

TRANSPIRATION AND THE SELECTIVE UPTAKE OF POTASSIUM BY BARLEY SEEDLINGS (*HORDEUM VULGARE* cv. BOLIVIA)

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Summary

Selective potassium uptake by barley seedlings decreases with increased solution concentrations above 20 m-equiv/l. This decrease is shown to be due to an action of transpiration. Total uptake of potassium and sodium was unaffected by transpiration, but increased transpiration rate increased sodium uptake and decreased potassium uptake. These changes in sodium and potassium content are difficult to explain in terms of "passive" metabolic components of uptake. It is suggested that sodium and potassium uptake to the shoot is controlled by active anion transport and that water flux acts on movement of sodium and potassium through the root to the site of active transport.

I. INTRODUCTION

Uptake of potassium and sodium to shoots of barley seedlings appears to be controlled by the same active process, but potassium is taken up in preference to sodium. In a previous paper (Pitman 1965*a*) it was suggested that the reduction in this selectivity which occurs with increased solution concentration was due to some action of transpiration.

Some workers in this field have suggested that transpiration can increase shoot uptake of salt due to increase in a "passive" component (e.g. Hylmö 1953, 1955, 1958). Such a model could explain the decrease in selectivity, which should be quantitatively related to the effect of transpiration on total uptake.

However, there is evidence that the *active* component of shoot uptake can be affected by transpiration. Brouwer, for example (1953, 1954, 1956), found that dinitrophenol (DNP) reduced salt passing through the root by more than would be expected for a transpiration component. He suggested that transpiration affected the "conductivity" of the root to ions, which were then taken up by active transport. An alternative mechanism for reduction in active uptake at low transpiration rates is that the resultant higher concentration in the transpiration stream reduces net uptake (Russell and Shorrocks 1959). Such a mechanism is analogous to the reduction in net salt uptake by beet tissue as the internal concentration increases (Sutcliffe 1952). According to these suggestions, transpiration could interact with the diffusion of ions across the root, and so influence the proportions of sodium and potassium presented at the site of uptake to the shoot.

This paper describes experiments to investigate the relation between potassium selectivity and transpiration and considers the results in relation to mechanisms of shoot ion uptake.

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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 with a day length of 16 hr.

Culture solutions contained varied amounts of KNO_3 , NaNO_3 , $\text{Ca}(\text{NO}_3)_2$, and MgSO_4 . The solution described as "10" contained 10 m-equiv/l of ($\text{KNO}_3 + \text{NaNO}_3$), 6 m-equiv/l of $\text{Ca}(\text{NO}_3)_2$, and 4 m-equiv/l MgSO_4 . The proportion of KNO_3 to NaNO_3 in the solution was either 1 : 3 or 1 : 19 and is given in the text where appropriate. Solutions of higher concentration contained these four salts in the same proportion; thus the solution "100" contained 100 m-equiv/l ($\text{KNO}_3 + \text{NaNO}_3$), 60 m-equiv/l $\text{Ca}(\text{NO}_3)_2$, and 40 m-equiv/l MgSO_4 .

All culture solutions contained 0.8 m-moles $\text{NH}_4\text{H}_2\text{PO}_4$; EDTA-Fe solution and trace elements were according to Arnon (1938) as in preliminary experiments (Pitman 1965a). The proportion of nitrate and sulphate to these nutrients was therefore raised with solution concentration. Such differences did not appear to affect growth or the ion uptake processes studied here. For example, large variations in proportions of nitrate, phosphate, and sulphate produced by replacement with chloride did not affect potassium and sodium uptake except when plant growth was restricted by obvious nutrient deficiency.

Seedling dry weight and potassium and sodium content increases exponentially during at least the first 21 days of development, and the proportion of potassium to sodium in the shoot is constant (Pitman 1965a). Samples taken at intervals of 2-3 days can therefore be used to determine relative growth rates or the proportions taken up of potassium to sodium. Transference of plants from one solution to another with higher concentration but the same proportion of potassium was used to determine the uptake at different concentrations. This procedure was justified because the behaviour in relation to potassium and sodium uptake was the same as in plants grown continuously on the higher solution.

Harvesting and estimation of potassium and sodium content were as described previously (Pitman 1965a), but more replicates were used for each experiment. Standard errors of the mean are given where appropriate.

"High" and "low" transpiration levels were achieved by using a pair of similar chambers with the same illumination and by increasing the humidity in one chamber to as near saturation as possible. In general, the increase in humidity decreased transpiration by about 50%. Further reduction in transpiration required a reduction in light intensity which had effects on growth as well as transpiration.

III. EXPERIMENTAL RESULTS

(a) *Effect of Transpiration on Uptake at Higher Concentrations*

Uptake by barley seedlings growing in culture solutions of different concentrations is inevitably liable to effects of both transpiration and concentration. Both

these factors could affect either or both of two different but related aspects of uptake, i.e. the proportions of potassium to sodium taken up and their combined uptake. To some extent the proportion of potassium to sodium can be ignored when considering total uptake to the shoot. It was shown previously (Pitman 1965*a*) that uptake of sodium and potassium at lower concentrations was independent of the proportions in the solution and appeared to be limited by the same active process. Behaviour at higher concentrations is also consistent with this view; as an example, Table 1 gives uptake of sodium and potassium by plants growing in culture solutions "60" either containing K/Na = 1 : 3 or no sodium. The plants were grown together in the same conditions and both relative content and total uptakes are remarkably similar. Each value

TABLE 1

DRY WEIGHTS OF SHOOTS AND ROOTS OF *H. VULGARE* SEEDLINGS AND COMPARISON OF THEIR UPTAKE OF POTASSIUM AND OF POTASSIUM PLUS SODIUM FROM CULTURE SOLUTIONS OF DIFFERING SODIUM AND POTASSIUM CONTENT

Culture solution "60" either without sodium or with K/Na ratio = 1 : 3 used in these experiments

Age of Plants (days)	Dry Weight (mg)		Potassium Uptake (μ -equiv/mg dry wt.) (no sodium)	Potassium + Sodium Uptake (μ -equiv/mg dry wt.) (K/Na ratio = 1 : 3)
	No Sodium	K/Na Ratio = 1 : 3		
	<i>Shoots</i>			
7	22.2	20.6	2.15 \pm 0.11	2.15 \pm 0.01
10	32.4	33.0	2.35 \pm 0.04	2.38 \pm 0.14
12	44.5	45.5	2.35 \pm 0.08	2.38 \pm 0.04
	<i>Roots</i>			
7	6.6	6.3	1.49 \pm 0.04	1.56 \pm 0.04
10	9.2	8.9	1.64 \pm 0.06	1.64 \pm 0.02
12	10.7	11.7	1.45 \pm 0.01	1.62 \pm 0.04

was the mean of four replicates. It seems reasonable then to compare total uptake of plants irrespective of the proportion of potassium and sodium (except when potassium is deficient or sodium toxic, but these conditions were outside the extremes of the present experiments).

Measurement of "uptake" needs some qualification when a quantitative comparison is to be made at different concentrations and transpiration conditions. The two possible units are " μ -equivalents/plant" and " μ -equivalents/mg", i.e. "total uptake" and "relative uptake". As potassium uptake is so dependent on metabolism, both these measurements are affected by growth. For example, growth of barley seedlings can decrease at higher concentrations. While uptake relative to growth (i.e. to dry weight increase) is relatively constant, total uptake can *decrease* with increased concentration over the same period of time due to this growth reduction. Similar problems of interpretation arise from effects of transpiration rate on growth. This problem is shown in Figures 1* and 2 and in the tabulation of dry weights.

* Figure 1 is similar to Figure 2 of Pitman (1965*a*) but is based on other data.

These figures give the relative increase in sodium and potassium content (μ -equiv/mg), i.e. uptake of potassium and sodium/increase in dry weight, for

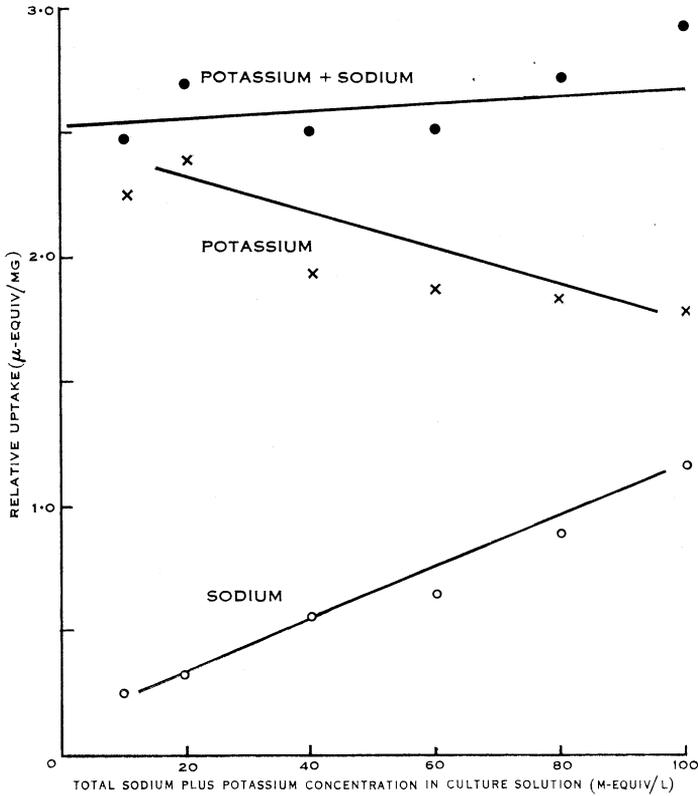


Fig. 1.—Relative uptake of sodium and potassium at different concentrations of culture solution.

plants in a range of concentrations of culture solution. The solutions used for Figure 1 contain 1 K : 3 Na and for Figure 2 no sodium was present. The plants were

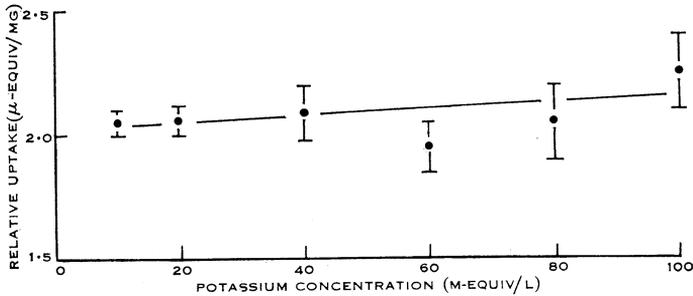


Fig. 2.—Relative uptake of potassium at different concentrations of culture solution.

grown in solutions "10" to 7 days of age and then transferred to the various concentrations for a further 3 days. Harvests were taken before and after the treatment. The

transfer from one solution to another possibly gave the plants some osmotic "shock", but the range of dry weight increase was less than if the plants had been grown in the high concentration solutions from seed, and it was found that the pattern of uptake was the same as in plants grown for longer periods in the solutions. The effect of concentration on plant size and transpiration are shown by the following tabulation:

Culture solution	"10"	"20"	"40"	"60"	"80"	"100"
Shoot dry weight increase (mg)	32.0	27.1	29.6	25.7	23.1	26.9
Transpiration (mg/g fresh wt. shoot/hr)	440	400	440	310	230	205

The initial shoot dry weight was 25.3 mg. Transpiration relative to shoot fresh weight was reduced by about 50% at the higher concentration, but this reduction in stomatal conductivity evidently had very much less effect on carbon dioxide uptake.

TABLE 2

EFFECT OF TRANSPIRATION ON TOTAL AND SELECTIVE UPTAKES BY *H. VULGARE* SEEDLINGS OF SODIUM AND POTASSIUM FROM CULTURE SOLUTION "60"

	Transpiration Level	
	Low	High
(a) Total uptake		
Shoot K + Na content (μ -equiv/plant)	108 \pm 2.5	106 \pm 4
Shoot relative K + Na content (μ -equiv/mg)	2.70	2.25
Transpiration (mg/g fresh wt. shoot/hr)	150	300
(b) Selective uptakes		
(1) For K/Na ratio in culture solution = 1 : 3		
Shoot potassium uptake (μ -equiv/plant)	48.8	47.0
Shoot sodium uptake (μ -equiv/plant)	13.7	19.0
Mean K/Na ratio		
Shoot	3.56 \pm 0.25	2.5 \pm 0.1
Root	3.1 \pm 0.1	2.9 \pm 0.1
(2) For K/Na ratio in culture solution = 1 : 19		
Shoot potassium uptake (μ -equiv/plant)	39.0	29.5
Shoot sodium uptake (μ -equiv/plant)	23.0	24.5
Mean K/Na ratio		
Shoot	1.72 \pm 0.14	1.22 \pm 0.09
Root	1.25 \pm 0.05	1.25 \pm 0.01

In general, uptake of potassium from solutions of potassium nitrate by cereal seedlings appears to increase but little with concentration (Kihlmann-Falk 1961) and barley plants are no exception. In Figures 1 and 2 the increase in combined potassium and sodium relative uptake with solution concentration was small. The linear regressions of relative uptake (y , μ -equiv/mg) and solution concentration (x , m-equiv/l) for these two figures were (limits are $P = 0.05$):

$$y = 2.45 + x(0.004 \pm 0.004) \quad \text{Figure 1 (K + Na)}$$

$$y = 2.00 + x(0.001 \pm 0.004) \quad \text{Figure 2 (K)}$$

The small increase in relative uptake with increased concentration might have been an underestimate of the effect of concentration due to the decreasing rate of transpiration, but Table 2 shows that transpiration has little effect on uptake. A comparison was made of uptake from solutions "60" at two transpiration levels, using two ratios of K/Na, 1 : 3 and 1 : 19. As in previous experiments plants were transferred from solutions "10" and uptake measured over a subsequent 3-day period. Each determination was the mean of four replicates, which have been combined to eight replicates for total uptake where K/Na ratio was not relevant. Transpiration rate increased with plant size from about 65 mg/plant/hr* to about 120 mg/plant/hr and was half this rate in the humid chamber.

Considering first the effect of transpiration on total uptake, the pooled results from the eight replicates were contents of 106 ± 4 and 108 ± 2.5 μ -equiv/plant at the high and low transpiration levels. At the start of the experiment the shoots weighed 22.6 mg and contained 46 ± 1.0 μ -equiv/plant. Uptake relative to dry weight, how-

TABLE 3
UPTAKE OF POTASSIUM AND SODIUM AT LOW CONCENTRATION BY *H. VULGARE* SEEDLINGS AT DIFFERENT TRANSPIRATION LEVELS
Ratio of K/Na in culture solution = 1 : 3. Means of duplicate samples given

K + Na Concentration (m-equiv/l)	Transpiration Level	Shoot Increase in:				K/Na Ratio
		Dry Weight (mg)	Potassium (μ -equiv/ plant)	Sodium (μ -equiv/ plant)	K + Na Relative Uptake (μ -equiv/mg)	
1.4	Low	7.9	24.1	3.9	3.55	6.2
	High	8.0	22.3	3.8	3.25	5.9
10.0	Low	9.3	26.3	4.5	3.30	5.8
	High	9.7	28.8	4.8	3.45	6.0

ever, was about 20% higher at the lower transpiration level. This difference is taken to be due to small environmental differences; for example, the higher leaf temperature in the humid chamber could have increased respiration at the expense of net assimilation. In view of these results, there seems to be no evidence that increased transpiration rate led to any appreciable increase in uptake.

The other aspect of uptake, the selectivity of potassium uptake, is shown both in Figure 1 and in Table 2. The lower transpiration level in Table 2 resulted in greater selectivity for potassium at both solution ratios of K/Na. This difference was the result of a 50% reduction in transpiration, which was the largest practicable without introducing too big a difference in growth. Hence the increased uptake of sodium with concentration in Figure 1 can be interpreted as due to some action of transpiration, which has a longer effect at higher solution concentrations.

This view is supported by the ratio of K/Na in the roots. This ratio was independent of transpiration level (Table 2) and furthermore it decreased much less with

* i.e. c. 300 mg/g fresh wt./hr or 3-4 mg/cm root/hr.

concentration than the ratio in the shoot, as shown by the following tabulation (taken from the data of Fig. 1):

Culture solution	"10"	"20"	"30"	"40"	"60"	"80"	"100"
K/Na ratio in root	2.7	3.3	3.0	2.7	2.8	2.8	2.5
K/Na ratio in shoot	8.6	7.6	5.3	3.4	2.9	2.1	1.5

(b) *Transpiration and Uptake at Lower Concentrations*

The uptake of potassium or sodium from culture solutions in the range "1.4"–"10" would be expected to be predominantly due to "metabolic" or active components, i.e. any "passive" component should be at its smallest level. Hence reductions in uptake due to reduction in transpiration or external concentration should be due to reductions in active components. Control of metabolic level in such experiments is particularly important.

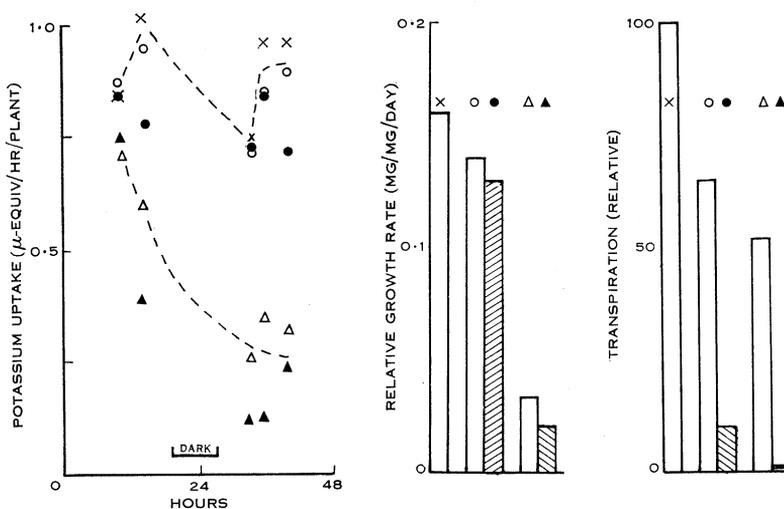


Fig. 3.—Potassium uptake, relative growth rates, and transpiration (relative to controls) for plants in different light and humidity conditions: X high light, high transpiration; ● moderate light, high transpiration; ○ moderate light, low transpiration; ▲ low light, high transpiration; △ low light, low transpiration.

Table 3 compares uptake of potassium and sodium to shoots of plants grown from seed in solutions "10" or "1.4" stirred by aeration. The solution ratio K/Na was 1 : 3. Plants were grown to 7 days in normal transpiration conditions and then some put into a low humidity chamber. At this stage the shoots weighed 17.9 mg and contained 25.2 μ-equiv potassium and 4.0 μ-equiv sodium. Uptake was measured by a harvest 2 days later. Transpiration at the "high" level was 70–80 mg/plant/hr* during the day but fell to an average of 20 mg/plant/hr at night. In the humid chamber transpiration was 35 mg/plant/hr and about 5–10 mg/plant/hr respectively, i.e. a reduction of 50%. This reduction in transpiration had no effect on the proportions of potassium to sodium taken up at either concentration. Total uptake and

* i.e. 350–400 mg/g fresh wt. shoot/hr or 4–5 mg/cm root/hr.

growth was a little smaller at the lower concentration at both transpiration levels, but relative uptake showed no conclusive response either to concentration or to transpiration.

The effects of larger reductions in transpiration on potassium uptake from the solution "1.4" were investigated by growing plants at lower light intensities to keep leaf temperatures low. Plants grown in solution "1.4" at the conditions of control plants used in Table 3 were transferred to moderate or to low light intensities, each either at full or reduced transpiration. At the time of transfer the plants weighed 33.5 mg and root length was about 20 cm. Transpiration in the humid chamber and

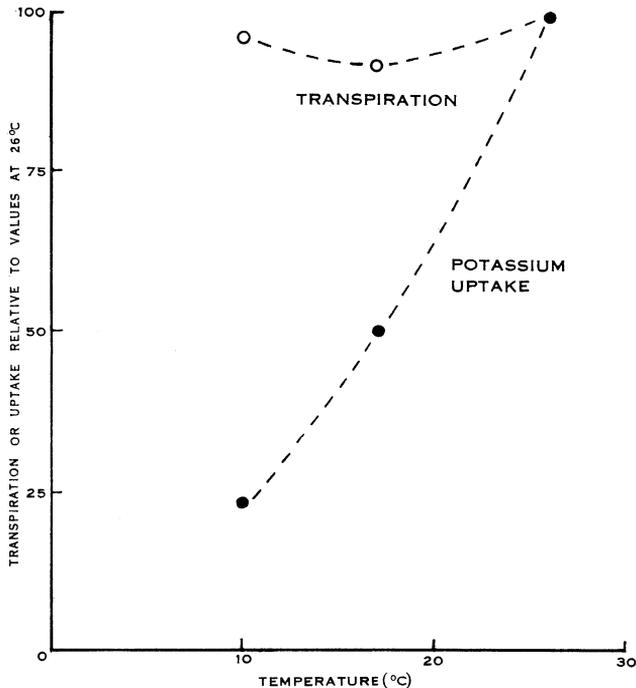


Fig. 4.—Transpiration and potassium uptake at different temperatures measured relative to behaviour at 26°C. 100% = 62 mg/plant/hr and 0.30 μ -equiv/plant/hr, respectively.

at the moderate light level was reduced to about 7 mg/plant/hr and at low light to a negligible level. Transpiration was water lost from the plant and not water uptake; plant growth was equivalent to about 1–2 mg/hr and guttation may have accounted for a further 5 mg/hr, so a more realistic minimum level was about 6 mg/hr.

Figure 3 shows that relative growth rates were reduced with light intensity as expected and at low light the extra shading of the humidity chamber reduced growth still further. Relative growth rate is used as a measure of growth as dry weight increases exponentially at this stage of seedling development. Two points in particular are shown in the figure. Firstly uptake to plants in these conditions corresponded very closely to relative growth rate—and not to transpiration. This was shown particularly well at moderate light, where a large reduction in transpiration was without effect

on uptake. Secondly, as in Table 3, there was no evidence that a reduction in uptake took place at low transpiration, i.e. a xylem concentration of about 80 m-equiv/l did not reduce active uptake.

Figure 3 also shows the persistence of uptake when metabolic status was changed; here the uptake fell slowly at low light intensity from that at the previous light intensity. This persistence is equivalent to the continued uptake of potassium at night in a normal day/night regime (Pitman 1965*a*). A temperature difference of 3 degC accounted for the difference in uptake during day and night at the higher light level.

The effect of solution temperature on uptake and on transpiration is shown in Figure 4. Plants in solution "1.4" were used first at 26°C and then transferred to solutions of varied temperatures at the same light and humidity conditions, and measurements made over a period of about 4 hr. The plants were then returned to solution at 26°C to check that no difference in metabolic status had been brought about by the change in temperature. Uptake and transpiration during the middle period are plotted relative to behaviour in the control periods at 26°C. The changes in temperature were without effect on transpiration, but the uptake was reduced at low temperatures. The temperature coefficient (Q_{10}) for uptake was about 2.3.

IV. DISCUSSION

These experiments show that increased transpiration decreases selective potassium uptake at higher concentrations (60 m-equiv/l) but has negligible effect at lower concentrations. As shoot uptake is a measure of the transport within the root to the transpiration stream, these results are perhaps better described as showing that water flux through the root can interact with ion fluxes, particularly at higher concentrations. The behaviour is shown best in Table 2, and can explain the increase in relative sodium uptake with solution concentration (Fig. 1) as being due to the combined effects of concentration *and* transpiration. The relative importance of concentration and transpiration is difficult to decide as it is experimentally difficult to reduce transpiration to an insignificant level without interfering with growth, particularly at high concentrations. One guide to the effect of concentration is the ratio of K/Na in root cortex cells. These cells are freely exposed to the solution and by virtue of their position should be more affected by solution contents than by transpiration (cf. Table 2). The tabulation on p. 993 showed that roots grown in solutions of the same K/Na ratio but increased concentration contained about the same proportions for culture solutions in the range "10"–"100". By comparison, the proportions taken up to the shoot were very much affected by concentration, and it is considered that this decrease was due to transpiration. At higher concentrations (culture solutions above "100") it is expected, from comparison with behaviour of *Sinapis alba* (Pitman, unpublished data), that concentration has its own effect in reducing selectivity.

In spite of the relatively large effect of transpiration on selectivity, there was much less effect on the combined potassium and sodium uptake. Total relative uptake was also virtually independent of solution concentration in spite of large increases in sodium uptake (Fig. 1). Both these aspects of uptake are suggested to be due to the

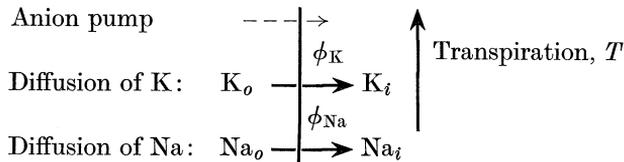
dependence of uptake on metabolism, which showed most clearly at lower concentrations (Figs. 3 and 4). Some increase in relative content might be expected at higher concentrations where higher leaf concentrations of salt are required to maintain transpiration against the osmotic effect of the solution, but in these experiments this increase was small.

There is, of course, a good reason why shoot uptake should appear to be controlled by plant growth. Active transport in the root, which determines this uptake, depends on sugars translocated from the shoot; this supply of metabolites is in turn closely related to shoot photosynthesis and so to growth. Under normal conditions uptake continues throughout the night period due to translocation of reserves from the shoot and reserves held in the root.

The active process responsible for potassium and sodium uptake is analogous to the uptake of salt by plant cells, and driven by an anion pump. The best evidence for this suggestion is Bowling's and Spanswick's (1964) measurements of negative potentials between solution and stele. Anions used in this process are derived mainly from the solution, but can also include organic acids from sugar breakdown. This active anion uptake provides a suitable mechanism for control of potassium and sodium uptakes as an equivalent uptake of cation must take place to balance the net negative charge transport of the active process.

The increased sodium uptake at higher concentrations or transpiration rates could have been explained by an increase in a "passive" component of uptake. In view of the present results, this explanation seems unlikely unless the passive component can in some way regulate the metabolic uptake so that the sum of active and passive components is constant. While such a mechanism might be possible it seems a more reasonable interpretation of behaviour that all uptake of potassium plus sodium to the shoot is controlled by the active process, and that the change in selectivity was due to water flux.

There is insufficient evidence about the potential differences between stele and solution to warrant a detailed examination of the relation between cation selectivity and anion uptake. The simplest situation would be



At steady state transfer of K and Na,

$$K_i = \phi_K \cdot a/T,$$

where ϕ_K is net potassium flux, across an area a when transpiration rate is T . In this case the passive fluxes of potassium and sodium are given by

$$\phi_K = -P_K \cdot \frac{\ln \zeta}{1 - \{1 + (P_K a \ln \zeta)/T\}} \cdot K_o,$$

where $\zeta = \exp(ZEF/RT)$ and the Goldman equation for flux is used. The relation between selectivity and transpiration on this model is shown by

$$\frac{K_{\text{shoot}}}{Na_{\text{shoot}}} = \frac{\phi_K}{\phi_{Na}} = \frac{P_K}{P_{Na}} \cdot \frac{K_o}{Na_o} \cdot \frac{1 - \{1 + (P_{Na}\alpha \ln \zeta)/T\}}{1 - \{1 + (P_{K\alpha} \ln \zeta)/T\}},$$

i.e. at high transpiration rates

$$\frac{\phi_K}{\phi_{Na}} \rightarrow \frac{P_K \cdot K_o}{P_{Na} \cdot Na_o},$$

and at low transpiration rates

$$\phi_K/\phi_{Na} \rightarrow K_o/Na_o.$$

On this model increased transpiration should act to *increase* selectivity for potassium (assuming $P_K > P_{Na}$). The action of water flux on selectivity is thus not a simple result of an anion pump unless P_K/P_{Na} decreases with increased transpiration and concentration.

In this model, K_o and Na_o are concentrations "outside" the anion pump and modified from the concentrations external to the root by the diffusion process across the root. Apart from changes in P_K and P_{Na} , transpiration could also affect selectivity by an action on this diffusion in the root, leading to changes in K_o and Na_o . At the outer surface of the root (and in the cortical cells) active potassium and sodium transport maintains high ratios of K/Na in the cortical cells relative to the solution. Although diffusion of potassium and sodium across the endodermis does not appear to be restricted any more than diffusion elsewhere in the root (Pitman 1965*b*) a further increase in selectivity relative to the cortex is found in the stele. This increase in selectivity seems the stage at which transpiration could most influence uptake because

- (1) Movement of potassium and sodium at low selectivity in cell walls should increase with concentration and transpiration, by-passing selective transport in the cytoplasm of cortical cells.
- (2) Water flux could increase diffusion of sodium past the mechanism increasing the stele K/Na ratio, thus reducing K_o and Na_o .

It is not thought likely that transpiration has any action on diffusion through the cytoplasm of the cortical cells. Big differences were found in shoot selectivity when concentration or water transport were increased, but there was no corresponding reduction in the selectivity shown by the root cells. If the explanation of the selectivity decrease were a decrease in selectivity in the cytoplasm of the cortical cells, then a similar decrease should have been observed in the ratio of potassium to sodium in the vacuoles of these cells.

V. ACKNOWLEDGMENTS

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