SODIUM AND POTASSIUM UPTAKE BY SEEDLINGS OF *HORDEUM VULGARE*

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Summary

Uptake of potassium and sodium from culture solutions by barley seedlings under a range of experimental conditions has been determined. It was shown that both sodium and potassium transport to the shoot was due to an active process in the root which was limited by the plant's growth. This process was not available for uptake of divalent cations. Sodium uptake at higher concentrations showed some relation to transpiration and the resulting increase in sodium uptake with concentration reduced the selectivity in the plant for potassium to sodium. It was shown that potassium transport across the root was independent of water flow to the cytoplasm. The role of the cytoplasm in selective ion uptake to the shoot is discussed.

I. INTRODUCTION

The uptake of potassium by barley seedlings appears to be the result of an active process somewhere in the roots which secretes potassium into the transpiration stream (Broyer and Hoagland 1943; Sutcliffe 1957; Russell and Shorrocks 1959). This process is possibly distinct from the uptake of potassium to the cells of the root cortex, which exhibits similar properties. One piece of evidence is that the shoots show greater preference for potassium to sodium than do the roots (Sutcliffe 1957). In spite of this distinction, the processes are not unrelated and can compete with each other, particularly in regions of developing root cells, and when "low salt" plants are transferred to a solution of higher potassium content (Broyer and Hoagland 1943).

Potassium uptake to the shoot need not be an active potassium transport, but could be due to an anion transport with concomitant potassium uptake to balance the charge transfer. In this case, the uptake of potassium and sodium could be limited by the same process (i.e. active anion uptake), and the potassium to sodium preference determined either by a sodium extrusion pump or simply by the difference in potassium and sodium permeabilities in the membrane across which the anion transport occurred (cf. Briggs 1963). Though much work has been done on potassium and sodium uptake in excised barley roots to investigate the cell's role in such processes, little is known of the processes involved in their uptake by the shoot. Generally, interest has been either in potassium uptake by the shoot alone, or in sodium and potassium uptake at high salt concentrations in relation to "saline" environments.

Although the whole plant is a complex system, a useful simplification for studying the transport to the shoot is to grow plants in culture solutions of constant composition. Then the cells of the root come to flux equilibrium with the solution,

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and the root is part of the steady-state system relative to the process of uptake to the shoot. In these conditions determination of shoot contents measures the activity of this process, as translocation out of the shoot is negligible compared with the uptake (Greenway and Pitman 1965).

This paper describes experiments to investigate this steady state, and discusses the relation between potassium and sodium uptake to the shoot.

II. Experimental Methods and Materials

Seedlings were grown from hulled seed germinated in distilled water on acid-washed filter paper. The germinated seeds were selected for uniformity at 36 hr and transferred to polythene mesh supported on the surface of the culture solution by stainless steel wires. Crystallizing dishes 5 cm deep and 8 cm in diameter were used as containers for eight seedlings. After a further 36 hr in the dark the dishes were illuminated in a controlled environment. The day temperature was 21°C and the night temperature 18°C; day length was 16 hr and relative humidity *c.* 50–60%. The relative growth rate under these conditions was 0·21 g/g/day (Table 1).

The culture solutions were varied by addition or deletion of most of the components but the basic solution contained 10 m-equiv/l in all of KNO_3 plus $NaNO_3$, together with 4 m-equiv/l $MgSO_4$, 6 m-equiv/l $Ca(NO_3)_2$, 0·8 m-moles/l $NH_4H_2PO_4$, EDTA–Fe solution, and trace elements according to Arnon (1938).

At each harvest the plants were taken from the solution, rinsed in distilled water for 30 sec to remove surface solution, blotted lightly, and divided into "root" and "shoot" by cutting just above the scutellum. The seed was removed and discarded. The tissue was dried, weighed, and then treated with HNO_3 and boiling distilled water to extract potassium and sodium; recovery was 98% efficient. Potassium and sodium concentrations in the extract were determined with an E.E.L. flame-photometer.

In Section III the shoot and root dry weights are given and also potassium and sodium contents relative to the dry weight of each plant part (expressed as μ-equiv/mg.). This quantity is here called the "relative content". In some cases the potassium or sodium content is expressed as μ-equivalents per plant part, but in those cases where it is not given it can be calculated from the dry weights and relative contents.*

Duplicates were used in each experiment, and the average difference between 25 pairs of estimates was as follows: dry weight 4·5%; potassium content 7·0%; relative potassium content 5·2%; sodium content 14%; relative sodium content 12·4%; potassium/sodium ratio 13%. These values give a guide to the reliability of the means quoted in the tables, but doubtful experimental observations were repeated several times. The difference in reliability of potassium and sodium estimates is probably due to the greater concentration of sodium than potassium in the solution, but smaller sodium than potassium content of the plants. Small contaminations with solution would then have had a greater proportionate effect on sodium than potassium.

* "Uptake" in this paper means change in content, not in relative content, i.e. it has the units μ-equivalents and not μ-equiv/mg.

III. Results

(a) *Potassium and Sodium Uptake during Seedling Growth*

Seeds of this variety of barley weighed 44 mg and contained 8 μ-equiv. of potassium and 0·4 μ-equiv. of sodium. Three days from germination, when the coleoptiles were about 5 cm long, plants were put from the dark to the light. The first leaf emerged by the fourth day, the second leaf at about 7 days, and the third leaf at about 11 days from germination. By the time the third leaf appeared the first leaf had reached its maximum dry weight.

Table 1 gives root and shoot dry weights and relative contents of potassium and sodium over the period of 11½ days after germination for plants grown in the basic culture solution containing 7·5 m-equiv/l sodium and 2·5 m-equiv/l potassium.

Table 1

Potassium and Sodium Uptake during Growth by Barley Seedlings

Culture solution contained 2·5 m-equiv/l potassium and 7·5 m-equiv/l sodium

Time (days)	Shoot				Root			
	Dry Weight (mg)	Relative Potassium Content (μ-equiv/mg)	Relative Sodium Content (μ-equiv/mg)	K/Na Ratio	Dry Weight (mg)	Relative Potassium Content (μ-equiv/mg)	Relative Sodium Content (μ-equiv/mg)	K/Na Ratio
2·0	4·33	0·64	0·03	22	3·7	0·61	0·08	7·7
4·5	14·0	1·45	0·15	9·7	4·7	0·94	0·30	3·1
5·5	18·1	1·70	0·20	8·5	4·8	0·93	0·39	2·3
6·5	22·2	1·70	0·20	8·5	5·8	0·95	0·42	2·3
7·0	24·5	1·64	0·21	7·8	5·8	1·04	0·38	2·7
8·0	34·2	1·52	0·21	7·2	8·65	1·07	0·31	3·4
9·5	42·7	1·90	0·22	8·6	13·2	1·08	0·30	3·6
11·5	57·4	2·20	0·27	8·9	22·1	1·22	0·26	4·6

There was at first a higher K/Na ratio in the shoot due to potassium transport from the seed, but the ratio fell to a relatively steady value of 8·7. This is shown in Figure 1, where shoot potassium content is plotted against shoot sodium content.

In spite of the constant ratio of potassium to sodium in the shoot, there can be considerable redistribution of potassium or sodium within the plant. The distribution between the first, second, and third leaves at 11½ days is shown in the following tabulation:

	Dry Weight (mg)	Relative Potassium Content (μ-equiv/mg)	Relative Sodium Content (μ-equiv/mg)	K/Na Ratio
Leaf 1	16·0	2·40	0·32	7·5
Leaf 2	17·9	2·20	0·15	15·4
Leaf 3	4·9	1·30	0·05	23
Rest of shoot	18·6	2·40	0·36	6·7

This distribution, previously demonstrated by Greenway (1962), has been shown to be due to translocation of potassium from the oldest leaf (Greenway and Pitman 1965). As the youngest leaf matures, the K/Na ratio in the oldest leaf can fall from about 8 to about 2. The relative content of both potassium and sodium in the roots did not show any appreciable trend in spite of root development (Table 1). These results support the view that the cells in the root are in flux equilibrium with the culture solution and show that this equilibrium does not change appreciably over the period of the experiment with age. Such a change would have shown as the proportion of young to older cells decreased.

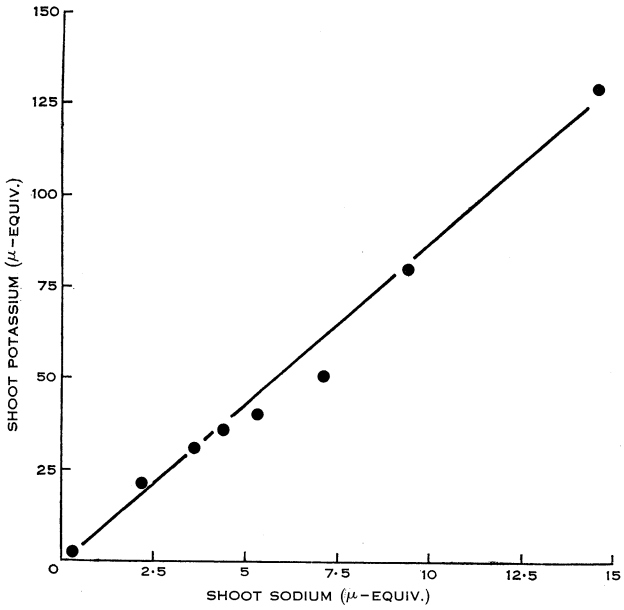

Fig. 1.—Regression of shoot potassium content on shoot sodium content. The regression line has a slope of 8·75 and potassium content = −2 m-equiv. at zero sodium content.

The pattern of uptake by shoots and roots shows that concentrations in the root relative to the transport process to the shoot are more or less constant although the amount of transport, and of root, increases with growth. By measuring the K/Na ratio in the shoot at, say, 7 days, an estimate therefore can be made of the effect of variations in the culture solution on the transport mechanism, so long as the contribution of the seed is small compared with the total uptake. This procedure was used in some of the experiments, but in others at low potassium concentration two harvests were made to eliminate the effect of seed contribution.

(b) Effect of Variation in Culture Solution Content on Potassium and Sodium Uptake

The anion content of the culture solution had little or no effect on the amounts of potassium and sodium taken up to the shoot, except in conditions of evident major nutrient deficiency. Substitution of chloride for nitrate in the culture solution only altered the shoot K/Na ratio when nitrate was obviously deficient, and variation

in sulphate concentration was also without effect. Consequently only the relation between solution cation content and shoot sodium and potassium uptakes was investigated, and the range of variation excluded conditions in which growth could have been limited by nutrient deficiency. Deficiencies affect structure of the plant as well as growth, making it difficult to separate effects of ion competition and structural damage. There were three kinds of experiments: variation in divalent cation when potassium and sodium concentrations were constant, variation in the K/Na ratio when total (K+Na) concentration was constant, and variation in total (K+Na) concentration when the K/Na ratio was constant.

TABLE 2

EFFECT ON POTASSIUM AND SODIUM UPTAKE OF VARIATION IN CALCIUM AND MAGNESIUM LEVELS IN A BASIC CULTURE SOLUTION

Solution contained 2·5 m-equiv/l potassium and 7·5 m-equiv/l sodium. Results are for two separate experiments

(Ca+Mg) Concentration (m-equiv/l)	Shoot Dry Weight (mg)	Shoot Relative Contents		Shoot K/Na Ratio	Root K/Na Ratio	Shoot (K+Na) Content (μ-equiv.)
		Potassium (μ-equiv/mg)	Sodium (μ-equiv/mg)			
Experiment 1						
1	21·2	1·60	0·28	5·8	2·6	40·6
5	21·6	1·64	0·23	7·3	2·7	40·4
10	23·0	1·70	0·19	8·7	3·6	43·7
15	21·3	1·63	0·19	8·3	3·4	39·1
20	21·1	1·64	0·19	8·7	3·0	38·4
Experiment 2						
10	32·9	1·99	0·22	8·9	2·9	72·9
30	33·8	1·85	0·20	9·2	3·1	69·4
50	35·0	1·77	0·20	9·0	3·1	69·0
70	33·4	1·89	0·23	8·2	3·1	70·7
90	32·9	1·72	0·22	7·8	2·1	63·8

Table 2 shows how divalent cation concentration affected uptake to the shoot from a solution containing 2·5 m-equiv/l potassium and 7·5 m-equiv/l sodium. The Ca/Mg ratio was constant at 3 : 2, but other experiments have shown uptake of potassium or sodium to be independent of the proportion of calcium to magnesium. Over the range 10–70 m-equiv/l of (Ca+Mg), uptakes of potassium and sodium to both root and shoot were independent of divalent cation concentration; and K/Na ratio showed little change. At lower concentrations of calcium and magnesium there was an increased sodium uptake to the shoot and the K/Na ratio was lower at these levels. The K/Na ratio for roots was also decreased but by a smaller extent than for the shoots.

A similar rise in K/Na ratio with increased (Ca+Mg) concentration was found at higher (K+Na) concentrations. For plants grown in solutions containing 60

m-equiv/l (K+Na) (K/Na ratio = 1/19), and varied (Ca+Mg) concentrations of 1, 10, 30, 60, and 90 m-equiv/l, the K/Na ratios taken up to the shoot were 0·85, 1·20, 1·20, 1·40, and 1·40 respectively. As before, the largest change in K/Na ratio was between 1 and 10 m-equiv/l of (Ca+Mg) and further increase was small. The maximum K/Na ratio in this example was 1·40; by contrast, the ratio was 2·8 from a solution of the same K/Na ratio (1/19) but of lower concentration [0·5 m-equiv/l potassium, 9·5 m-equiv/l sodium, and 10 m-equiv/l (Ca+Mg)]. This difference was due to greater sodium uptake and lower potassium uptake at the higher concentration; the K/Na ratio in the roots was the same in both cases.

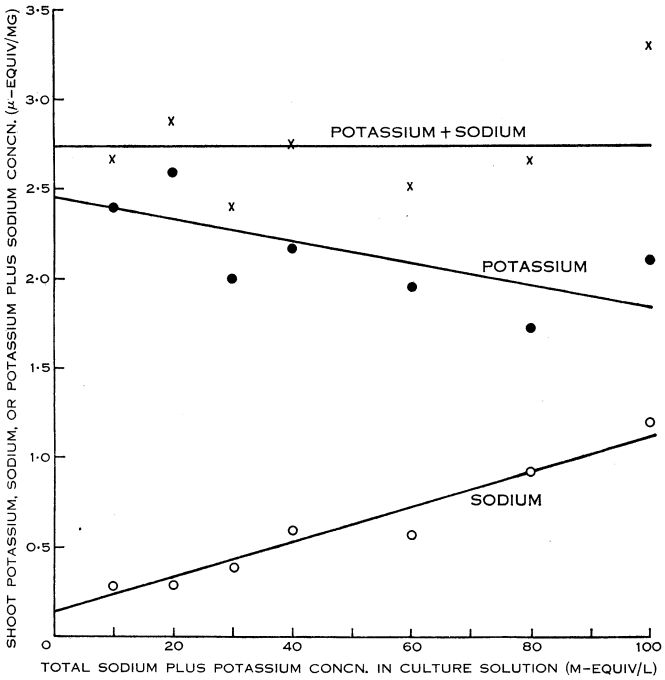

Fig. 2.—Effect of total potassium plus sodium concentration in culture solution on shoot uptake of potassium and sodium.

This behaviour shows there were two factors acting to increase sodium uptake (and so reduce the K/Na ratio): one was low divalent cation concentration; the other was high (K+Na) concentration. Whereas the low (Ca+Mg) level induced a lower K/Na ratio in the roots as well as in the shoot, (K+Na) concentration had little effect on K/Na ratio in the roots.

Figure 2 shows another example of (K+Na) concentration affecting shoot K/Na ratio. Plants grown for 7 days on a solution of 2·5 m-equiv/l potassium, 7·5 m-equiv/l sodium, and 10 m-equiv/l (Ca+Mg) were transferred to a range of concentrations containing the same proportions of potassium, sodium, calcium, and magnesium, and were harvested 3 days later. This procedure minimized the growth reduction at higher concentrations, but did not prevent it entirely. Consequently, to compensate

for differences in growth, potassium and sodium uptakes are given in Figure 2 as change in potassium or sodium content/change in dry weight. As in the previous examples root cell contents were unaffected by (K+Na) concentrations in this range and the root K/Na ratio was effectively constant at 2·8. Uptake to the shoot was strongly affected by concentration, and shoot K/Na ratio fell from 9 at the lowest to 1·7 at the highest concentration. This decrease was due to changes in both potassium and sodium uptakes but the large variability in the ratio change in potassium/change in dry weight makes it impossible to show equivalence of sodium increase and potassium decrease. The regression of (K+Na) against concentration has a slope of $0 \cdot 0017 \pm 0 \cdot 007$.

TABLE 3

POTASSIUM AND SODIUM UPTAKE TO THE SHOOT AS AFFECTED BY TOTAL POTASSIUM PLUS SODIUM CONCENTRATION

Solution K/Na ratio = 1 : 3; total calcium plus magnesium concentration equal to total potassium plus sodium concentration

Solution (K+Na) Concentration (m-equiv/l)	Shoot Dry Weight (mg)	Relative Potassium Content (μ-equiv/mg)	Relative Sodium Content (μ-equiv/mg)	Shoot K/Na Ratio	Root K/Na Ratio
1·25	24·5	1·21	0·52	2·3	0·85
2·50	25·9	1·38	0·39	3·6	0·90
5·0	24·8	1·40	0·31	4·5	1·60
10·0	24·3	1·60	0·25	6·5	2·50

The increased sodium uptake with concentration appears to be related to transpiration. In the above experiment plants in the 60 m-equiv/l solution transferred to the dark took up proportionately less sodium (K/Na ratio = $8 \cdot 5 \pm 1 \cdot 0$) than plants in the light (K/Na ratio = $3 \cdot 4 \pm 0 \cdot 2$). In another experiment using similar solutions but at lower transpiration K/Na ratios were 9·3, 9·6, 8·2, and 5·5 in solutions of 10, 20, 40, and 60 m-equiv/l respectively. In both these examples, at low transpiration the K/Na ratio at high concentrations tends towards that at lower concentrations. How transpiration acts is uncertain. Increased sodium uptake could be due to an action on diffusion across the cortex to the site of uptake, or else uptake of potassium and sodium could be the sum of two processes, one selective for potassium and independent of transpiration, the other non-selective but proportional to transpiration and concentration.

Uptake of potassium and sodium at concentrations below 10 m-equiv/l, is given in Table 3. As the total concentration was increased from 1·25 to 10 m-equiv/l with the K/Na ratio = 0·33, there was an increase in relative potassium content in the shoot from 1·2 to 1·6 μ-equiv/mg and a decrease in relative sodium content from 0·52 to 0·25 μ-equiv/mg, i.e. the ratio of K/Na in the shoot rose from 2·3 to 6·5. Uptake to the roots followed a similar pattern, and the corresponding change in the K/Na

ratio was from 0·85 to 2·5, though as in previous examples the sum of the relative contents of potassium and sodium in the root was less than in the shoot. This drift to lower shoot K/Na ratio at low total (K+Na) concentrations was independent of calcium concentration. Since the effects of transpiration and concentration are minimal in the range (K+Na) = 10–20 m-equiv/l, these concentrations have been used in experiments where K/Na ratio was varied.

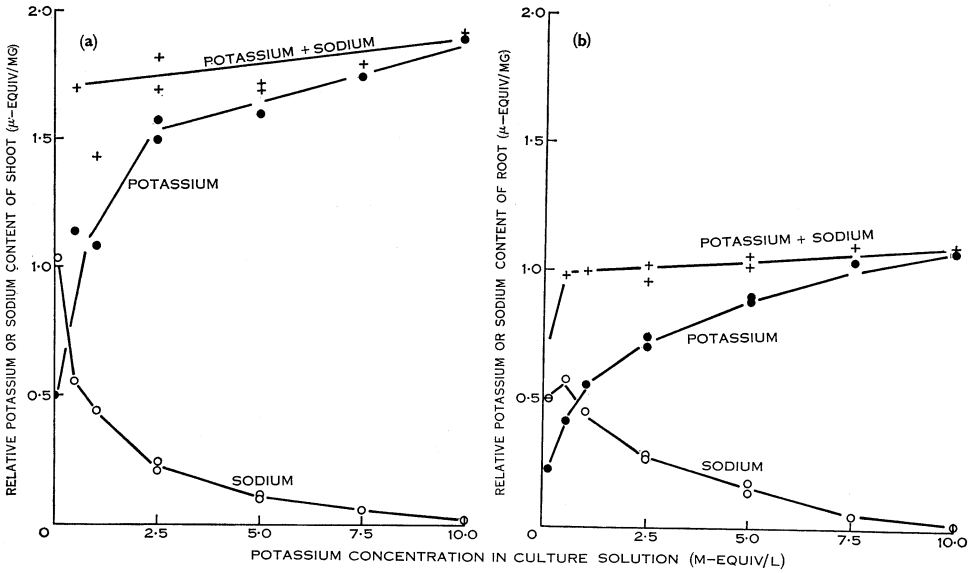

Fig. 3.—Variations in relative contents of sodium and potassium in the shoot (*a*) and in the root (*b*) with solution content of sodium and potassium. Total solution concentration was 10 m-equiv/l but the K/Na ratio was varied. ● Relative potassium content. ○ Relative sodium content. + Relative potassium plus sodium content.

Variation in the K/Na ratio in the solution had a marked effect on the proportion of potassium to sodium in both shoot and root, but had negligible effects on growth, except where potassium was deficient. Increased potassium concentration produced a disproportionately greater increase in relative potassium content of the plant at low concentrations, but had little effect at higher concentrations (Fig. 3). The concomitant decrease in sodium concentration reduced sodium uptake, so that the K/Na ratio in shoot and root increased with increasing K/Na ratio of the solution (Fig. 4). As in the previous example, shoot K/Na ratio was nearly proportional to root K/Na ratio. In this and other experiments given above, the sum of shoot potassium and sodium uptakes was unaffected by the proportion of potassium to sodium in the shoot, i.e. sodium behaves as if its uptake were limited by the same factors as for potassium uptake, though there is preferential uptake of potassium. In this way sodium differs markedly from the divalent cations. Although the shoot contains about one-third as much divalent as univalent cation, the total uptake of potassium and sodium was unaffected by divalent concentration increase from 10 to 70 m-equiv/l (Table 2). Thus the process of potassium and sodium uptake to the shoot does not seem to be the same as that responsible for divalent cation uptake.

(c) *Exudation from Cut Shoots*

It is common knowledge that exudate from a cut shoot can contain potassium at a relatively high concentration. This observation has been used by many authors to support the view that potassium uptake results from active uptake, as both potassium and anions such as bromide can be in a high concentration in the exudate. If potassium and sodium in the exudate are taken up by the same process as in shoot transport, then potassium should be replaced by sodium to the same extent as in the shoot.

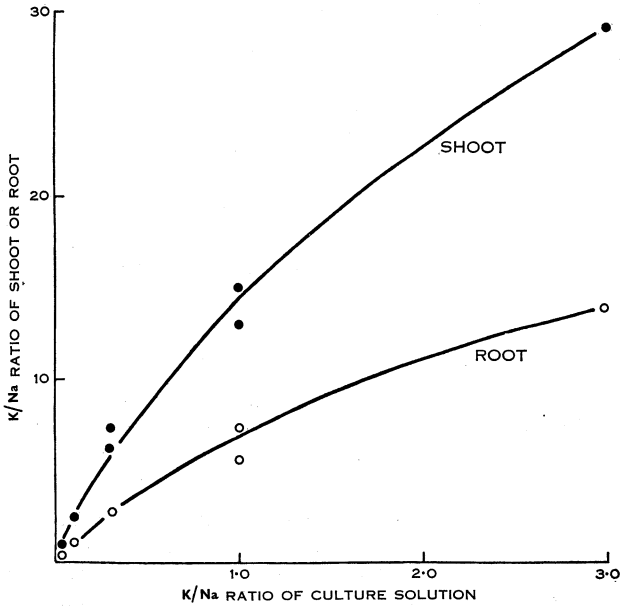

Fig. 4.—K/Na ratio of shoot and of root plotted against K/Na ratio of culture solution. Total (K+Na) concentration of solution = 10 m-equiv/l.

Table 4 gives some measurements of potassium and sodium in exudate from cut shoots, and in the shoots which were cut off. The plants were grown in the basic solution containing 10 m-equiv/l (K+Na), but with varied K/Na ratios. Each determination was made in duplicate. The concentration in the exudate decreased a little with time from cutting and the values given here were for the period 30–90 min. The amount of exudate and total (K+Na) concentration was independent of concentration, but the K/Na ratio showed the same drift as found for shoot uptake (Fig. 4). If allowance is made for the potassium derived from the seeds, this ratio in the exudate is the same as that in the shoots as a whole. For example, the shoots of plants grown in 0·5 m-equiv/l potassium and 9·5 m-equiv/l sodium weighed 18·2 mg and contained 18·5 μ-equiv. potassium and 5·4 μ-equiv. sodium. The seeds contained 8 μ-equiv. at the start and 1·5 μ-equiv. at harvest, i.e. 5–6 μ-equiv. in the plant came from the seeds and the ratio of potassium to sodium taken up from the solution would then be 2·2–2·4.

In these examples the sodium concentration was not higher than 12 m-equiv/l, which is little different from 9·5 m-equiv/l, the solution concentration. Higher concentrations can be reached in plants grown in solutions of sodium alone, but then the exudate is reduced to about 2–3 mg/hr/plant. High values were also obtained, though, in plants which grew for 3 days on 0·5 m-equiv/l potassium, 9·5 m-equiv/l sodium, and then were transferred to a solution containing sodium alone. In this

TABLE 4

EXUDATION FROM CUT BARLEY SHOOTS: POTASSIUM AND SODIUM CONTENT OF EXUDATE AND WHOLE SHOOTS

Solution Concentration (m-equiv/l)		Amount of Exudate (mg/hr/plant)	Concentration in Exudate (m-equiv/l)		K/Na Ratio in Exudate	Whole Plants	
Potassium	Sodium		Potassium	Sodium		Shoot K/Na Ratio	Root K/Na Ratio
0·5	9·5	7·3	25	12	2·1	3·4	0·8
1·0	9·0	7·4	24	8	3·1	4·0	1·1
2·5	7·5	6·4	30	4	7·1	8·1	1·9
6·0	4·0	7·1	35	1·6	22	18	6·7
8·0	2·0	6·8	36	1·0	36	30	8·9

case the potassium and sodium concentrations were 1·3 and 25 m-equiv/l respectively, and the exudate 6·8 mg/hr/plant. The difference in exudate volume was possibly due to potassium deficiency in the plants grown continuously on 10 m-equiv/l sodium solution.

TABLE 5

UPTAKE OF POTASSIUM AND SODIUM FROM BASIC CULTURE SOLUTION BY PLANTS GROWN EITHER IN THE LIGHT OR THE DARK

Culture solution contained 2·5 m-equiv/l potassium and 7·5 m-equiv/l sodium

Age of Plant (days)	Conditions	Shoot Dry Weight (mg)	Relative Potassium Content (μ-equiv/mg)	Relative Sodium Content (μ-equiv/mg)	Shoot K/Na Ratio	Total Uptake (μ-equiv.)
5	Light	15·2	1·29	0·18	7·0	21·9
	Dark	15·2	1·15	0·18	6·4	20·3
6·5	Light	21·9	1·63	0·22	7·5	40·5
	Dark	21·2	1·46	0·20	7·3	35·2

(*d*) *Uptake of Potassium and Sodium in Relation to Energy Source*

When seeds were grown in the dark for 5–6 days from germination there was little difference in dry weights and potassium and sodium uptake between these and similar plants grown at the same temperature in a normal day/night regime (Table 5). The pattern of behaviour was different for plants transferred to the dark

after growing for about 7 days in the light—i.e. 16 hr day, 8 hr night (Fig. 5). During the period 9–11 days there was a small decrease in dry weight and potassium and sodium uptakes were stopped completely. During the first 2-day period there was some increase in dry weight (from seed reserves) and an appreciable potassium and

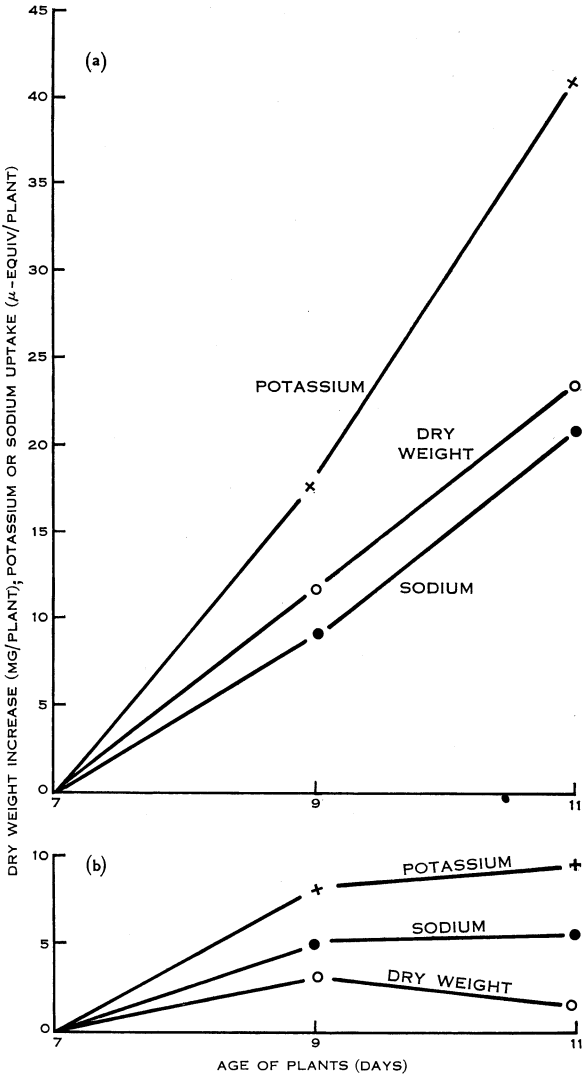

Fig. 5.—Uptakes (μ-equiv/plant) of potassium and sodium and increases in dry weights (mg/plant) (*a*) by plants in normal day/night regime and (*b*) by plants kept in the dark from day 7 onwards.

sodium uptake. This uptake was presumably analogous to that which takes place during the night in normal growth. For example, seedlings grown in a basic solution containing 0·5 m-equiv/l potassium to 9·5 m-equiv/l sodium took up 0·50 μ-equiv. potassium/hr/plant during the day, and 0·37 μ-equiv. potassium/hr/plant at night.

In this case day and night temperatures differed by 2·8°C which was enough to account for the different rates of uptake.*

During the first 5 days in the dark, uptake of potassium and sodium follows growth and uses seed reserves. By 7 days these are depleted and then transference to the dark stops photosynthesis and growth. Eventually this restriction stops potassium and sodium uptake, but for some time this process can utilize food reserves translocated from the leaves or stored in the roots.

The K/Na ratio taken up in the dark was lower than in the light and, as in other examples, there was a parallel decrease in root K/Na but sodium uptake stopped when potassium uptake stopped, although there continued to be some water uptake and transpiration. The accumulation of potassium and sodium by the roots was stopped in the dark at the same stage as uptake to the shoots.

IV. Discussion

In the present experiments, the measurement of shoot contents of plants grown under uniform conditions is really an estimate of a root process. The shoot is an incidental sink used here to estimate transport through a system that appears to be in a steady state relative to the uptake process. This view is supported by the demonstration that the proportions of potassium to sodium in the plant can be maintained at the same level over 11½ days. Calculations based on data given by Greenway (1962) show this holds at least until the plants are 25 days old, and in another example (Greenway, personal communication) until flowering. Although the uptake increases with development the plant appears to maintain the same diffusion path and uptake restrictions in the root relative to the uptake process.

In some experimental conditions, uptake to the shoot can be in direct competition with uptake to root cells, particularly if the plant is transferred from a solution of low to one of higher concentration. This complication can be largely avoided by growing seedlings in the same relatively high concentration [10 m-equiv/l (K+Na)].† In these conditions root cells have little or no net uptake when their development has finished, though they still have a not insignificant flux into and out of the vacuoles. According to Wiebe and Kramer (1954) most of the rubidium uptake (which behaves like potassium) to the shoot takes place through the regions of mature cortical cells away from the root apex. As a result of their negligibly low net uptake in the present experiments, these cells cannot compete with the shoot uptake process for potassium and sodium. This view is not contradictory to the observations that root cells compete with the shoot for *isotope* in experiments with labelled solutions, for competition here depends on the influx and not the net flux.

At higher concentrations (60 m-equiv/l) uptake of potassium and sodium to the shoot is affected by transpiration and may be the sum of several processes, but at lower concentrations (10 m-equiv/l) uptake behaves like a single active process. This view is supported by the similarity between exudates and shoot contents.

* Q_{10} for potassium uptake is 2·4–2·6.

† At lower concentrations there appears to be some competition between the two processes, leading to a reduced K/Na ratio in shoot and root (cf. Table 3).

Although differing in selectivity, the behaviour of potassium and sodium at these lower concentrations is the same in many important respects. Both potassium and sodium uptakes depend on metabolic reserves and are stopped when these are depleted. The sum of potassium and sodium uptake is independent of the proportion of potassium to sodium in a number of experiments where total concentration, calcium level, or K/Na ratio were varied in the solution. In particular, this substitution of sodium for potassium is also shown in root exudates. Finally, both potassium and sodium uptakes are unaffected by increase in (Ca+Mg) concentration above a certain level. This similarity in behaviour can be adequately explained by a single active process determining both potassium and sodium uptakes. Moreover, this process must be independent of divalent cation uptake, as there is no interference with potassium and sodium uptake by calcium and magnesium. The uptake of calcium and magnesium (which is as large as one-third of the potassium plus sodium uptake) must then be due to a separate process.

Insufficient evidence is presented here to distinguish between possible mechanisms of selectivity in the active process. The relation between potassium and sodium uptakes and solution content could be explained as well by a "carrier–competition" model as by an active anion uptake determining cation uptake analogous to cell-uptake processes (Briggs 1963).

Several locations have been suggested for the active uptake process of potassium and the topic has been discussed in many papers without satisfactory solution. The above results give more examples of the difference in K/Na ratio between root and shoot quoted by Sutcliffe (1957). He suggested that this difference showed the need for a process in the root separate to the uptake responsible for plasmalemma transport. This argument would be conclusive if it could be shown that K/Na ratio in the cytoplasm of cortical cells was less than that in the shoot uptake. The answer to this problem requires the determination of the salt relations of the cortical cells, and in particular investigating the presence of active potassium or sodium pumps at the tonoplast. In any case it is useful to think of the uptake as separate from root cell uptake, to avoid the assumption that root uptake (i.e. by excised roots) is the same as shoot uptake.

In spite of the indeterminacy about the mechanism and location of the active process of the shoot, the cytoplasm must play an important part in transport of potassium and probably sodium across the cortex. This view is supported by observations on tomatoes (Jackson and Weatherly 1962) and on barley for transport of calcium (Barber and Koontz 1963), and by the following examples.

The flux of potassium across the stele can be as high as 0·3 μ-equiv/plant/hr from a solution containing only 0·5 m-equiv/l potassium [+9·5 m-equiv/l sodium+ 10 m-equiv/l (Ca+Mg)]. The roots in this case were about 10 cm long and had an outer radius of 200 μ, giving a minimum flux of 65 p-equiv/cm^2 root surface/sec. Transpiration was about 50 mg/plant/hr, i.e. only 5 p-equiv/cm^2 root surface/sec of potassium could have been transported as a mass flow of solution. At least 60 p-equiv/cm^2 root surface/sec must have diffused across the roots independently of water uptake.

Diffusion across a cylindrical stele in the steady state is

$$J = D(C_2 - C_1)/R_2 \ln(R_2/R_1),$$

where J = flux, D = diffusivity, and C_2 and C_1 are concentrations at R_2 and R_1, the external and internal radii. If diffusion of potassium were taking place across the roots only in the cell walls, which behave as free space for potassium and sodium, the flux J would be 20×60 p-equiv/cm^2/sec, as the walls occupy not more than 5% of the area.* D for sodium is *c.* 3×10^{-7} cm^2 sec^{-1} when the solution concentration is 10 m-equiv/l and (Ca+Mg) concentration = 10 m-equiv/l (Pitman, unpublished data). R_2 and R_1 are 200 μ and 80 μ respectively, ignoring the stele, and so $(C_2 - C_1)$ would have to be 70 m-equiv/l. Even if D were as large as 10^{-6}cm^{2}sec^{-1} the difference in concentration would still be about 10 times larger than the solution concentration. This concentration difference is also larger than could be expected for potassium in the Donnan phase of the cell walls. The Donnan concentration is *c.* 400–500 m-equiv/l in about 1–2% of the tissue (50% of the cell walls), and for this particular solution, the (K+Na) concentration would have been only about 60 m-equiv/l, of which 3 m-equiv/l was potassium.

It does not seem possible for diffusion or flow of water in cell walls to account for the high fluxes of potassium across the root at these low concentrations, and the most reasonable alternative is that movement of potassium across the root takes place in the cytoplasm. Fluxes into and out of the vacuoles are not large enough and, in any case, the specific activity of uptake to the shoot becomes nearly equal to that in the solution long before the specific activity of the vacuoles rises (Greenway and Pitman 1965).

In this example potassium transport is obviously greater than cell wall diffusion, but the behaviour of plants in a solution of 0·5 m-equiv/l potassium+9·5 m-equiv/l sodium is not very much different from that of plants growing in solutions of higher concentration and the same K/Na ratio. It is most likely that in these other solutions potassium uptake to the shoot is also supplied predominantly by diffusion in the cytoplasm, and, moreover, that sodium may also diffuse in this phase. Movement of potassium and sodium mainly in the cytoplasm across the root would account for the striking relationship between K/Na ratios in root and shoot K at lower concentrations, or when low calcium in the solution increased cell wall potassium and sodium cell wall diffusion might be more important, and for this reason lead to a reduction in the K/Na ratio in the shoot.

The structure of the stele in barley plants does not favour cell wall diffusion and here movement in the cytoplasm must be important. The diffusion of univalent ions in the cytoplasm of the cortex would do no more than extend the pathway. There is less information about anion movement in the root, but the Donnan concentration in the cell walls would not favour anion diffusion. It is possible that films of water in the intercellular spaces could be a pathway of anion movement in the root, but

* The value estimated from photographs is about 3% of which about 50% will be unavailable as a pathway—hence this could be an underestimate by a factor of about 4.

cytoplasmic transport could explain the differences that exist in uptake of anions as well as of univalent cations.

Potassium and sodium content of the root has not been emphasized in this discussion as much has been published on uptake of potassium and sodium by excised barley roots. Moreover, the contents of the roots are an average of the positions of flux equilibrium of cells in different parts of the roots, and can be very different from the content of, say, cortical cells. In one example, the average K/Na ratio for the root as a whole was 2·4, for the stele 4·1, and for the cortex 2·1. These differences make it very difficult to relate shoot uptake to root content, beyond the observation that the K/Na ratio in the shoot appears to be proportional to the K/Na ratio in the root.

The transpiration-dependent uptake, which will be the subject of a further paper, may be equivalent to the transpiration-dependent uptake observed for potassium and nitrate in wheat (Kihlman-Falk 1961). Its effects at high salt concentrations (i.e. saline media) would be particularly important if the action of transpiration is on the pre-selective part of potassium and sodium uptake to the shoot, i.e. on the processes of diffusion across the cortex.

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VI. References

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