

Potassium and the Absorption of Calcium and Magnesium by Potato Plants from Soil

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Potato plants were grown in soil in pots with various additions of K_2SO_4 . Before and after the tubers formed, plants were taken and detopped just above the soil. The xylem sap exuded from the stump was collected; the stems and petioles were macerated under distilled water and the diluted "whole stem sap" (representative of all stem cells) retained. The soil was extracted with distilled water.

The K_2SO_4 increased the Ca and Mg concentrations in the soil extract, but consistently decreased the Ca concentration in the exuded xylem sap. Before the tubers formed, the Mg concentration in the exuded sap decreased with the smaller K additions but increased again with the larger; after the tubers formed, K had little effect on it. Giving K_2SO_4 sharply decreased the concentrations of both Ca and Mg in the "whole stem sap".

Explanations for these observations are offered in terms of the possible influence of K nutrition on the potential difference between the xylem sap and the soil solution and on the phloem translocation of Mg into the roots from the tops.

1. Introduction

Adding a potassium salt to soil will influence Ca and Mg uptake by plant roots both by altering Ca and Mg concentrations in the soil solution and by altering the relationship between ion concentrations inside and outside the root. The relative importance of these effects was studied for potato plants (*Solanum tuberosum*, var. King Edward).

Added potassium increases the activity ratio, $a_K/\sqrt{a_{Ca+Mg}}$, in the soil solution.^{1,2} If the total cation concentration in the soil solution remains constant, this implies a decrease in the Ca and Mg concentrations as K is added. However, the anion in the K fertiliser increases the total anion concentration unless it is removed from the system (e.g. by precipitation or absorption), permitting the total cation concentration to increase, so Ca and Mg concentrations may increase.

Potassium nutrition may influence the relationship between Ca and Mg concentrations inside and outside the root in three ways.

1. Limited anion uptake may limit total cation uptake,³ so that increasing the number of K-ions absorbed decreases the numbers of other cations taken up.

2. There is usually a potential difference between the xylem solution inside a plant root and the external solution, the xylem being negative. This probably facilitates the entry of cations, particularly Ca and Mg, which have been suggested to enter

passively.^{4,5} Increasing the K concentration in the external solution may decrease this potential difference,^{6,7} and so decrease the passive absorption of Ca and Mg.

3. Giving K may alter the composition of the phloem translocation stream coming to the roots from the tops. K may influence the amounts of respirable carbohydrate or adenosine triphosphate (ATP) reaching the roots and this might influence Ca or Mg uptake if either were actively absorbed (i.e. with metabolic intervention). In addition, K increases the translocation of Mg into other sinks in the potato plant,⁸ if the same is true of the roots the extra Mg coming to the roots from the tops might either be lost or tend to repress further Mg uptake by what might crudely be called a "mass action" effect. Ca is relatively immobile in the phloem by comparison with Mg and should not be affected in this way.

In this experiment, the effects of added K_2SO_4 on Ca and Mg concentrations in a water extract of the soil were measured and compared with effects on their concentrations in the sap exuded from the stumps of plants detopped just above the soil, and in the sap of the whole stems, at different times before and after the tubers formed.

2. Experimental

Potato plants were grown (in 1969) from excised sprouted eyes in pots containing 400 g of Rothamsted soil (containing 160 mg/kg exchangeable K; pH 7.8) mixed with 200 g of quartz, and with $Ca(NO_3)_2$, $Ca(H_2PO_4)_2$ and $Mg(NO_3)_2$ supplying 100 mg of N, 100 mg of P and 20 mg of Mg per pot. K_2SO_4 was added to give 0, 20, 80, 160, 300 or 500 mg of K per pot. Water was maintained in saucers under the pots.

Two replicates of each K treatment were harvested 28, 44, 63 and 80 days after planting and two were allowed to grow until the tops died. (No sap was collected from the last two plants and they are not discussed further here.) More N (25 mg/pot) was given between the second and third harvests. Tubers were just starting to form at 44 days.

At each harvest, the tops were removed 12 mm above the soil and bent capillary tubes attached to the stumps with rubber tubing and sealed with "vaseline". The exuded sap was conducted to a small tarred glass vial, collected for 24 hours, weighed, diluted and analysed. The composition of this sap suggested that it was xylem sap and that it was not much contaminated by phloem sap, which is far richer in K (by a factor of about 20).⁹

When the leaves had been removed, the stems and petioles were weighed fresh, macerated under distilled water and filtered; the resulting solution was diluted and analysed, and the solid matter dried and analysed, so that soluble and insoluble fractions of ions in the stems could be calculated. From the amounts of water and water-soluble nutrients in the stems and petioles, nutrient concentrations in the "whole stem sap" were calculated, representing a weighted average for all categories of cell. This indicates the extent to which the nutrients were more concentrated in the other cells of the stem than they were in the xylem.

A water extract of the soil was obtained by shaking one aliquot of distilled water successively with three aliquots of the moist soil at a 1:2.5 soil:solution ratio, centrifuging at 6000 revs/min and analysing the supernatant solution. This was done as soon as possible after each harvest.

K was determined by flame photometry, and Ca and Mg by flame emission and atomic absorption, respectively, on an SP900 spectrophotometer.

3. Results

Table 1 shows the effects of K nutrition on the K, Ca and Mg concentrations in the soil extract, in the exuded xylem sap, and the “whole stem sap”, for the first and last harvests, the latter about 35 days after the tubers started to form. Data for the other harvests are held¹⁰ but are not reported in detail.

TABLE 1. Effects of added K on concentrations of K, Ca and Mg in the soil extract (s), exuded xylem sap (x) and whole stem sap (w) in the 28- and 80-day harvests

K added (mg/pot)	Concentration (mm) of								
	K			Ca			Mg		
	s	x	w	s	x	w	s	x	w
28 days									
0	0.023	1.85	73	3.3	6.4	49	0.14	1.10	17
20	0.022	1.63	78	3.6	4.9	42	0.12	0.89	17
80	0.135	2.67	111	4.9	4.4	21	0.21	0.76	10
160	0.352	3.82	126	6.4	4.8	15	0.26	0.92	8
300	0.948	5.55	144	7.6	3.7	8	0.31	0.94	9
500	1.874	6.28	147	7.6	2.8	5	0.29	0.93	6
Mean	0.559	3.63	113	5.6	4.5	23	0.22	0.92	11
80 days									
0	0.004	0.16	8	1.4	3.5	46	0.03	0.83	33
20	0.005	0.28	9	4.3	4.2	43	0.03	0.84	35
80	0.006	0.58	10	3.4	3.6	46	0.03	0.75	32
160	0.014	0.66	22	4.8	5.6	48	0.05	1.27	15
300	0.060	0.58	62	4.9	4.0	39	0.05	0.78	11
500	0.244	0.84	97	5.9	3.1	7	0.10	0.83	4
Mean	0.056	0.52	35	4.1	4.0	38	0.05	0.88	22

3.1. Overall concentration changes during absorption

K, Ca and Mg differed greatly in the extents to which they became concentrated as they moved into the plant. At the first harvest, K was on average 6.5 times and 203 times more concentrated in the exuded xylem sap and “whole stem sap” than in the soil extract. The corresponding factors for Ca were 0.8 and 4.2 and for Mg 4.2 and 51. By the last harvest, the overall trend had not changed greatly, except that K and Mg, which had become depleted in the soil solution, were even more vigorously acquired; it should be noted that concentrations in the “whole stem sap” at these harvests reflect gains and losses over the whole previous growth period.

3.2. Effects of K nutrition

3.2.1. Soil extract

The Ca and Mg concentrations in the soil extract increased with added K_2SO_4 (Table 1). This occurred at all harvests. Calculations suggested that these increases were a consequence of the increased total anion concentration and showed that the relationship between K, Ca and Mg ions accorded fairly well with the known potassium quantity/intensity relationship for this soil.² Ca was less concentrated than the calculations would have predicted, probably because it was precipitated as the sulphate. This meant that other cations were also less concentrated than would have been predicted, because the appropriate activity ratios were maintained.

3.2.2. Exuded xylem sap

In spite of the increase in the Ca concentration in the soil solution, giving K decreased the concentration of Ca in the exuded sap (Table 1).

The Mg concentration was less simply related to added K (Table 1). It decreased with the first two additions but then increased slightly. This pattern was repeated at the second harvest, but not at the fourth, when the tubers had formed.

3.2.3. Relationships between soil extract and exuded sap concentrations

Because Ca and Mg concentrations in the soil solution were allowed to vary, the best measure of the influence of K nutrition on Ca and Mg uptake was probably the ratio

$$\frac{\text{concentration in exuded sap}}{\text{concentration in soil extract}}$$

which was called the "accumulation ratio". At the first harvest, for K and Ca this ratio decreased in a smooth curve as the K concentration in the soil extract increased, but for Mg the relationship was not continuous (Figure 1).

Figure 1 also shows \log_{10} (accumulation ratio) plotted against \log_{10} (K molarity), the latter referring to the soil extract. For K and Ca, but not Mg, there was a linear relationship, and calculating the linear regressions showed r^2 to be highly significant (Table 2). The corresponding relationships for K and Ca in later harvests were also highly significant. There thus seemed to be a consistent effect of K on Ca uptake. For Mg the relationship between \log_{10} (accumulation ratio) and \log_{10} (K molarity) improved after the tubers formed (Table 2); the meaning of this observation is discussed later.

3.2.4. The whole stem sap

At the first harvest, the added K sharply decreased the concentrations of both Ca and Mg in the whole stem sap (Table 1). The regressions of these concentrations on \log_{10} (K molarity) in the soil extract were highly significant ($P < 0.001$; $r^2 = 0.91$ and 0.84 , respectively). Similar, but less significant, relationships occurred at the other harvests, though by the last harvest only the largest K additions much altered these concentrations (Table 1).

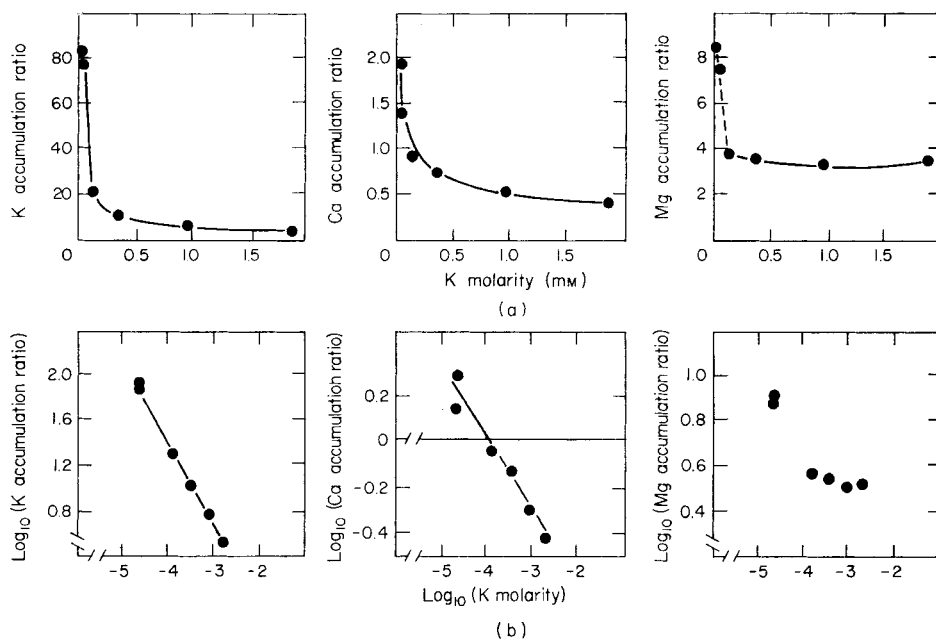


Figure 1. (a) Accumulation ratios plotted against the K molarity of the soil extract. (b) The corresponding log:log relationships.

3.3. Cation:anion relationships in the exuded sap

Figure 2 shows the sum of the cation concentrations K + Ca + Mg + Na in the exuded sap plotted against the sum of the nitrate and phosphate concentrations (all concentrations in mequiv./l) for the first harvest. Most points fell close to a 1:1 relationship except at small concentrations, and the regression was significant at $P < 0.001$. At the second, third and fourth harvests the relationship persisted ($r^2 = 0.57, 0.75$ and 0.66 , respectively, all significant at $P < 0.01$), but the sum of the cation concentrations was always greater than the sum of the nitrate and phosphate concentrations, suggesting

TABLE 2. Values of r^2 for the regressions of \log_{10} (accumulation ratio) on the \log_{10} (K molarity) of the soil extract. The accumulation ratio always decreased as the K molarity increased

Harvest	r^2 for		
	K	Ca	Mg
28 days	0.98***	0.91***	0.53**
44 days	0.97***	0.76***	0.52*
63 days	0.71**	0.75***	0.62**
80 days	0.88***	0.75**	0.79***

Significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

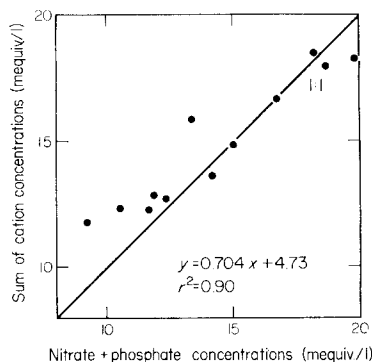


Figure 2. Relationship of the sum of the cation concentrations in the exuded xylem sap to the sum of the nitrate and phosphate concentrations.

either that organic anions were increasingly generated in or translocated to the roots, or that other inorganic anions were absorbed more after the first harvest.

No similar relationships were found in the whole stem sap.

4. Discussion

4.1. Concentration changes during absorption

The accumulation ratios shown are exaggerated because the soil extract was more dilute than the original soil solution (by a factor of about 4.8 for non-absorbed anions, Ca and Mg, and by $\sqrt{4.8}$ for K). However, since the dilution factor was the same for Mg as for Ca, it appears that Mg was accumulated more than Ca (in relation to their respective concentrations in the soil solution), and that K was accumulated more than Mg.

If Ca and Mg had both been absorbed passively by the roots their accumulation ratios should have been similar. The larger ratio for Mg may mean that Mg brought from the tops in the phloem translocation stream before detopping re-ascended in the xylem and contributed to the Mg concentration measured in the exuded xylem sap. Alternatively, there might have been an active component of Mg uptake by the roots.

K, Ca and Mg were all considerably more concentrated in the whole stem sap than in the xylem sap, suggesting there might have been some active secretion from the xylem into other stem cells. If so, K seemed to be more actively secreted than Mg, and Mg more than Ca; i.e. the order was the same as in root uptake. In addition, K may have passed in the xylem to the leaves, from there have been re-exported in the phloem, which contains K at a larger concentration than the xylem and have diffused or been secreted from the phloem into other stem cells. Ca does not seem to be re-exported from leaves;^{11, 12} whether Mg can be is doubtful.⁸

The concentrations of K in the whole stem sap (Table 2) are of the same order as those found in the phloem exudate of *Ricinus* by Hall and Baker,⁹ suggesting that the K concentration in the phloem solution may not differ much from that in adjacent cells in the stems. The concentrations of Ca and Mg in the whole stem sap are mostly much larger than Hall and Baker found in the phloem exudate.

4.2. Effects of added K

Ca and Mg absorption also differed in respect of the effect of added K.

For Ca, \log_{10} (accumulation ratio) was well and consistently related to the \log_{10} (K molarity) of the soil extract. Dunlop and Bowling⁷ found that in maize roots, giving K decreased the negative potential difference (p.d.) between the xylem sap and the external solution, such that the p.d. was linearly related to the \log_{10} (K molarity) of the external solution. For ions accumulated passively, \log_{10} (accumulation ratio) should, on the basis of the Nernst equation, be related to the p.d., so the added K may simply have decreased the p.d. between the xylem sap and the soil solution, thereby lessening the passive absorption of Ca.

This simple explanation was not adequate for the behaviour of Mg. At both the first and second harvests, the Mg concentration in the exuded xylem sap first decreased as K was added and then increased again with further K, but not to the original value. A possible interpretation is that giving K decreased the passive uptake of Mg as it did of Ca, but that before detopping it also increased the phloem translocation of Mg into the roots from the tops (as it did into the tubers);⁸ some of this Mg possibly re-ascended in the xylem, causing an increase in the Mg concentration in the xylem sap that was super-imposed on the decrease caused by the lessening of passive absorption.

This suggestion could also explain why the relationship between \log_{10} (Mg accumulation ratio) and \log_{10} (K molarity) improved when the tubers formed (Table 2). The tubers are a "dominant" sink in the potato plant¹³ and their formation probably disrupted the existing pattern of phloem translocation so that less occurred towards the roots.¹⁴ This would partly have eliminated the component of xylem Mg concentration suggested to arise from phloem-translocated Mg, leaving only the passive component of Mg uptake, so that the \log_{10} (Mg accumulation ratio): \log_{10} (K molarity) relationship improved.

An alternative, or additional, explanation of these observations is possible if there is an active component of Mg uptake depending on respirable carbohydrate or ATP brought to the roots through the phloem. Added K might have enhanced either the translocation or utilisation of these energy sources for Mg uptake, causing the active component of Mg uptake to increase while the passive component decreased.

Section 3.3. showed a relationship between the sum of the cation concentrations in the exuded xylem sap and the sum of the nitrate and phosphate concentrations. There is insufficient evidence to show whether this could have been a contributory factor in the effects of K nutrition on Ca and Mg uptake. It may simply imply that anion uptake depends on cation uptake rather than *vice versa*.

The effect of added K on the Ca concentration in the whole stem sap seems at least partly attributable to the cumulative effect of decreased Ca concentrations in the xylem sap. For Mg, this explanation is less tenable because the Mg concentration in the xylem sap was decreased less; however, Mg may have been increasingly moved to sinks as K was given, so that less accumulated in the stems and leaves.⁸

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References

1. Beckett, P. H. T. *J. Soil Sci.* 1964, **15**, 9.
2. Addiscott, T. M. *J. agric. Sci., Camb.* 1970, **74**, 131.
3. Cunningham, R. K. *J. agric. Sci., Camb.* 1964, **63**, 97.
4. Bowling, D. J. F.; Macklon, A. E. S.; Spanswick, R. M. *J. exp. Bot.* 1966, **17**, 410.
5. Shone, M. G. T. *J. exp. Bot.* 1968, **19**, 468.
6. Davis, R. F.; Higinbotham, N. *Pl. Physiol., Lancaster* 1969, **44**, 1383.
7. Dunlop, J.; Bowling, D. J. F. *J. exp. Bot.* 1971, **22**, 445.
8. Addiscott, T. M. *J. Sci. Fd Agric.* 1974, **25**, 1173.
9. Hall, S. M.; Baker, D. A. *Planta, Berlin* 1972, **106**, 131.
10. Addiscott, T. M. Ph.D. Thesis, Univ. Lond. 1972.
11. Biddulph, O.; Cory, R.; Biddulph, S. *Pl. Physiol., Lancaster* 1959, **34**, 512.
12. Ringeot, A.; Sauer, G.; Gielink, A. J. *Planta, Berlin* 1968, **80**, 15.
13. Moorby, J. *Ann. Bot., Lond.* 1968, **32**, 57.
14. Biddulph, O.; Cory, R. *Pl. Physiol., Lancaster* 1965, **40**, 119.