

UPTAKE AND TRANSPORT OF IONS IN BARLEY SEEDLINGS

III.* CORRELATION BETWEEN TRANSPORT TO THE SHOOT AND RELATIVE GROWTH RATE

By M. G. PITMAN†

[Manuscript received 30 November 1971]

Abstract

Determinations of potassium transport are described for plants growing at varied relative growth rates. These determinations were based on differences in total potassium content of the shoot over a 3-day period for plants growing on culture solution. It is shown that rate of transport from root to shoot is correlated with relative growth rate. The concentration of potassium in the shoot was independent of ratio of root to shoot, and little affected by relative growth rate (potassium was the only available univalent cation).

Measurements of tracer uptake were used to estimate fluxes into the root and into the stele. Low rates of net uptake were due to low fluxes into the root as well as into the stele. At low rates of growth, rate of uptake was limited by the availability of energy substrates such as sugar. At higher growth rates sugar levels built up in the plant without corresponding increases in ion fluxes. The balance between growth and potassium uptake must have been achieved by other means in these conditions, such as translocation of growth substances.

I. INTRODUCTION

Net transport of potassium through the plant involves many processes; active transport into and across the root, movement in the transpiration stream, retranslocation in the phloem, and possibly an overall control based on photosynthesis in the leaves. In previous papers (Pitman 1971, 1972) it was suggested that transport through the roots could be related to a system like that shown in Figure 6 of Part I (Pitman 1971). There appeared to be three active transport processes involved. These were located at the outer surface of the cytoplasmic phase (ϕ_{oc}), at the boundary between cytoplasm and vacuole (ϕ_{cv}), and between symplast and xylem (ϕ_{cx}). From the stele, ions were carried to the shoot in the transpiration stream. Net transport from root to shoot was described as R' , which was equal to $(\phi_{cx} - \phi_{xc})$; net uptake to the root, R , was equal to $(\phi_{oc} - \phi_{co})$. When levels in the root were steady, ϕ_{cv} was equal to ϕ_{vc} , and R' was equal to R .

Measurements of tracer uptake to both high-salt and low-salt roots have shown that influx (ϕ_{oc}) rises continuously with concentration, at least up to 50 mM (Epstein 1966; Latices 1969; Cram and Latices 1971). However, the relationship between net transport to the shoot and external concentration contrasts with this relationship between influx and concentration.

* Part II, *Aust. J. biol. Sci.*, 1972, 25, 243-57.

† School of Biological Sciences, University of Sydney, Sydney, N.S.W. 2006.

If over 20 μM , concentrations of potassium and sodium in solution do not seem to limit transport of these ions to shoots of barley seedlings. Using whole plants, Johansen, Edwards, and Loneragan (1968) found that rates of potassium transport from solutions of 0.02, 0.2, and 2.0 mM potassium were independent of concentration, that is, 2.2, 2.6, and 2.7 $\mu\text{-equiv g}_{\text{root}}^{-1} \text{hr}^{-1}$ respectively. Over a higher concentration range of from 1 to 100 mM, uptake of potassium from potassium solutions or of potassium plus sodium from solution containing both ions was independent of total concentration, and of the ratio of potassium to sodium in solution (Pitman 1965*a*, 1965*b*). These results imply that some factor within the plant (as opposed to the solution) limits uptake.

A more direct dependence of uptake on factors related to growth is shown in other examples. Both transport and growth were stopped when plants were put from light to dark (Pitman 1965*a*). Similarly, there was correlation between rate of transport of potassium and chloride and the changing relative growth rate at different stages of development from germination to flowering (Greenway 1965; Greenway *et al.* 1965).

In order to explain the constant levels of cation in seedlings of barley, and the effect of transpiration on total and selective uptake of potassium and sodium, it was suggested that transport to the shoot was controlled by active anion transport into the xylem, and that this transport was regulated by supply of metabolites from the shoot (Pitman 1965*a*, 1965*b*, 1966). If a feedback control operates from shoot to root it would be expected that in seedlings of the same age, net transport to the shoot (R') would be related to relative growth rate.

If cation level in the shoot is the factor controlling uptake, then level in the shoot should be independent of relative growth rate as well as of external concentration. Nye and Tinker (1969) used the concept of "plant demand" to consider uptake to plants from the soil and showed that over a period when concentration in the plant was constant, the rate of transport to the shoot should be proportional to relative growth rate.

This paper is concerned with the effects of relative growth rate on active transport processes in the root and the relationship of these processes to net transport from root to shoot. The net rate of transport of potassium is shown to be proportional to relative growth rate.

Measurements of tracer uptake are used to investigate how the system of fluxes in the root adjusts to achieve this control of net uptake in relation to growth. It is also shown that translocation of metabolites from the shoot to root can have a controlling effect on ion uptake. This observation is considered in relation to the overall process of transport in the plant.

II. MATERIALS AND METHODS

(a) Plants

Seeds of *Hordeum vulgare* cv. Cape were germinated for 18 hr on blotting paper and then planted out on gauze on 0.5 mM CaSO_4 . These seedlings were kept in the dark until 3 days old, when the CaSO_4 solution was replaced with a nutrient solution containing: 10 mM KNO_3 , 3 mM $\text{Ca}(\text{NO}_3)_2$, 2 mM MgSO_4 , 0.8 mM $\text{NH}_4\text{H}_2\text{PO}_4$, Fe-EDTA solution (90 μM Fe), and trace elements according to Arnon (1938). The plants were then transferred to the light regime to be used in the experiments. By 7 days the plants had depleted seed reserves both for growth and as a source of potassium.

(b) *Growth Conditions*

Plants were grown in a controlled-environment cabinet. The light source was a bank of high intensity warm-white fluorescent tubes supplemented by incandescent bulbs giving an intensity of $1.9 \times 10^3 \text{ J m}^{-2} \text{ s}^{-1}$. Humidity was not controlled but relative humidity was between 50 and 60%.

Variation in relative growth rate of plants growing on culture solution was produced by variation in length of photoperiod, or in a few cases by reduction of light intensity in photoperiods of 16 or 24 hr. The ratio of weight of shoot to root was between 2.5 and 3.7, a high value due to growing the plants without aeration on nitrate solutions in the light. The percentage dry weights ranged from 6.6, when relative growth rate was low, to 12.5 when it was high.

The smaller percentage dry weight of plants with lower relative growth rate was consistent with their appearance. Plants growing in the 2-hr photoperiod were pale green and showed characteristics of etiolation. Plants grown in the 16-hr photoperiod at the same light intensity were shorter and were dark green in colour.

(c) *Estimation of Relative Growth Rate and Potassium Transport*

These quantities were estimated from two harvests three days apart. At the first harvest (H_1) the seedlings were 10 days old (T_1) and at the second harvest they were 13 days old (H_2 , T_2). At each harvest eight samples each of five plants were taken; the plants were rinsed in distilled water to remove surface potassium and then cut into root and shoot at the junction with the seed. (The seed was discarded.) The samples were blotted and fresh weight measured. Four samples were then dried to measure dry weight and used to determine potassium content. (The other samples were used to determine the level of reducing sugar.)

During this early period of growth, dry weight increased exponentially and relative growth rate (G) was calculated as

$$G = (\log_e W_2 - \log_e W_1) / (T_2 - T_1), \quad (1)$$

where W_1 and W_2 are weights at H_1 and H_2 . Relative growth rate based on total dry weight is referred to as G_D , and on shoot fresh weight as G_S .

The rate of transport of potassium to the shoot (R_K) is defined as "rate of change in amount of potassium in the shoot divided by root fresh weight", i.e.

$$R_K = (dK_S/dt) \cdot (1/W_R).$$

In practice, R_K was calculated from the difference in content of the shoot (K_{S_1} , K_{S_2}) divided by the logarithmic mean fresh weight of the roots (W_{R_1} , W_{R_2}), and by $(T_2 - T_1)$ to express the results as $\mu\text{-equiv g}_{\text{root}}^{-1} \text{ hr}^{-1}$. Thus

$$R_K = \frac{(K_{S_2} - K_{S_1})(\log_e W_{R_2} - \log_e W_{R_1})}{(T_2 - T_1)(W_{R_2} - W_{R_1})}. \quad (2)$$

A related quantity M_K , which is the rate of transport relative to shoot weight, can be calculated using mean shoot weight instead of mean root weight. In this case

$$M_K = \frac{(K_{S_2} - K_{S_1})(\log_e W_{S_2} - \log_e W_{S_1})}{(T_2 - T_1)(W_{S_2} - W_{S_1})}. \quad (3)$$

The rate of uptake to the plant as a whole (U_K) can be calculated similarly, replacing potassium content in the shoot (K_S) by total potassium content (K).

Least significant differences have been calculated at the 5% level.

(d) Measurement of Potassium Content

Dried samples of plants were extracted with hot 1.0N HNO₃ followed by four extractions with hot distilled water. This solution was used to estimate potassium with a flame-photometer.

Levels of potassium in the root or shoot are expressed as the appropriate potassium content divided by fresh weight (μ -equiv g⁻¹) or as the potassium content divided by water content [μ -equiv (g water)⁻¹].

(e) Tracer ⁸⁶Rb Uptake

Solutions of culture solution were labelled by addition of ⁸⁶Rb to give suitable counting rates. The total potassium concentration in solution was 10 mM.

Uptake of ⁸⁶Rb is expressed as μ -equiv, using as specific activity the ratio of radioactivity (⁸⁶Rb) to chemical concentration of potassium in the solution (Epstein 1966).

Uptake, accumulation, and transport were measured by the procedure described in Part I (Pitman 1971). Plants were transferred from unlabelled to labelled culture solution and immersed so that the solution came to the junction of root and shoot. After the selected period in solution the plants were rinsed in unlabelled culture solution, blotted, cut into root and shoot, and weighed. The plant material was cut up and dried onto 5-cm planchets for counting.

(f) Sugar Extraction and Estimation

Replicate samples of plants were weighed as soon as harvested and put into hot 80% (v/v) ethanol. Sugars were extracted and estimated as described previously (Pitman, Mowat, and Nair 1971).

(g) Translocation of ¹⁴C-labelled Compounds

Plants were set up with shoots in a sealed box and the roots in a culture solution. The air space in the box was stirred with a small fan. Labelled CO₂ was liberated into the box, left for 15 min, then flushed out with air. Plants were sampled, divided into root and shoot, and weighed. The samples of root were extracted with 80% (v/v) ethanol, as described above, and the extract used both for ¹⁴C determination and for chromatography. Solvents used were as described previously (Pitman, Mowat, and Nair 1971).

(h) Transpiration

Plants were sealed in 3 by 1 in. sample tubes containing culture solution. The seal was a collar of polythene tubing pushed into a hole in the plastic lid of the sample tube and made airtight with silicone grease. Transpiration was estimated from the change in weight of batches of four plants. The results quoted are as milligrams per plant per hour. Fresh weights of the shoot and leaf areas are given where appropriate to allow conversion to other units.

III. RESULTS

(a) Potassium Levels and Relative Growth Rates

Figure 1 shows the level of potassium in the shoot plotted as potassium concentration against relative growth rate (G_D). The concentration increased by 10–20% over the range of relative growth rate. When the level is expressed as μ -equiv (g fresh weight)⁻¹ there is less change with G_D as the water content of the leaf decreased too with G_D by about 6% (p. 907). The concentrations in the leaves at H₂ were about 6% larger than at H₁. The levels of potassium in the roots are not shown, but were between 135 and 155 mM. Figure 1 also includes concentrations of potassium plus sodium in shoots of plants grown in sand and soil. The total of potassium plus sodium instead of potassium alone was used since earlier work had shown that the total uptake of these ions was independent of the proportions in the external solution, provided the total

supply of ions was adequate (Pitman 1965*a*). In the case of plants growing on sand the lower total uptake indicates that supply of ions was inadequate. The ratio W_S/W_R was 1.8 for plants in soil and 1.0 for plants in sand. Dry weight was 9% of fresh weight.

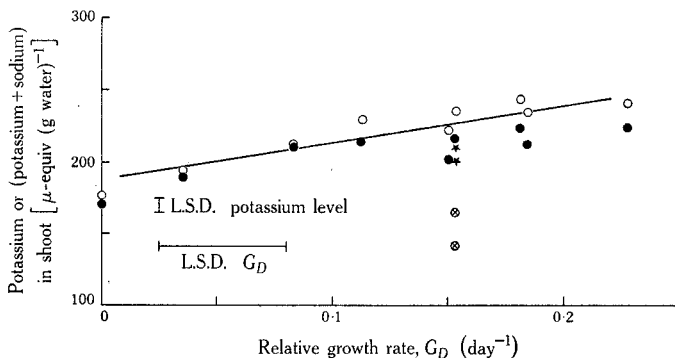


Fig. 1.—Level of potassium in the shoot plotted against relative growth rate (G_D). ● Plants in culture solution at harvest 1. ○ Plants in culture solution at harvest 2. ★ Potassium plus sodium level for plants growing in soil. ⊗ Potassium plus sodium level for plants growing in sand. L.S.D. shown at 5% level. Note origin not at zero concentration.

(b) *Potassium Transport and Relative Growth Rate*

The rate of transport of potassium from the root, R_K , is defined as

$$R_K = (dK_S/dt) \cdot (1/W_R).$$

When K_S/W_S is constant,

$$(dK_S/dt) = \text{constant} (dW_S/dt) = (K_S/W_S)(dW_S/dt).$$

Relative growth rate of the shoot is defined as

$$G_S = (1/W_S)(dW_S/dt),$$

so when K_S/W_S is constant,

$$R_K = (K_S/W_S)(W_S/W_R)G_S. \quad (4)$$

In most situations G_S is either the same as G_D , or over a range of G_D , G_S is correlated with G_D so it can be expected that R_K will be proportional both to G_S and to G_D if both the level in the shoot (K_S/W_S , not potassium concentration) and the shoot weight/root weight ratio (W_S/W_R) are constant. In these experiments R_K was calculated as the mean over the period ($T_2 - T_1$) using equation (2).

Values of R_K are plotted against G_D in Figure 2(a), and against G_S in Figure 2(b). As expected from the steady levels of potassium in Figure 1 there is good correlation of transport and relative growth rate with the exception of the plants growing on soil or sand for which the ratio W_S/W_R was less. At lower relative growth rates, the increment of shoot fresh weight was larger than the increment of dry weight, and G_S was larger than G_D . This difference is a consequence of the tendency to etiolation in

short photoperiods. Correlation with G_S was better than with G_D , mainly due to the smaller fiducial limit for G_S . When plotted against G_S the rates of transport lie close to a line through the origin.

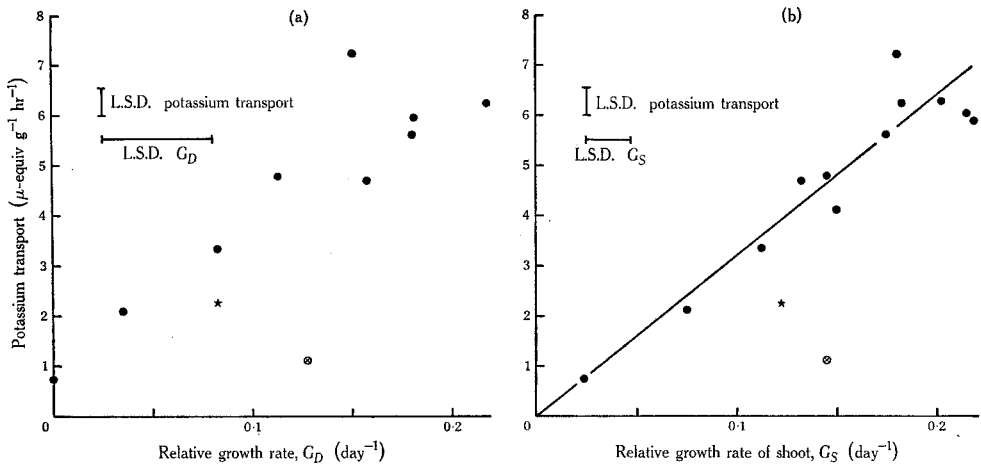


Fig. 2.—(a) Potassium transport relative to root weight plotted against relative growth rate based on dry weight (G_D); potassium plus sodium transport for plants in soil (★) and sand (⊗) are shown. L.S.D. shown at 5% level. (b) As for (a) but plotted against relative growth rate of the shoot (G_S).

The rate of transport relative to shoot weight, M_K , should also be proportional to relative growth weight but independent of W_S/W_R . Thus

$$M_K = (1/W_S)(dK_S/dt) = (1/W_S)(K_S/W_S)(dW_S/dt) = (K_S/W_S)G_S.$$

Figure 3 shows M_K calculated using equation (3) plotted against G_S . There was good correlation between M_K and G_S and now there was much less difference between plants growing on solution and plants growing on soil or sand.

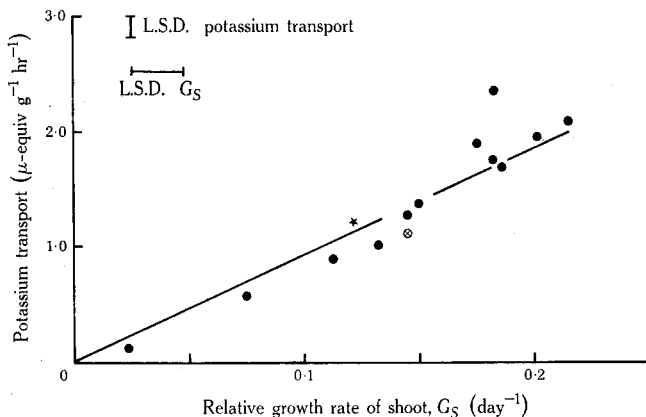


Fig. 3.—Potassium transport relative to shoot weight plotted against G_S . Potassium plus sodium transport for plants in soil (★) and sand (⊗). L.S.D. shown at 5% level.

The rate of uptake to the plant as a whole was approximately 10% higher than the rate of transport to the shoot, since the amount of potassium in the root was only 10% of the total in the plant.

(c) *Tracer Measurements*

The change in net transport with relative growth rate raises the problem of how a difference in net transport is related to individual fluxes. Does reduction in relative growth rate lead to reduction in entry to the root (ϕ_{oc}), in transport to the shoot (R'), or in both fluxes? Is accumulation in the vacuole (ϕ_{oc}) also affected?

A fair approximation for these fluxes can be made using efflux analysis when the material is short lengths of root (5 cm) containing cells at the same stage of development (Pitman 1971). This method has its limitations as assumptions must be made about the relationships of components in the path of uptake to the root, and about the homogeneity of cell types. In a whole root system there are many possible degrees of difference between cell types and between cells of different ages. Efflux measurements in this case should be treated with some suspicion unless there is clear agreement between these and other measurements of tracer and net potassium uptake.

For the purpose of the present paper absolute values of fluxes are less useful than knowledge of the way they change with change in relative growth rate. A comparison is made of plants growing in the usual conditions (p. 907) either with a 16-hr or 2-hr photoperiod in each 24 hr. One difference was that temperatures were the same in light and dark to avoid responses of fluxes to temperature. Uptake of tracer has a high temperature coefficient ($Q_{10} = 2-4$).

(i) *16-hr Photoperiod*

Figure 4 shows tracer taken up by plants growing in 16 hr light and 8 hr darkness, and the distribution of this tracer between root (accumulation) and shoot (transport). The plants were growing on a normal culture solution labelled with ^{86}Rb as a tracer for potassium.

Separate measurements were made of total K^+ uptake and transport to the shoot as described above (p. 907). Potassium was taken up at an average rate of $6.9 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$ and transported to the shoot at a rate of $5.9 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$ (relative to the root). Potassium concentrations in the roots were the same at each harvest ($135 \mu\text{-equiv g}^{-1}$). Relative growth rate, G_D , was 0.185 day^{-1} .

During the early stages of uptake S_v was small (S_v is the specific activity of potassium accumulated in the vacuoles of root cells). At this stage the rates of tracer uptake, accumulation, and transport were:

$$\text{Uptake to roots } (\phi_{oc} - \phi_{co} \cdot S_c) = 7.9 \mu\text{-equiv g}^{-1} \text{hr}^{-1}.$$

$$\text{Accumulation in roots } (\phi_{cv} \cdot S_c) = 4.4 \mu\text{-equiv g}^{-1} \text{hr}^{-1}.$$

$$\text{Transport to the shoot } (R' \cdot S_c) = 3.5 \mu\text{-equiv g}^{-1} \text{hr}^{-1}.$$

If the root is treated as a collection of cells, each with similar fluxes, then these figures can be used to estimate fluxes, though with the reservations already mentioned. Since $R' = 5.9$, $S_c = 3.5/5.9 = 0.59$; hence $\phi_{cv} = 7.5$, $\phi_{oc} = 9.3$, and $\phi_{co} = 2.4 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$.

As the amount of tracer in the vacuoles increased, S_v increased too, leading to changes in rates of accumulation and transport. The rate of accumulation is $(\phi_{cv} \cdot S_c - \phi_{vc} \cdot S_v)$, which decreased as $\phi_{vc} \cdot S_v$ became larger. Increase in S_v also led to an increase in S_c and so to an increase in tracer transport to the shoot ($R' \cdot S_c$). Using fluxes calculated from the uptake data above, time courses of tracer level in root and shoot have been determined and are shown as the solid lines in Figure 4. There was reasonable agreement between these calculations and observed uptake over the whole 47 hr. The flux estimations were based on tracer uptake over the first 6 hr.

This extrapolation over 47 hr assumes that the fluxes are the same in light and dark periods. This seems a justifiable conclusion as the following measurements show.

At the end of a 16-hr period of light some 10-day old plants were retained in the light and others put in the dark. Comparison was made of tracer uptake, accumulation, and transport in successive periods of 90 min for a total of 6 hr. The following tabulation shows the means for plants kept in the light compared with means for plants in the dark.

	Mean rates ($\mu\text{-equiv g}^{-1} \text{hr}^{-1}$)	
	Light	Dark
Accumulation in roots	5.1 ± 0.2	4.9 ± 0.5
Transport to shoot	1.2 ± 0.2	1.0 ± 0.1
Total uptake	6.3 ± 0.1	5.9 ± 0.5

Over the 6 hr following the 16-hr light period, there was no difference between plants in light and dark. Presumably the plants had enough reserves at the end of the 16-hr light period for rates of ion uptake to be maintained for at least 6 of the 8 hr of the following dark period. These results also give some justification for thinking that fluxes were constant over the 47 hr of Figure 4.

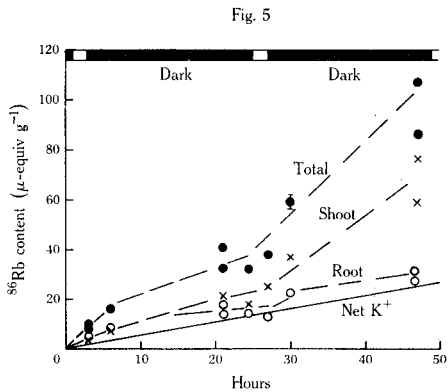
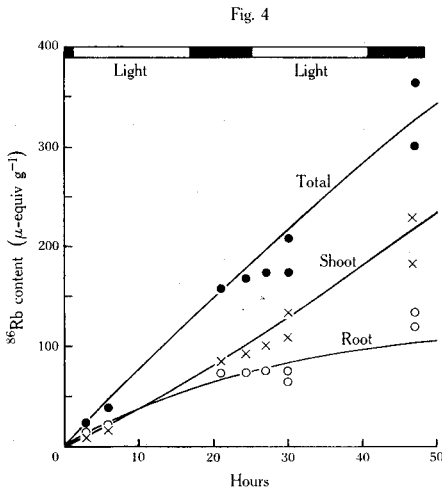


Fig. 4.—Uptake of ^{86}Rb . Plants were grown in 16 hr light periods as shown. ● Uptake to the plant as a whole. ○ Accumulation in the roots. × Transport to the shoot. — Calculated uptake (see text).

Fig. 5.—Uptake of ^{86}Rb by plants growing in 2 hr photoperiod. As for Figure 4, but solid line shows net uptake estimated from harvests 3 days apart.

(ii) 2-hr Photoperiod

Tracer uptake over 47 hr is shown in Figure 5; these measurements were made at the same time as those in Figure 4. The relative growth rate (G_D) was $0 \pm 0.05 \text{ day}^{-1}$; the relative growth rate of the shoot (G_s) was $0.025 \pm 0.03 \text{ day}^{-1}$. Net potassium uptake over 3 days was $0 \pm 0.5 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$ and transport was $0.7 \pm 0.5 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$. The accuracy of these measurements was not high since it involved a small difference between two large amounts. The 5% fiducial limits

are given. The potassium concentration in the shoot was the same at each harvest ($160 \mu\text{-equiv g}^{-1}$) but fell in the root from 125 to $100 \mu\text{-equiv g}^{-1}$ over the 3 days.

The average rate of tracer uptake to the plant as a whole was $2.0 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$. Since net uptake was less than $0.5 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$ there must have been some exchange of potassium between roots and solution. Clearly ϕ_{c0} was not negligible, and at least $1.5 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$. The average rate of transport to the shoot was $1.3 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$, compared with net potassium transport of $0.7 \pm 0.5 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$. It appears that there may have been some exchange between shoot and root but to a limited extent since the difference is only just significant at the 5% level.

For comparison with Figure 4 the initial rates of tracer uptake accumulation and transport were 2.7, 1.4, and $1.3 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$. All processes seem to be taking place less rapidly than in plants growing in a 16-hr photoperiod.

Due to the uncertainty of the estimation of net potassium transport, estimation of fluxes is not warranted from these data, as was done in Figure 4. Apart from these statistical errors, there was another source of uncertainty since there is no basis for thinking uptake was constant over the 47-hr period. In Figure 5 uptake of tracer appears to have been larger following the light period than just before it. Net uptake too may have fluctuated in this way.

A more sensitive way of showing that uptake is related to light period in these 2-hr plants is shown in Figure 6. Plants were put into labelled culture solution for short periods of 90–120 min, starting at successive times during the end of one dark period, the light period, and the start of the next dark period.

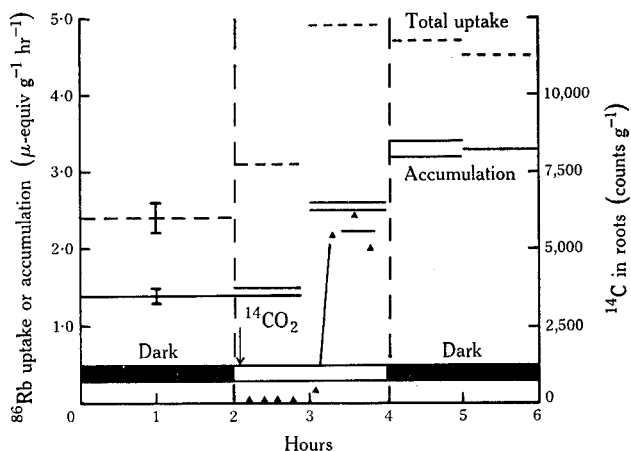


Fig. 6.—Rates of ^{86}Rb uptake and accumulation relative to root weights. Measurements were made using separate samples of plants in labelled solution for 1–2 hr. --- Uptake. — Accumulation. \blacktriangle ^{14}C content of the root. Light was on between 2 and 4 hr.

Both rate of uptake and rate of accumulation in the roots was larger in the light period than in the dark period. The rate of accumulation in particular showed a lag of about an hour before it increased; it then continued at a high level into the following dark period. Transport was $1.0 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$ in the dark, then rose to $1.6 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$ in the first hour and $2.3 \mu\text{-equiv g}^{-1}$ in the second hour of the light period.

In the following dark period transport fell again to $1.4 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$. Transport showed some correlation with transpiration, which was 7.6 mg hr^{-1} per plant in the dark periods, rising to 29.4 mg hr^{-1} in the 2 hr of light; new levels were reached within 15 min of the transition from light to dark (leaf area = 12.3 cm^2 per plant; root weight = 52 mg per plant).

The lag of 1 hr before accumulation increased seems to be due to the lag in translocation of sugars to the root following the start of photosynthesis. Figure 6 also shows the rate at which ^{14}C appeared in the root following a pulse of $^{14}\text{CO}_2$ supplied to the shoot at the start of the light period. There was a lag of about 1 hr before the level of ^{14}C rose in the root. Chromatography of the alcoholic extract from the roots shows that at least 95% of the ^{14}C in the roots was present as sugars: 85% as sucrose and 10% as glucose and fructose. There was no evidence of translocation of organic acids.

TABLE 1
COMPARISON OF UPTAKE AND FLUXES FOR PLANTS IN 2-HR AND 16-HR PHOTOPERIODS

Parameter	Photoperiod 2 hr	Photoperiod 16 hr
Relative growth rate, G_D (day^{-1})	0 ± 0.05	0.185 ± 0.05
Potassium in shoot ($\mu\text{-equiv g}^{-1}$)	160	210
Potassium in root ($\mu\text{-equiv g}^{-1}$)	100-125	135
Potassium transport, R_K ($\mu\text{-equiv g}^{-1} \text{hr}^{-1}$)	0.7 ± 0.5 (av.)	5.9 ± 0.5
Tracer uptake ($\mu\text{-equiv g}^{-1} \text{hr}^{-1}$)		
Dark	1.3-3.0	6.0-8.0
Light	4.5-5.5	
Fluxes ($\mu\text{-equiv g}^{-1} \text{hr}^{-1}$)		
ϕ_{oc}	3.5	9.3
ϕ_{co}	2.2	2.4
ϕ_{cv}	0.8-1.0	7.5
R'	0.9-1.1	5.9

Interpretation of the low rates of uptake depends on knowing $\phi_{co} \cdot S_c$, for low uptake to the root could be due to high efflux as well as to low influx. Even though fluctuations in fluxes prevent use of standard efflux analysis procedure, $\phi_{co} \cdot S_c$ can be estimated from efflux measurements. At $t = 0$, the rate of loss of tracer outwards from the surface of the root is a combination of loss from the free space plus the tracer efflux $\phi_{co} \cdot S_c$. Though the free space has a large content it exchanges rapidly with a half-time of about 2 min. Extrapolation of rate of loss of tracer over the period 15-60 min to $t = 0$ gives an estimate of $\phi_{co} \cdot S_c$ irrespective of what other compartments are involved.

Efflux measurements were made using the whole root system of plants cut off about 5 mm below the seed. The plants were grown for 36 hr with a 2-hr photoperiod in a culture solution labelled with ^{86}Rb . The roots were excised 4.5 hr after the end of the light period, blotted lightly, and set up in apparatus to measure efflux from cut end and surface separately, as described previously (Pitman 1971). Cutting did not affect the efflux, since loss from the excised roots was the same as loss from whole plants over at least 10 hr.

From the extrapolated rate of loss $\phi_{co}.S_c$ was estimated at $2.2 \pm 0.3 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$. Parallel uptake measurements using plants grown on unlabelled culture solution showed that tracer uptake was $1.3 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$ and ϕ_{oc} was therefore $2.2 + 1.3 = 3.5 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$. Accumulation in the roots ($\phi_{cv}.S_c$) and transport to the shoot ($R'.S_c$) were 0.6 and $0.7 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$. Net uptake was not determined but from the previous example lies between zero and $0.7 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$; in this case ϕ_{cv} is $1.0\text{--}0.8$ and R' $1.1\text{--}0.9 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$.

Fluxes and uptake in 16-hr and 2-hr photoperiod are summarized in Table 1. The response of the plant to change in relative growth rate seems to be in the fluxes ϕ_{oc} , ϕ_{cv} , and R' ; the efflux from the cytoplasm to the solution (ϕ_{co}) seems less affected than these other fluxes.

(d) Sugar Levels and Potassium Uptake

Measurements were made of reducing sugars in roots and shoots of plants growing at different relative growth rates. The results are shown in Table 2. At low relative

TABLE 2
COMPARISON OF SUGAR LEVELS, RELATIVE GROWTH RATE (G_D), AND
NET POTASSIUM TRANSPORT (R_K)

G_D (day ⁻¹)	R_K ($\mu\text{-equiv g}^{-1} \text{hr}^{-1}$)	Sugar level in shoot (μmoles)	Sugar level in root (μmoles)
0.0	0.7	13	<0.8
0.08	3.4	11	2.3
0.11	4.8	22	4.6
0.21	6.3	55	14.5
0.185	5.6	63	22.0

growth rates when sugar level was low, there was a correlation between rate of uptake and rate of transport. At higher relative growth rates sugar level increased without any corresponding increase in rate of transport. While sugar level may be important as a factor regulating transport (and uptake) at low levels, some other factors become more important at higher relative growth rates. These results are consistent with observations of effects of light on plants in 2-hr and 16-hr photoperiod.

IV. DISCUSSION

(a) Regulation of Uptake to the Shoot

The level of potassium in the shoot as a whole increased by only 15% over the range of relative growth rate studied, and so seems reasonably independent of the growth of the plant. Part of this increase may have been due to the greater development of seedlings when G_D was high. Usually the level of potassium in the shoot increases with age and with plant size.

Seedlings 13 days old have their second leaf well developed. Concentration of potassium in leaf 2 is initially lower than in leaf 1, but may eventually rise to be higher. The difference in individual leaves is better shown when the plants are growing with both potassium and sodium available. Older leaves tend to accumulate more sodium

relative to potassium than younger leaves. (This difference is due to translocation of potassium in the phloem from old to younger leaves.) However, the ratio of potassium to sodium in the shoot as a whole remains constant despite these differences between leaves (Pitman 1965*a*; Greenway and Pitman 1965). In barley seedlings the shoot thus behaves as a whole organ. Uptake appears to be regulated to the shoot as a whole, rather than regulation being achieved by individual leaves.

As expected for constant potassium level in the shoot, the rate of transport was proportional to relative growth rate, but there seemed to be better correlation with G_S than with G_D . At low relative growth rates G_S was greater than G_D , i.e. the shoot was increasing in fresh weight more rapidly than the plant increased in dry weight, leading to some of the symptoms of etiolation. It was striking that uptake calculated relative to the shoot was proportional to relative growth rate and independent of the ratio of shoot to root. The results of Figure 3, the behaviour of the shoot as a whole, and the dependence of R_K on G_S rather than G_D support the view that the plant is able to regulate transport from the root to the shoot according to shoot growth.

Comparison of rates of ion movement into the root, and then into root cells or to the shoot, showed that changes in net transport were accompanied by changes in other fluxes in the root. When net transport was low, the other active fluxes (ϕ_{oc} , ϕ_{cv} , and R') were also reduced. This reduction appeared to be due to restricted supply of metabolic substrates available for supply of energy for ion transport. Thus sugar level was low when net transport was low, and the rate of tracer accumulation was related to translocation of sugar from shoot to root during the light period. This dependence of ion intake in "high-salt" roots on sugar level has been noted by other workers (e.g. Humphries 1956).

When relative growth rate was larger sugar level was clearly not the controlling factor. Plants growing at high G_D were able to build up high levels of sugar in their leaves and in the roots, without any corresponding increase in rate of ion transport. Table 2 showed that uptake increased only 20%, while sugar level increased fivefold. Though rates of uptake changes in the light when plants were in 2-hr photoperiod, reserves in 16-hr plants were sufficient for uptake to continue for at least 6 of the 8 hr of darkness, and probably much longer. Plants transferred to the dark for 4 days took up potassium and sodium equivalent to about 14 hr uptake at normal rates in the light (Pitman 1965*a*). It seems that at high relative growth rates some other factor than sugar levels is controlling transport from root to shoot.

Figure 7 summarizes processes concerned with ion transport in the plant as a whole. Both cation and anion are transported from root to shoot, but for simplicity only potassium is shown in the figure. The level of potassium in the leaf cells is assumed to be maintained by active transport from the free space. The leaf as a whole receives ions from the xylem and can export potassium (preferentially to sodium) in the phloem, mainly to younger leaves (Greenway and Pitman 1965), but also to the roots. The level of ions in the free space of the leaves will be determined by the balance between these three processes (see also Robinson 1971). In the roots there is an active transport of ions into the root cells and, it has been suggested, into the stele (Pitman 1972). The level of potassium (or potassium plus sodium) in the shoot can be regulated either by control of entry into the shoot or by retranslocation of potassium back from the shoot to the root.

When growth is limited by available light it seems that sugar level in the root can control export to the shoot. A possible mechanism of control when photosynthesis is not limiting uptake could be through cytokinins and abscisic acid. Osmotic stress has been shown to lead to increased abscisic acid level in the shoot (Mizrahi, Blumenfeld, and Richmond 1970). In the root, abscisic acid can inhibit secretion of ions into the stele (Cram and Pitman 1972). Excess transport of ions to the shoot would have the same effect as drought stress on osmotic pressure in the vacuoles and so could be expected to lead to changes in abscisic acid and cytokinin production. Translocation of these substances to the root would then reduce transport to the shoot. Such a system could provide a delicate feedback control regulating transport to the shoot as well as levels of (potassium plus sodium) in the leaf cells.

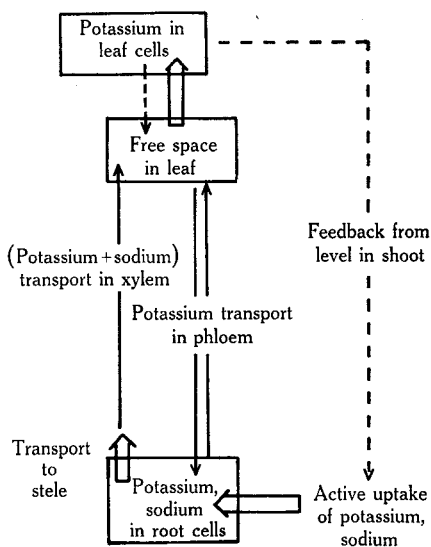


Fig. 7.—Processes involved in uptake and transport of potassium and sodium in the plant. See text for discussion.

Tracer measurements show that potassium in the leaves can be retranslocated to the roots. This process would achieve a balance between root and shoot analogous to the influx–efflux balance in plant cells. Excess ions in the shoot would be returned to the root. The results of Figures 4 and 5 show that the extent of this retranslocation is limited, since tracer transport and net potassium transport are the same within about $0.5 \mu\text{-equiv g}^{-1} \text{hr}^{-1}$. It is suggested that this process is less important in regulation of potassium uptake than control of the input processes, i.e. ϕ_{oc} and R' .

(b) *Relationship between Uptake, Concentration, and Growth*

For whole plants, Barley (1970) suggested that it was adequate to use a simple expression of the form

$$V = V_{\max} C_o / (C_o + \rho), \quad (5)$$

where V is rate of uptake, V_{\max} is maximum rate, C_o is concentration, and ρ is a

constant. [Experiments with culture solutions suggest ρ is about 10^{-5}M or less (Johansen, Edwards, and Lonergan 1968)]. Uptake to the whole plant clearly depends upon growth as well as on availability of nutrients so that an expression combining both concentration effects and "growth" is needed. Such an expression could be described generally as

$$\text{Uptake} = \text{function (concentration, growth)}$$

In equation 5 the term V_{\max} is taken as a constant for a particular set of conditions; in fact it includes an implicit term relating to growth. (It is also assumed that ρ is independent of V , i.e. the relationship is a Michaelis-Menten one, not a diffusive one.)

It would be convenient in some studies of growth and uptake if V_{\max} could be made explicitly related to growth. In the present experiments concentration was not limiting uptake and V_{\max} is the same as uptake to the plant (M_K) provided V_{\max} is measured as a long-term average. Uptake is proportional to transport, and G_D is proportional to G_S . Figure 3 showed that transport to the shoot was proportional to G_S , but in view of these other relations, generally, V_{\max} should be proportional, too, to G_D , and substituting in equation (5)

$$V = kG_D C_o / (C_o + \rho), \quad (6)$$

where k is a constant relating V_{\max} to G_D . Uptake of different nutrients would be described by a set of these expressions. The expression is basically an empirical relationship of convenience for it ignores the problem of substituting for V_{\max} if ρ is a function of V or V_{\max} .

Apart from the data in Figures 1, 2, and 3 there are other sets of data in the literature showing that V is proportional to G_D . For example, in barley total uptake of potassium plus sodium to the shoot was proportional to the weight of the shoot over the whole period of development from germination to flowering (Greenway *et al.* 1965). Equally there are other examples where this relation does not appear to hold even with adequate nutrient supply. A common example which does not show uptake proportional to weight is uptake of nitrogen to cereals (e.g. Halse *et al.* 1969). During the early stages of development (to 10 weeks) uptake of nitrogen is rapid but then falls despite increase in dry weight. In this example nitrogen is being retranslocated around the plant so that the plant acts as its own source of nitrogen.

The value of including a term for plant growth in expressions of the type in equations (5) and (6) is the extension of the predictive scope of the expression. The hypothesis that the shoot regulates its content and therefore uptake by the plant also provides a useful basis for looking at uptake to the plant as a whole.

V. ACKNOWLEDGMENTS

This work was supported by the Australian Research Grants Committee and University of Sydney Research Grant. I am grateful to Dr. W. J. Cram for helpful discussion, and to Mrs. J. Le Claire and Miss M. Corderoy for assistance with experiments.

VI. REFERENCES

- ARNON, D. I. (1938).—*Am. J. Bot.* **25**, 322–4.
- BARLEY, K. P. (1970).—*Adv. Agron.* **22**, 159–201.
- CRAM, W. J., and LATIES, G. G. (1972).—*Aust. J. biol. Sci.* **24**, 633–46.
- CRAM, W. J., and PITMAN, M. G. (1972).—*Aust. J. biol. Sci.* **25**, in press.
- EPSTEIN, E. (1966).—*Nature, Lond.* **212**, 1324–7.
- GREENWAY, H. (1965).—*Aust. J. biol. Sci.* **18**, 763–81.
- GREENWAY, H., GUNN, A., PITMAN, M. G., and THOMAS, D. A. (1965).—*Aust. J. biol. Sci.* **18**, 525–41.
- GREENWAY, H., and PITMAN, M. G. (1965).—*Aust. J. biol. Sci.* **18**, 235–47.
- HALSE, N. J., GREENWOOD, E. A. N., LAPINS, P., and BOUNDY, C. A. P. (1969).—*Aust. J. agric. Res.* **20**, 987–98.
- HUMPHRIES, E. C. (1956).—*Ann. Bot. (N.S.)* **20**, 411–17.
- JOHANSEN, C., EDWARDS, D. G., and LONERGAN, J. F. (1968).—*Pl. Physiol., Lancaster* **43**, 1722–6.
- LATIES, G. G. (1969).—*A. Rev. Pl. Physiol.* **20**, 89–116.
- MIZRAHI, Y., BLUMENFELD, A., and RICHMOND, A. E. (1970).—*Pl. Physiol., Lancaster* **46**, 169–71.
- NYE, P. H., and TINKER, P. B. (1969).—*J. appl. Ecol.* **6**, 293–300.
- PITMAN, M. G. (1965a).—*Aust. J. biol. Sci.* **18**, 10–24.
- PITMAN, M. G. (1965b).—*Aust. J. biol. Sci.* **18**, 987–98.
- PITMAN, M. G. (1966).—*Aust. J. biol. Sci.* **19**, 257–69.
- PITMAN, M. G. (1971).—*Aust. J. biol. Sci.* **24**, 407–21.
- PITMAN, M. G. (1972).—*Aust. J. biol. Sci.* **25**, 243–57.
- PITMAN, M. G., MOWAT, J., and NAIR, H. (1971).—*Aust. J. biol. Sci.* **24**, 619–31.
- ROBINSON, J. B. (1971).—In "Salinity and Water Use". pp. 193–206. (MacMillan: London.)

