# UPTAKE OF POTASSIUM AND SODIUM BY SEEDLINGS OF SINAPIS ALBA

# By M. G. Pitman\*

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#### Summary

Seedlings of *Sinapis alba* (mustard) have a lower potassium selectivity than those of barley, as shown by the lower ratio of potassium to sodium in the shoots of plants grown on the same solution. The ratio in the shoots is usually lower than in the roots, whereas in barley it is higher. In spite of this difference in selectivity, the uptake of potassium and sodium by mustard has much in common with that by barley. The total potassium and sodium uptake to the shoot is independent of the ratio in the solution; the ratio of potassium to sodium in the shoot is proportional to that in the roots, but not to that in solution; and potassium selectivity can be reduced by transpiration. Thus it appears that the same general model for ion uptake can be used for both plants, although they have different levels of selectivity. In this model it is suggested that total potassium and sodium uptake is controlled by an active anion transport coupled with plant growth by means of metabolism, but selectivity is determined during movement of ions into the stele through cytoplasm and cell walls.

#### I. INTRODUCTION

Collander's (1941) experiments with a range of plant species demonstrated clearly the different degrees of potassium/sodium selectivity in plants. At one end of the scale *Fagopyrum* and *Zea* were extremely selective for potassium and at the other end some species of *Atriplex* took up more sodium than potassium from the solutions, which contained equal equivalent concentrations of the major cations. In previous papers (Pitman 1965a, 1965b) barley seedlings were used to investigate potassium and sodium uptake because they show a marked preference for potassium. In the present paper similar experiments are described for *Sinapis alba* (mustard) which Collander's experiments showed to have little preference for potassium. The behaviour of mustard is compared with that of barley seedlings in similar experiments.

# II. EXPERIMENTAL

Seeds of S. *alba* were germinated on moist filter paper and when the roots were about 1 mm long were transferred to terylene gauze on aerated culture solutions. When 5 days old, the seedlings were about 5 cm high and the first pair of leaves after the cotyledons were just visible. At this stage four seedlings were transplanted to a plastic container which held about 600 ml of culture solution. The seedlings were loosely held in the lids with cotton wool. Solutions were well aerated and changed frequently so that there was no problem from bacterial or fungal contamination.

\*Department of Botany, University of Adelaide.

The culture solutions were as described in previous publications (Pitman 1965*a*, 1965*b*). Briefly, all culture solutions contained  $0.8 \text{ m-moles/l NH}_4\text{H}_2\text{PO}_4$ , 0.2 m-moles/l Fe-EDTA, and trace elements according to Arnon (1938). In addition the solutions contained varied concentrations of KNO<sub>3</sub>, NaNO<sub>3</sub>, Ca(NO<sub>3</sub>)<sub>2</sub>, and MgSO<sub>4</sub>. The standard solution (referred to as "10") contained 10 m-equiv/l (KNO<sub>3</sub> + NaNO<sub>3</sub>) and 10 m-equiv/l [Ca(NO<sub>3</sub>)<sub>2</sub> + MgSO<sub>4</sub>]; "20" and "60" solutions contained these salts at 20 m-equiv/l and 60 m-equiv/l, respectively. The ratio of K to Na was 1:3 (m-equiv/l) in most cases, but in some cases was varied. The ratio of Ca(NO<sub>3</sub>)<sub>2</sub> to MgSO<sub>4</sub> was always 3:2 (m-equiv/l) but in some experiments solutions were prepared with varied amounts of these salts (Figs. 4 and 6). In other experiments the divalent cation salts were constant but the (KNO<sub>3</sub> + NaNO<sub>3</sub>) varied (Fig. 5). Such details are given in the text.

At harvest the roots were rinsed in distilled water for 1 min to remove culture solution from the root surface and then cut into root and shoot at the level of insertion into the culture vessel. This was just above the origin of lateral roots. Plant parts were dried and digested in a mixture of nitric, sulphuric, and perchloric acids. The sodium and potassium contents were estimated by flame-photometry and calcium and magnesium by atomic absorption spectrometry.

Growth of the mustard plants was much less uniform than that of barley seedlings in spite of selections made at transplanting. Variability between samples was consequently larger and experimental determinations were the mean of either three or four replicates. Mean standard errors of the mean for 12 examples were 5.9% for dry weight; 8.2% for potassium content; 5.8% for sodium content; 4.7% for relative potassium content; and 5.0% for relative sodium content.

Plants for some experiments were grown in an air-conditioned glasshouse and the relative growth rate was then about 0.12 mg/mg/day. In other experiments fluorescent and incandescent lighting was used, and relative growth rates were about 0.2-0.3 mg/mg/day.

# III. RESULTS

Increase in dry weight of mustard seedlings is exponential at least over the plant weight range of 10–500 mg. Below 10 mg plants grow relatively more slowly due to the small proportion of leaf area to total dry weight, and exponential growth starts between 7 and 15 days from germination, depending on the conditions. Over the period studied (i.e. up to 500 mg dry wt.)\* the total content of potassium and sodium is proportional to dry weight, both in root and shoot (Fig. 1). The constant of proportionality (i.e. relative content) is influenced by the conditions for growth; for example, plants grown at high humidity and a low light intensity have a much larger relative content of potassium and sodium than plants grown at higher light intensities (see Table 5). These differences are not surprising, as relative content depends on the rate of uptake of ions and on plant relative growth rate, and both these components are sensitive to the environment.

\*At this stage flower buds were present but had not opened.

As found for barley seedlings (Pitman 1965b) the ratio of potassium to sodium in the shoot was very nearly constant during the exponential stage of growth, as shown in the following tabulation:





The proportion of potassium to sodium in the roots increased during early stages of development due to the relatively large amount of sodium in the roots at the start of seedling growth, but became constant from about 11–13 days onwards. The values for root content are more variable than those for the shoot due mainly to the difference in size. The plants used in these experiments were grown on solutions containing 10 m-equiv/l of potassium plus sodium. At higher concentrations selectivity may decrease with age, because in this concentration range selectivity decreases with transpiration (see Table 5).

The overall constant proportion of potassium to sodium in mustard masked the differences in distribution between young and older leaves. "Young" leaves contained about six to seven times as much potassium to sodium, but this ratio fell as the leaf increased in size. For example during development of the second leaf:

> Leaf dry weight (mg):  $3 \cdot 8$  $7 \cdot 6$  $16 \cdot 3$  $24 \cdot 2$  $36 \cdot 2$  $45 \cdot 3$  $57 \cdot 7$ K/Na ratio:  $6 \cdot 5$  $5 \cdot 3$  $3 \cdot 0$  $4 \cdot 1$  $3 \cdot 4$  $2 \cdot 4$  $3 \cdot 0$

This pattern of behaviour is common to many plants and is due to a change in the main uptake process from predominantly phloem transport (where the K/Na ratio is high) to predominantly transpiration transport (lower K/Na ratio) (Greenway and Pitman 1965).



Fig. 2.—Effect of varied K/Na ratios in the culture solution on the potassium, sodium, and potassium plus sodium uptake to both shoots and roots.

Uptake to mustard is thus very much like uptake to barley seedlings. The relative contents of potassium and sodium in the roots were constant and the same was true for the shoots in spite of very different distributions in young and old organs. The quality of uptake remained unchanged in spite of the increased quantity of uptake with plant growth. Like uptake to barley shoots, that to mustard shoots appears to be due to a transport system in a kind of steady state relative to the roots; this process limits uptake, but distribution within the shoot is controlled by other means. The root cells are considered to be in flux equilibrium with the solution from an early stage of development. In a "10" solution, these cells contain about 180–200 m-equiv/l potassium and sodium, with the K/Na ratio about  $4 \cdot 2$  compared with 0.33 in the solution. The most striking difference is the much smaller selectivity in the shoot—K/Na ratio of 2.4 compared with 4.2 in the roots. In barley seedlings comparable values would be 7–9 in the shoots and 3–4 in the roots (Pitman 1965b).

The constant proportion of potassium to sodium found in the shoots and roots over a period of at least 1–2 weeks simplifies the investigation of effects of solution content on uptake of these ions. Samples taken at 7 and 14 days, for example, enable the relative growth rate and the proportions of potassium and sodium in the plant to be determined without establishing the complete pattern of growth and uptake over this period.

This approach was used to determine the effect of the ratio of potassium to sodium in the solution on the uptake to the plant. Seedlings were transplanted at 7 days into "10" solution in which the K/Na ratio was varied from 1:19 to 9:1, and



Fig. 3.—Relation between K/Na ratio in the shoots to K/Na ratio in the roots for mustard plants when grown on culture solutions "10" and "20", and for barley plants grown on culture solution "10" (see Pitman 1965b).

were harvested 8 days later. The mean weights of shoot and root were  $55 \cdot 3 \pm 1 \cdot 4$  mg and  $8 \cdot 3 \pm 0 \cdot 25$  mg respectively at the final harvest and relative growth rate was  $0 \cdot 26$  mg/mg/day. The plant weights were independent of the proportions of potassium to sodium in the solution. Relative contents of these plants are given in Figure 2. Both in roots and shoots, the total relative potassium and sodium content was independent of the ratio of potassium to sodium in the solution, but the proportion of potassium to sodium decreased with decrease in the K/Na ratio in solution.

At any one concentration the K/Na ratio in the shoot is proportional to that in the root. This proportionality is shown in Figure 3 where the K/Na ratio in the shoot is plotted against the ratio in the roots for plants grown on solutions of constant total concentration, but varied proportions of potassium and sodium. In spite of the big difference in inherent selectivity between barley and mustard there is in each case a remarkable correlation between root and shoot uptake.

Figure 3 also shows that selectivity in the shoot falls at higher concentrations. This feature is shown in more detail in the following results, but there is an experimental problem in investigating concentration effects. Alteration in concentration of the culture solution involves more than change in potassium or sodium; of necessity, either ion balance in the solution or concentrations of other ions must also be affected. Each of these changes may influence the proportions of potassium and sodium taken up. Moreover, altering osmotic pressure of the solution may have its own effect on plant growth. To study the effect of altering both monovalent and divalent cation concentrations in culture solution, the following experiments were carried out.



Fig. 4.—Effect of varying the calcium plus magnesium concentration in the culture solution (from 10 to 60 m-equiv/l), whilst maintaining potassium plus sodium concentration constant at 10 m-equiv/l, on uptake of sodium and potassium by mustard plants.

Plants were grown in solutions containing a constant level of potassium and sodium (2.5 and 7.5 m-equiv/l respectively) but with various levels of calcium and magnesium (10-60 m-equiv/l). The relative potassium and sodium contents of the shoots are shown in Figure 4. Sodium relative content decreased slightly and potassium selectivity was correspondingly higher at higher levels of calcium plus magnesium. There was less variation in selectivity in the roots, but the higher concentrations reduced growth by 15-20% and increased relative content from  $1.7-1.9 \mu$ -equiv/mg (Table 1). Similar reductions in growth of mustard with concentration were found in other experiments (Table 3), and were larger than the changes in growth of barley under similar conditions (Pitman 1965b). The calcium and magnesium relative content of the shoot rose from about 0.8 to  $1.1 \mu$ -equiv/mg in this range of concentration (Table 1).

Interactions of mono- and divalent cations are also shown in Tables 2 and 3 and in Figure 5, but in these examples calcium plus magnesium was constant at 10 m-equiv/l and sodium plus potassium varied from 0.5 to 60 m-equiv/l, with the K/Na ratio constant and equal to 1:3. Table 2 and Figure 5(a) give data for the range 0.5-10 m-equiv/l; Table 3 and Figure 5(b) for the range 1-60 m-equiv/l.

The relative content of potassium in both root and shoot was relatively unaffected by concentration, but that of sodium increased considerably. This behaviour also showed as changes in selectivity and in total relative content. Over the range 0.5-10 m-equiv/l the increase was due to increased uptake as dry weights were little affected by concentration. At higher concentrations (40 and 60 m-equiv/l) there was a large reduction in growth (cf. Table 3) and increased relative content may have been due to changes in both growth and uptake. These results (and those of Fig. 1) could be interpreted as a potassium relative uptake independent of concentration, plus a sodium relative uptake that increased with concentration, i.e. implying separate mechanisms. However, I prefer to regard the constancy of

 Table 1

 RATIO OF POTASSIUM TO SODIUM IN SHOOTS AND ROOTS OF MUSTARD PLANTS GROWN ON SOLUTIONS

 CONTAINING VARIED CONCENTRATIONS OF CALCIUM PLUS MAGNESIUM

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	Calcium plus Magnesium Concentration (m-equiv/l)					
	10	20	30	40	50	60
K/Na ratio in shoot	$3 \cdot 5$	$3 \cdot 5$	3.9	4.4	$4 \cdot 3$	$4 \cdot 9$
K/Na ratio in root	<b>4</b> · 0	$5 \cdot 1$	$5 \cdot 2$	$5 \cdot 1$	$5 \cdot 3$	$5\cdot 2$
Potassium plus sodium in root ( $\mu$ -equiv/mg)	1.66	1.53	1.75	$1 \cdot 85$	1.90	1.93
Calcium in shoot $(\mu$ -equiv/mg)	0.46	0.51	0.43	0.65	0.52	0.64
Magnesium in shoot ( $\mu$ -equiv/mg)	0.35	$0\cdot 42$	0.44	0.48	0.49	0.51

Data of Figure 4

potassium content as partly fortuitous, and due to an increasing *total* uptake combined with decreasing selectivity. Figure 2 showed that the total potassium and sodium uptake is independent of the proportions of potassium and sodium in the solution and it is quite reasonable to suppose that the same argument applies to the results of Tables 2 and 3. The increase in sodium uptake occurs even over the low concentrations of Table 3, so it is not likely to be a simple additive effect of, say, transpiration. (If it were, then at higher concentrations virtually all the uptake would be of this kind. Table 5 (q.v.) shows that this is not so.)

Figures 5(a) and 5(b) show how the selectivity varied in these experiments. The most interesting feature is the change in selectivity of the ion supply to the shoot with decreasing concentration; in the range 1-2 m-equiv/l the selectivity was very much larger than that of the root and mustard behaved much like barley.

The solutions used for the results of Tables 2 and 3 contained varying proportions of monovalent to divalent ions as well as increased concentrations of sodium and potassium. The results of Figure 4 show that there was little effect of variation in calcium and magnesium level when potassium plus sodium was equal to 10-m equiv/l.

#### TABLE 2

DRY WEIGHTS AND RELATIVE POTASSIUM AND SODIUM CONTENTS OF SHOOTS AND ROOTS OF MUSTARD PLANTS GROWN ON SOLUTIONS CONTAINING VARIED CONCENTRATIONS OF POTASSIUM PLUS SODIUM Culture solutions contained 10 m-equiv/l calcium plus magnesium, whilst potassium plus sodium concentrations varied from 0.5 to 10 m-equiv/l

	Potassium plus Sodium Concentration (m-equiv/l)					
	$0\cdot 5$	1.0	$2 \cdot 0$	$5 \cdot 0$	10.0	
	Shoots					
Dry weight (mg) Relative potassium	$20 \cdot 9 \pm 1 \cdot 8$	$23 \cdot 6 \pm 1 \cdot 0$	$25 \cdot 3 \pm 1 \cdot 7$	$23 \cdot 3 \pm 0 \cdot 2$	$24 \cdot 0 \pm 0 \cdot 5$	
content ( $\mu$ -equiv/mg) Relative sodium con-	$1 \cdot 64 \pm 0 \cdot 07$	$1 \cdot 68 \pm 0 \cdot 02$	$1 \cdot 79 \pm 0 \cdot 04$	$1 \cdot 67 \pm 0 \cdot 08$	$1 \cdot 50 \pm 0 \cdot 03$	
tent ( $\mu$ -equiv/mg)	$0.17 \pm 0.005$	$0.17\pm0.005$	$0 \cdot 21 \pm 0 \cdot 02$	$0.39 \pm 0.005$	$0.65 \pm 0.02$	
1. S.			Roots			
Dry weight (mg) Relative potassium	$5\cdot3\pm0\cdot3$	$6 \cdot 0 \pm 0 \cdot 3$	$6 \cdot 2 \pm 0 \cdot 2$	$5\cdot9\pm0\cdot1$	$5 \cdot 8 \pm 0 \cdot 2$	
content ( $\mu$ -equiv/mg) Belative sodium con-	$1 \cdot 15 \pm 0 \cdot 06$	$1 \cdot 33 \pm 0 \cdot 04$	$1 \cdot 37 \pm 0 \cdot 03$	$1 \cdot 44 \pm 0 \cdot 04$	$1 \cdot 43 \pm 0 \cdot 01$	
tent ( $\mu$ -equiv/mg)	$0 \cdot 25 \pm 0 \cdot 003$	$0 \cdot 23 \pm 0 \cdot 02$	$0.21 \pm 0.01$	$0 \cdot 24 \pm 0 \cdot 01$	$0.32\pm0.01$	

#### TABLE 3

DRY WEIGHTS AND RELATIVE POTASSIUM AND SODIUM CONTENTS OF SHOOTS AND ROOTS OF MUSTARD PLANTS GROWN ON SOLUTIONS CONTAINING VARIED CONCENTRATIONS OF POTASSIUM PLUS SODIUM Culture solutions contained 10 m-equiv/l calcium plus magnesium, whilst potassium plus sodium concentrations varied from 1 to 60 m-equiv/l

	Potassium plus Sodium Concentration (m-equiv/l)							
	1	5	10	20	40	60		
	Shoots							
Dry weight (mg) Relative potassium con-	$40 \pm 2 \cdot 1$	$45 \cdot 6 \pm 3 \cdot 3$	$40.6 \pm 1.0$	$36 \cdot 8 \pm 3 \cdot 0$	$29 \cdot 5 \pm 1 \cdot 0$	$29 \cdot 5 \pm 1 \cdot 6$		
tent ( $\mu$ -equiv/mg) Relative sodium content	$1.75 \pm 0.12$	$1 \cdot 66 \pm 0 \cdot 05$	$1.72 \pm 0.06$	$1 \cdot 68 \pm 0 \cdot 12$	$1\cdot41\pm0\cdot05$	$1 \cdot 32 \pm 0 \cdot 07$		
$(\mu$ -equiv/mg)	$0.17 \pm 0.02$	$0\cdot38\pm0\cdot02$	$0.59\pm0.01$	$0.91 \pm 0.03$	$ 1\cdot 36\pm 0\cdot 08 $	$1.70 \pm 0.04$		
	Roots							
Dry weight (mg) Relative potassium con-	$6 \cdot 4 \pm 0 \cdot 8$	$7 \cdot 1 \pm 0 \cdot 6$	$7 \cdot 0 \pm 0 \cdot 2$	$5 \cdot 8 \pm 0 \cdot 6$	$5 \cdot 5 \pm 0 \cdot 5$	$5 \cdot 5 \pm 0 \cdot 2$		
tent ( $\mu$ -equiv/mg) Relative sodium content	$1 \cdot 38 \pm 0 \cdot 16$	$1 \cdot 72 \pm 0 \cdot 21$	$1 \cdot 23 \pm 0 \cdot 06$	$1 \cdot 43 \pm 0 \cdot 12$	$1 \cdot 38 \pm 0 \cdot 04$	$1 \cdot 42 \pm 0 \cdot 01$		
$(\mu$ -equiv/mg)	$0.42 \pm 0.01$	$0.47 \pm 0.04$	$0.52 \pm 0.01$	$0\cdot 66\pm 0\cdot 03$	$0.79 \pm 0.01$	$0.98 \pm 0.04$		
Relative growth rate (mg/mg/day)	0.18	$0 \cdot 20$	0.19	0.17	0.15	0.15		

In contrast the effect of such variations was found to be marked when potassium plus sodium was equal to 2 m-equiv/l (Fig. 6 and Table 4). Thus the increase in selectivity



Fig. 5.—Effect of varying potassium plus sodium concentration in the culture solution (from 0.5 to 10 m-equiv/l), whilst maintaining calcium plus magnesium concentration constant at 10 m-equiv/l on shoot and root selectivity (i.e. K/Na ratio).

between plants on solutions containing potassium plus sodium equal to 10 m-equiv/l and those on 0.5-2 m-equiv/l in Figure 5 is shown to be caused largely by the changed



Fig. 6.—Effect of varying calcium plus magnesium concentration in the culture solution (from 0.5 to 10 m-equiv/l) whilst maintaining potassium plus sodium concentration constant at 2 m-equiv/l on shoot and root selectivity(i.e. K/Na ratio).

ratio between calcium plus magnesium and potassium plus sodium rather than by the concentration change in potassium plus sodium alone. At the lower concentrations, there was a decrease in total uptake of potassium and sodium with increased concentration of calcium and magnesium but the most striking feature was the increased selectivity both in the shoot and the root (Fig. 6). In spite of the range of

#### TABLE 4

DRY WEIGHTS AND RELATIVE POTASSIUM AND SODIUM CONTENTS OF SHOOTS AND ROOTS OF MUSTARD PLANTS GROWN ON SOLUTIONS CONTAINING VARIED CONCENTRATIONS OF CALCIUM PLUS MAGNESIUM Culture solutions contained 0.5 m-equiv/l potassium and 1.5 m-equiv/l sodium, whilst calcium plus magnesium concentrations varied from 0.5 to 10 m-equiv/l

	Calcium plus Magnesium Concentration (m-equiv/l)				
	0.5	1	2	5	10
		1	Shoots		
Dry weight (mg)	$34 \cdot 0 \pm 0 \cdot 6$	$36 \cdot 8 \pm 1 \cdot 8$	$35 \cdot 7 \pm 1 \cdot 3$	$37 \cdot 4 \pm 1 \cdot 9$	$37 \cdot 2 \pm 0 \cdot 6$
Relative potassium con- tent ( $\mu$ -equiv/mg)	$1 \cdot 64 \pm 0 \cdot 01$	$1 \cdot 61 \pm 0 \cdot 02$	$1 \cdot 64 \pm 0 \cdot 04$	$1 \cdot 60 \pm 0 \cdot 06$	$1 \cdot 52 \pm 0 \cdot 05$
$(\mu$ -equiv/mg)	$0.42 \pm 0.01$	$0.35 \pm 0.02$	$0 \cdot 25 \pm 0 \cdot 01$	$0\cdot 21\pm 0\cdot 01$	$0 \cdot 16 \pm 0 \cdot 01$
			Roots		
Dry weight (mg)	$8 \cdot 2 \pm 0 \cdot 1$	$8\cdot5\pm0\cdot6$	$9 \cdot 1 \pm 0 \cdot 1$	$8 \cdot 3 \pm 0 \cdot 5$	$7 \cdot 5 + 0 \cdot 2$
Relative potassium con- tent ( $\mu$ -equiv/mg)	$0.86 \pm 0.06$	$1 \cdot 03 \pm 0 \cdot 04$	$1\!\cdot\!04\!\pm\!0\!\cdot\!02$	$1 \cdot 22 \pm 0 \cdot 09$	$1 \cdot 12 \pm 0 \cdot 03$
Relative sodium content $(\mu$ -equiv/mg)	$0.36 \pm 0.03$	$0 \cdot 27 \pm 0 \cdot 03$	$0\cdot22\pm0\cdot01$	$0 \cdot 22 \pm 0 \cdot 01$	$0.18\pm0.01$

values of K/Na, the ratio of selectivity in shoot to that in the root was fairly constant and equal to 1.62, 1.38, 1.47, 1.45, and 1.52, respectively, in the range 0.5-10 m-equiv/l. This behaviour is another example of the correlation shown in Figure 3.

#### TABLE 5

SELECTIVE UPTAKE OF POTASSIUM AND SODIUM BY PLANTS GROWING IN FULL LIGHT, IN LOW LIGHT, AND IN LOW LIGHT AND HIGH HUMIDITY

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Means of three replicates					
	Plants Grown in Full Light	Plants Grown in Low Light	Plants Grown in Low Light and High Humidity		
Relative growth rate (mg/mg/day) K/Na ratio in roots K/Na ratio in uptake to shoots Relative transpiration Relative potassium plus sodium content	$0.163.0\pm0.30.68\pm0.08100$	$0.07 \\ 2.5 \pm 0.1 \\ 0.73 \pm 0.07 \\ 70$	$0.06 \\ 2.4 \pm 0.1 \\ 2.6 \pm 0.1 \\ < 5$		
in shoots ( $\mu$ -equiv/mg)	$2 \cdot 50 \pm 0 \cdot 1$	$3 \cdot 20 \pm 0 \cdot 1$	$3 \cdot 25 \pm 0 \cdot 05$		

Though K/Na ratio in the shoot is proportional to that in the root at any one concentration, there is a decrease in selectivity of the ion supply to the shoot relative to that of the root contents, as potassium plus sodium is increased in the solution (Fig. 5). This decrease is partly (if not entirely) due to the action of transpiration, which reduces selectivity in the shoot uptake at higher concentrations. Table 5 gives

the ratio of potassium to sodium in plants grown under different conditions of light and humidity on solutions containing 15 m-equiv/l potassium, 45 m-equiv/l sodium, and 20 m-equiv/l calcium plus magnesium. Seedlings were grown on this solution at the same high light intensity for 3 days after transfer to the culture solution, and then uptake measured in a subsequent period of 7 days at the different conditions: high light, low light, and low light at high humidity. The K/Na ratio in the roots was little affected by the different relative growth rates or transpiration. Similarly, growth rate had little effect on selectivity in the shoot at high transpiration, but there was a large difference between plants growing at high and low transpiration levels. This behaviour was very much like that of barley (Pitman 1965b), where transpiration did not affect total uptake, but selectivity of potassium for sodium was much higher at low transpiration levels.

#### IV. DISCUSSION

The results given in the present paper provide a basis for comparing uptake of potassium and sodium by two plants of different structure and selectivity. The difference in selectivity is possibly more useful in these studies of comparative physiology than the difference in structure. Collander's (1941) results showed that there was no clear distinction between cereals and dicotyledonous plants in selectivity for potassium, although these plants have a very different root anatomy.

The difference in selectivity between mustard and barley (i.e. in the K/Na ratio in the plant) is largely one of degree and not of kind. There are many impressive similarities in these plants' patterns of ion uptake, that can be interpreted by a common basic model for potassium and sodium transport to the shoot. In both plants, uptake to the shoot appears to be governed by a root process, i.e. the average proportion of potassium to sodium in leaf cells is not entirely due to the properties of these cells but is a measure of the proportions supplied to the shoot from the root. In the present work, the proportion of potassium to sodium in mustard shoots was relatively constant over long periods of development despite uneven distribution within the shoot [cf. barley (Pitman 1965b)].

Although potassium is preferred in this uptake (K/Na ratio in the shoot is greater than K/Na ratio in the solution), sodium can substitute for potassium in uptake to both root and shoot, and at both 10 and 20 m-equiv/l total uptake is independent of the proportions in the solution. The process thus appears to be limited by the capacity of some other factor and not simply by the separate potassium and sodium concentrations. By analogy with barley, it seems reasonable to suggest that in mustard total uptake of potassium and sodium is largely controlled by an active anion transport within the root [but probably at the xylem parenchyma and not at the endodermis (Pitman 1965c)].

The proportions of potassium to sodium taken up by this process in both mustard and barley show similar relations to solution content and to transpiration. In particular, at the same potassium plus sodium concentration in the solution, the K/Na ratio in the shoot was linearly correlated with that in the root but *not* with that in the solution. Another similarity between mustard and barley is the effect transpiration has in reducing the selectivity in uptake to the shoot, though it

does not affect the selectivity shown by the root, or the total uptake (Table 5). Again, as in barley, calcium and magnesium do not substitute for potassium in the way sodium does, and their uptake appears to be by a separate process, independent of potassium uptake.

It was argued from observations on barley seedlings (Pitman 1965b) that the total uptake of potassium and sodium to the shoot was controlled by an independent process related to metabolism, such as an active transport of anion. In view of the similarity between the two plants investigated it is suggested that the model of Figure 7 is a useful way of summarizing the results and showing the kind of experiments needed to study this system. No component directly proportional to transpiration and concentration is included (passive component) as there seems to be no evidence for it in either barley or mustard, but such a component may be important in uptake of divalent cations.



Fig. 7.—Suggested processes involved in uptake of potassium and sodium to the shoot. Total uptake is controlled by an active transport of anions. Selectivity can be determined by movement in the cytoplasms of cells in the root (high selectivity) and by movement in cell walls or intercellular spaces (low selectivity). The high selectivity of root cells is controlled by an active cation transport.

In the model, total uptake of potassium and sodium to the shoot is controlled by the anion transport process. The proportion of potassium and sodium supplied to the shoot would be partly determined by the relative permeability to these ions at this site of transport, but also by selectivity of ions reaching this site, a kind of preselection. It is suggested, therefore, that the properties of the root cell play an important part in this preselectivity. In support of this view is the marked correlation between root and shoot selectivity at the same level of potassium plus sodium either when the K/Na ratio or the ratio (K+Na)/(Ca+Mg) was varied in the solution. As little of the transport through the root cortex is likely to take place through the vacuoles (due to the relatively low fluxes into and out of them), it is considered that it is movement in the cytoplasm of some root cells that contributes to preselectivity.

By contrast, the effect of transpiration in selectivity of the supply to the shoot, unaccompanied by any effect in root selectivity, is taken to show that some other pathway is important in these conditions. Such a pathway appears to be of low

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selectivity and it is suggested that the free space (cell walls and intercellular spaces) fills this category quite adequately. At low solution concentrations the cytoplasmic pathway may be from cells in the cortex to cells in the stele, but at higher concentrations it seems adequate to postulate movement in cytoplasm only through the xylem parenchyma (which contain much cytoplasm—P. Smith, unpublished data).

The selectivity in the root cells appears to be determined by active transport of potassium and sodium (Pitman, unpublished data). At low concentrations this process may be important to take ions into the root from the solution, and so in these conditions have more control on the supply of ions to the shoot than the process controlled by anion transport within the stele.

# V. Acknowledgments

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