (k Sec^{-1} x 10^6)	Water flux Vo (cm^{-3} cm^{-2} Sec^{-1} x 10^{6})	Uptake/pot (m moles)		Flux into roots+ (p moles . cm^{-1} Sec^{-1})$^+$	
				K	Rb	K	Rb
Zanesville	11-21	0.86 c*	1.12 e	0.15 e	0.02 c	0.39 b	0.02 e
	21-31	1.21 bc	2.20 d	0.33 b	0.03 b	0.54 b	0.03 de
Zanesville + K	11-21	0.94 c	1.17 e	0.20 de	0.02 c	0.46 b	0.02 e
	21-31	0.93 c	2.15 d	0.28 bc	0.02 c	0.51 b	0.02 e
Raub	11-21	1.03 c	2.86 c	0.14 e	0.03 b	0.44 b	0.07 a
	21-31	1.40 ab	3.39 b	0.25 cd	0.04 a	0.40 b	0.06 ab
Raub + K	11-21	0.88 c	3.21 b	0.22 cd	0.02 c	0.87 a	0.04 bc
	21-31	1.65 a	4.60 a	0.46 a	0.03 b	0.85 a	0.04 bc

* Numbers in each column not followed by the same letter are significantly different as judged by Duncan's multiple range test at 0.05 probability.
+ Calculated using Eq. 1

Table 6. Comparison of K/Rb ratios of plant uptake at different stages of growth with K/Rb ratio in soil solution and on the exchange phase

Soil and treatment	K/Rb ratio							
	Uptake (days)		Displaced soil solution (days)			Exchangeable (days)		
	11-21	21-31	0-11	11-21	21-31	0-11	11-21	21-31
Zanesville	28.3	21.9	27.7	26.7	25.9	8.8	8.5	8.7
Zanesville + K	46.6	61.5	36.3	42.4	40.8	13.8	14.5	14.2
Raub	6.8	7.7	8.4	9.4	8.8	3.4	3.3	4.3
Raub + K	26.9	25.1	24.5	25.8	24.4	7.9	7.9	7.6

It is compared with the average K/Rb ratio on the exchange sites and in solution determined before and after each period of growth. The K/Rb ratios of uptake were corrected (Table 7) by dividing by 1.91, the ratio of K/Rb uptake from solution as compared to the K/Rb ratio in solution. The corrected ratio for uptake from Zanesville soil was between the ratio on the exchange sites and the ratio in solution. On the Raub soil the corrected ratio was similar to the ratio on the exchange sites on the soil without added K and between the exchangeable and solution values where K was added. On these soils mass-flow supplied an average of 44% of the K and Rb absorbed on the Zanesville soil and an average of 20% of the Raub soil. The greater proportion supplied by mass-flow on the Zanesville soil could explain why corrected K/Rb ratio of uptake was nearer that of the solution phase.

Potassium and Rb uptake by Jerusalem artichoke appears to have come from both solution and exchange sites. Since mass-flow only supplied a portion of uptake, there would be depletion at the root and diffusion to the root. Mass-flow would supply K and Rb into the depletion zone. The results with Jerusalem artichoke are somewhat different from those of corn, in that with corn the exchange phase appeared to be the sole source of supply. Possibly solution cations supply the initial amounts of K and Rb uptake by the root and then after the soil becomes depleted near the root the K and Rb on the exchange sites may be regulating the supply.

Comparison of Jerusalem artichoke with Corn

Since corn was grown with similar soil treatments in the same growth chamber it is useful to compare the uptake parameters of each (Table 8). Both corn and Jerusalem artichoke were grown on Raub and Zanesville soils under the same light and temperature conditions in a growth chamber. Only the data from the Raub soil are used since the samples of Zanesville soil differed greatly. Corn plants having a larger seed, grew more rapidly and produced many more roots. Average root radius was larger for Jerusalem artichoke than for corn. The root length per gram of shoot was much greater for corn and as a result of this, water flux and mean K influx were both greater for Jerusalem artichoke when measured per unit of root length or area. Because of a lower root density the mean distance between Jerusalem artichoke roots was much grater than for corn. When this distance is compared with the average K depletion zone about the root (calculated as $(2\ \overline{D}_e\ T)^{½}$, Newman and Andrews, 1973) interroot distance was less than the depletion zone for corn indicating interroot competition. For Jerusalem artichoke the depletion zone was much less than the mean distance between roots. A mathematical model simulating K uptake by plant roots was used to calculate the K concentration at the root surface as a fraction of that present initially in the soil. There was little difference between corn and Jerusalem artichoke when concentrations were calculated after 57 hours of uptake. This is sufficient time for the concentration at the root surface to approach a constant value. Corn roots had root hairs that averaged 0.6 mm in length so that after uptake reduced K level in the soil between root hairs to a low level, the corn root would have an effective radius that was 0.6 mm larger.

Corn took up 47% of the exchangeable and solution K in the pot while Jerusalem artichoke only absorbed 6%. The difference in amount per pot removed could be the reason for the difference between these species in the source of K absorbed as indicated by K/Rb ratio of uptake. However, corn grown for 11 days only removed 11% of exchangeable and solutions K and its K/Rb ratio of uptake was similar to that for corn grown for 17 days.

Table 7. Means of K/Rb ratio of K and Rb uptake, in solution and on the exchange phase

Soil and treatment	K/Rb ratio of			
	Uptake	Uptake/2.0	Solution	Exchangeable ions
Zanesville	25.1	13.3	26.8	8.7
Zanesville + K	54.1	28.5	39.8	14.2
Raub	7.3	3.9	8.9	3.7
Raub + K	26.0	13.8	24.9	7.8

Table 8. Comparison of corn and Jerusalem artichoke root morphology and K absorption properties

Characteristics	Corn (17 days)	Jerusalem artichoke (31 days)
Root length		
m/pot	35.4	11.9
m/g of shoot	50	15
Root density, L_V, cm/cm^3	16.5	0.89
Mean distance between roots, cm	0.15	0.63
Mean root radius, mm	0.17	0.30
Root growth rate, $Sec^{-1} \times 10^6$	4.0	1.6
Water flux, cm^3/cm^2 per Sec $\times 10^6$	0.70	2.1
Average K influx, *p* moles/cm per Sec	0.36	0.63
Average depletion zone after 57 hours, cm	0.23	0.20
K conc. at root after, 57 hours, % of initial C	12	14

CONCLUSIONS

Potassium uptake was calculated using the simulation model of Claassen and Barber (1976) and the results were compared with observed K uptake by corn and Jerusalem artichoke. For Jerusalem artichoke, the correlation between observed and predicted K uptake only had an r of 0.41, whereas the same comparison for corn gave an r of 0.88. Hence, agreement between observed and predicted was much closer for corn. The slope of the regression line was 2.51 for corn and 5.31 for Jerusalem artichoke. So, while for both the model predicted much more than was taken up, the difference was much greater for Jerusalem artichoke.

Solution diffusion and exchange diffusion of K may be important mechanisms for K supply to the root. In the experiments, K absorbed by corn appeared to come from the exchange site and exchange diffusion may have been the mechanism. For Jerusalem artichoke, the K/Rb ratio of uptake indicated that both solution and exchange K were influencing uptake. The difference of the results for Jerusalem artichoke from those for corn may have been because of absence of root hairs on Jerusalem artichoke, greater influx rate for water by Jerusalem artichoke or greater K influx by Jerusalem artichoke.

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الملخص العربي

تأثير نسبة البوتاسيوم والروبيديوم علي إمتصاص البوتاسيوم لجذور نبات الطرطوفة

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من الاعتقاد الشائع أنه يتم امتصاص العناصر الغذائية عن طريق جذور النباتات من المحاول الأرضي.

أجري هذا البحث لمحصول الذرة باستخدام نسبة كل من البوتاسيوم والروبيديم لتقييم مصدر امتصاص كل من K وRb عن طريق جذور النباتات ومعرفة نسبة كل من K وRb المتبادل.

أجري هذا البحث لمعرفة مصدر كل من K و Rb الممتص من التربة بواسطة جذور الشعيرات الجذرية لجذور نبات الطرطوفة والذي يؤثر علي ميكانيكية امتصاص كل من K وRb.

أوضحت النتائج أنه في حالة نبات الطرطوفة يكون امتصاص نسبة K/Rb متوسط بين نسبة K وRb المتبادل، ونسبة الكاتيونات في المحاول الأرضي.

وعند مقارنة نباتي الذرة والطرطوفة فإن امتصاص البوتاسيوم يكون بمعدل ۱/۳ ولكن يكون امتصاص الماء بمعدل أسرع ثلاث مرات لذلك فإن معدل التدفق الكتلي للماء تساهم في زيادة نسبة K الممتص بواسطة نبات الطرطوفة عنها في نبات الذرة.

هذه الزيادة النسبية تكون عن طريق الشعيرات الجذرية حيث أن الاختلاف الملحوظ يكون في امتصاص K بين نباتي الذرة والطرطوفة.