

## ABSCISIC ACID STIMULATED INTERCELLULAR FLUXES OF POTASSIUM IN EXCISED ROOTS OF MAIZE

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### Abstract

Compartmental analysis were carried out to determine the influence of ABA on the intercellular fluxes of K in excised roots of *Zea mays* L. The rate of influx was sensitive to ambient temperature and the tissues take about 24 hours to reach an equilibrium. ABA stimulated K influx rate at 15-25°C, but did not alter the pattern of influx. The cytoplasmic content 'Qc' and the efflux at both the plasmalemma and tonoplast membrane were also increased by ABA, the net tracer uptake, however was little affected by ABA. In excised maize root, K was actively transported inwards. It is concluded that externally applied ABA promotes intercellular fluxes of K and that interacts with energy-linked K pump. A model based on these results is described.

### Introduction

Abscisic acid (ABA) has been known to play an important role in the regulation of stomatal aperture in water-stressed plants (Jones & Mansfield, 1972; Milborrow, 1974). The levels of ABA rise dramatically in the buds (Wright, 1975), leaves (Walton *et al.*, 1977), and roots (Walton *et al.*, 1976). The increased concentration of ABA in the leaves and ABA translocated from shoot to the root (Hocking *et al.*, 1972) affects on the solute transport into and out of the guard cells. The action of ABA is to inhibit H/K exchange (Raschke, 1977) or to stimulate the efflux of both K and Cl from the guard cells (MacRobbie, 1981). The inhibition of K movement into the guard cells or the leakage of K from the guard cells causes stomatal closure due to the reduced turgor.

There are contradictory reports whether ABA stimulates hydraulic conductivity of the root (Cram & Pitman, 1972; Collins & Kerrigan, 1974; Pitman *et al.*, 1974a; Pitman & Wellfare, 1978; Collins & Morgan, 1980; Glinka, 1980; Fiscus, 1981). However, unequivocally it has been reported that externally applied ABA at least affects two processes in the plant roots. Firstly, ABA acts on the salt transport to the xylem (Pitman *et al.*, 1974a; Dieffenbach *et al.*, 1980) and secondly, it affects the mechanism that regulates processes involved in the vacuolar saturation (Behl & Jeschke, 1979).

From the earlier work with maize, millet and sorghum plants, we found that ABA stimulates volume flow, K selectivity and cytoplasmic content of K (Collins & Channa,

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1983; Channa & Collins, 1985a; Channa & Collins, 1985b). It was therefore suggested that ABA can increase both the water permeability of the membrane and ion fluxes in the roots. This report further explores the action of ABA on the fluxes of K and its intercellular compartmentation in the excised maize roots.

## Materials and Methods

*Growth Conditions:* Maize Seeds (*Zea mays*, L. cv. Anjou 210) soaked in tap water for about 1-2h were germinated on moist tissue at 25°C in dark for 48h. After germination the seeds were transferred to plastic containers containing 1/10 Long Ashron solution and grown for 72h. To facilitate root growth, the culture solution was aerated continuously. The seedlings were then removed from the culture solution for flux studies.

*Root material:* Roots were equilibrated at the relevant temperatures for at least one hour prior to the experiment using a water bath and cooling unit. ABA was added during the equilibration period. ABA was used from a stock solution prepared by dissolving the ABA in dimethyl sulphoxide (DMSO) and stored at 4°C. The concentration of the stock solution was usually  $10^{-2}$ M. Control roots were treated with DMSO at the same V/V percentage. ABA used was 2-cis-4trans isomer, which is a synthetic crystalline product and is approximately 95% pure, supplied by Sigma Chemical Company, U.S.A.

*Isotope:*  $K^{42}$  obtained from the Joint Universities Nuclear Reactor Risley, Cheshire, U.K. was added in the loading solution of appropriate concentration.

*Compartmental Analysis:* The measurement of the kinetics of isotope exchange between a radioactively loaded tissue and a nonlabelled external solution offers an indirect way for the analysis of concentrations in particular compartments and of fluxes at the boundaries of such compartment. The theory of compartmental analysis is complex, but has been comprehensively discussed by Walker (1975). The following paragraphs set out the fundamental equations used in this investigation.

The efflux rate constants for the cytoplasm,  $K_c$ , and the vacuole,  $K_v$ , was obtained from the slope of the 'unloading' curves (Fig. 1). The apparent radioisotope contents for the cytoplasm,  $I_c$ , and for the vacuole,  $I_v$ , was calculated from the intercepts of the cytoplasmic and the vacuolar efflux curves divided by the external specific activity ( $S_o$ ). The vacuolar content of the ion,  $Q_v$ , was obtained by chemical analysis of parallel samples of tissue at the beginning of the wash-out period minus the apparent contents of the cytoplasm and cell wall calculated from the tracer experiment. Thus the primary parameters obtained were:

The intercepts:  $I_c$ ,  $I_v$ , in c.p.m. g-1.

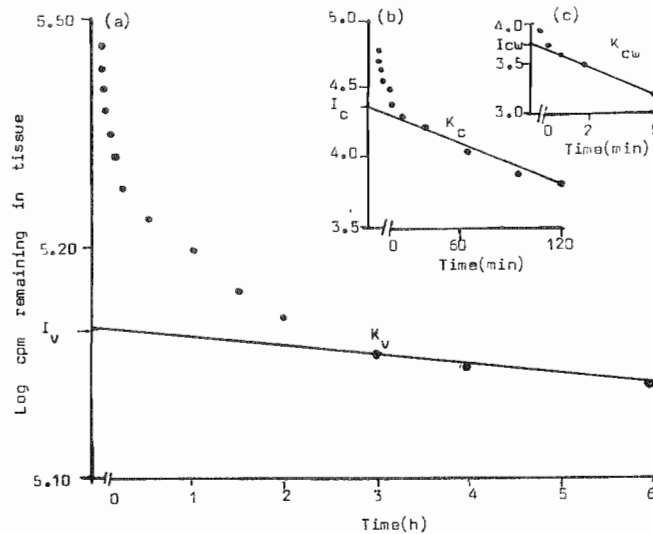


Fig. 1 Loss of  $K^{42}$  from an excised maize root. (a) Total loss from excised root. Final linear phase attributed to the vacuole. (b) Loss after subtraction of the cytoplasm. (c) Loss after subtraction of vacuolar and cytoplasmic phase. Final linear phase attributed to the cell wall and intercellular spaces.

The rate constants (slopes);  $K_c$ ,  $K_v$  in  $h^{-1}$ .

Loading solution:  $S_0$  in c.p.m.  $\mu\text{mol}^{-1}$ .

Loading time:  $t$  in hours.

These were used to derive the following:

Flux from outside to cytoplasm

$$J_{oc} = (I_v/t + I_c \cdot K_c)/S_0.$$

Flux from cytoplasm to outside

$$J_{co} = I_c \cdot K_c/S_0 + K_v \cdot Q_v.$$

Flux from cytoplasm to vacuole

$$J_{cv} = J_{co} (I_v/t)/(I_c \cdot K_c).$$

Flux from vacuole to cytoplasm

$$J_{vc} = J_{oc} + J_{cv} - J_{co}$$

Cytoplasmic content

$$Q_c = (J_{oc} - J_{cv})/K_c$$

The flux equations were derived on the assumptions that:

- (i) The compartments are in series with regard to ion transport.
- (ii) The tissue is in a steady state with regard to ionic content and flux in each compartment.
- (iii) The vacuolar compartment is larger than the cytoplasmic compartment.
- (iv) There is no net flux into each cellular compartment after the loading time.

The net flux was therefore:

$$J_n = J_{oc} - J_{co} = J_{cv} - J_{vc}$$

- (v) The specific activity of compartments is assumed to be uniform.
- (vi) Mixing of the ions within the compartment is instantaneous.

*Influx:* Root segments (10 cm apical segments) were placed in a litre beaker containing loading solution identical to the growth medium, at the start of the influx  $K^{42}$  was added. At required intervals roots were removed from the loading solution, blotted gently, and their radioactivity was determined. Cerenkov method was employed for  $K^{42}$  counting using a Unicom Packered Liquid Scintillation Spectrometer, Tricarb Model 3320. The radioactivity of the loading solution was also determined at several intervals.

*Efflux:* Excised root segments (10 cm) were sealed into capillaries with a paraffin wax/rosen mixture. Individual roots were held in perspex holders suspended over a tube containing  $8 \text{ cm}^3$  of solution. To load the root a solution identical to the growth medium but without K was used, then  $0.4 \mu\text{Ci/mgK}$  was added from the isotope, this was usually about  $10 \mu\text{Ci/mgK}$ . The solution was aerated continuously at the required temperature in a laboratory water bath. Each root was loaded with  $K^{42}$  over an 18h period. The experimental set up is shown in Fig. 2.

To start the elution experiment, the root was fixed into a clean perspex holder and then transferred at various time intervals through elution tubes containing standard media. Initially, elution periods were 30 seconds and finally 2h. After a total of 6h the roots were removed, blotted, weighed and counted. All tubes, of both loading and elution solutions contained ABA or DMSO.

Efflux curves were constructed by plotting the logarithm of the c.p.m. remaining in the tissue as a function of time. The final linear part of the graph represents the loss of isotope from the vacuole. The counts from this compartment were subtracted from the total for each time and the difference replotted as another semi-logarithmic graph. Further analysis in this way revealed at least two additional phases, the first representing the cyto-

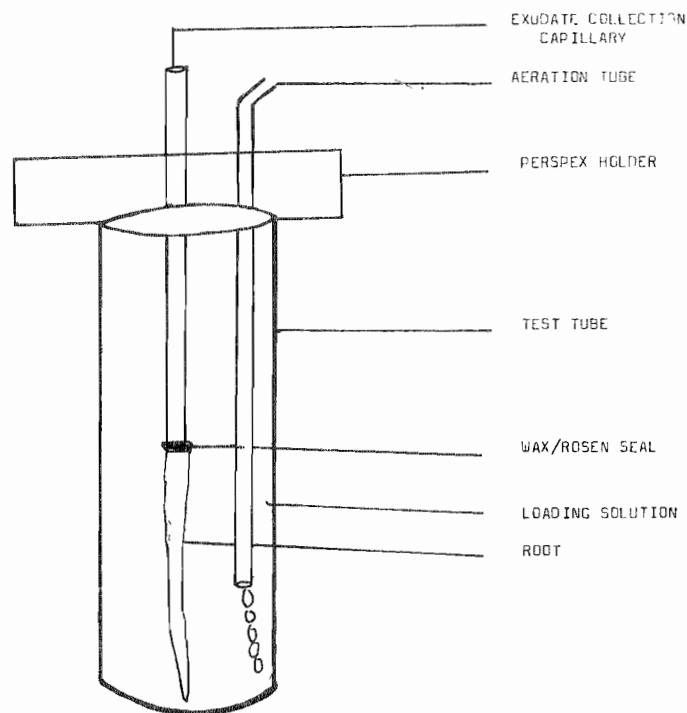


Fig. 2. Efflux experiment set up.

plasm and the second the free space of the root, including the cell wall and the intercellular spaces (Fig. 1).

## Results and Discussion

*Effect of ABA on K-accumulation:* The effect of ABA on K-accumulation rate is shown in Fig. 3. It was found that K-accumulation rate was rapid at first and then it slows, the tissue takes at least 24h to reach an equilibrium. The rate of accumulation was highly sensitive to ambient temperature and a maximum value reached at 20-25°C. Addition of ABA to the medium increased the rate of K-accumulation but did not change its pattern.

*Effect of ABA K-influx:* Calculations of influx rate is difficult for such a complex tissue as the root. A simple analysis of the data has been attempted by taking the slopes of the initial tracer influx, which represents the loading of the symplasm, and the slope of the steady influx rate at the long time periods, representing loading of the vacuole. These two parameters have been taken as estimates of  $J_{oc}$  and  $J_{cv}$ , respectively. As both calculations are based on the slope of the influx plot the free space 'fs' was eliminated.

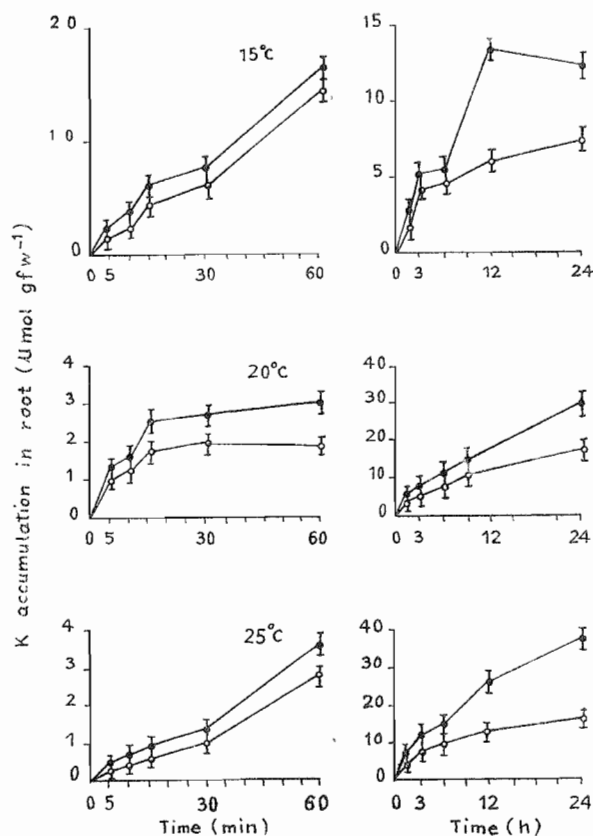


Fig. 3. Effect of ABA on  $\text{K}^{42}$  accumulation by maize roots. ● — ABA ○ — Control.

The data revealed the ABA increased K-influx across both the plasmalemma and the tonoplast membrane at temperature ranging from 15-25°C (Table 1). The energy of activation for the fluxes, across both the membranes was also high in the presence of ABA.

*Effect of ABA on K-efflux:* The data regarding the influence of ABA on K-efflux and cytoplasmic content is presented in Table 2. The efflux across the plasmalemma and tonoplast increased as the temperature was raised. The efflux at both the membranes was increased by ABA, though the net tracer flux ( $J_{oc} - J_{co}$ ) was unaltered or little affected by ABA (Table 3). The cytoplasmic content ( $Q_c$ ) of K was also sensitive to temperature and was increased by ABA. The values for cytoplasmic content found here are some what lower than those recorded by Davis & Higinbotham (1976) who also worked with maize. However, it should be pointed out that they have used a higher, K level, 1 mM, and were not using full growth medium as was done in our studies. Pitman (1963) also showed that as the outside K was increased so did the cytoplasmic content of this ion.

**Table 1. Effect of ABA on K-influx in excised maize roots.**

Treatment	Temperature °C						Energy of activation	
	15		20		25		Ea KJ mol <sup>-1</sup>	
	Joc	Jcv	Joc	Jcv	Joc	Jcv	Joc	Jcv
Control	1.20	0.17	2.81	0.61	2.72	0.44	119.4	176.9
ABA 10 <sup>-6</sup> M	1.50	0.38	3.78	1.08	3.44	1.28	129.7	146.5

All fluxes in  $\mu\text{mol g}^{-1} \text{fw h}^{-1}$ .

Energy of activation 'Ea' calculated for 15-20 C using arrhenius equation.

**Table 2. Effect of ABA on K fluxes and cytoplasmic content in excised maize roots.**

Temperature °C	Treatment	Joc	Jco	Jcv	Jvc	Qc
10	Control	0.61	0.46	0.29	0.14	0.79
		±	±	±	±	±
	ABA 10 <sup>-6</sup> M	0.80	0.13	0.07	0.04	0.07
		±	±	±	±	±
15	Control	1.02	0.85	0.68	0.48	0.84
		±	±	±	±	±
	ABA 10 <sup>-6</sup> M	0.20	0.25	0.25	0.25	0.05
		±	±	±	±	±
20	Control	0.56	0.36	0.30	0.10	0.80
		±	±	±	±	±
	ABA 10 <sup>-6</sup> M	0.13	0.01	0.08	0.02	0.06
		±	±	±	±	±
25	Control	1.05	0.64	0.90	0.49	1.41
		±	±	±	±	±
	ABA 10 <sup>-6</sup> M	0.20	0.04	0.05	0.06	0.08
		±	±	±	±	±
25	Control	1.53	0.95	1.36	0.78	1.61
		±	±	±	±	±
	ABA 10 <sup>-6</sup> M	0.30	0.30	0.40	0.11	0.23
		±	±	±	±	±
25	Control	2.00	1.57	0.93	0.50	2.70
		±	±	±	±	±
	ABA 10 <sup>-6</sup> M	0.10	0.16	0.12	0.12	0.27
		±	±	±	±	±
25	Control	2.16	1.73	0.73	0.30	1.70
		±	±	±	±	±
	ABA 10 <sup>-6</sup> M	0.21	0.16	0.06	0.09	0.20
		±	±	±	±	±
ABA 10 <sup>-6</sup> M	3.13	2.79	1.82	1.48	3.37	
	±	±	±	±	±	
ABA 10 <sup>-6</sup> M	0.65	0.65	0.24	0.18	0.35	
	±	±	±	±	±	

Fluxes in  $\mu\text{mol g}^{-1} \text{fw h}^{-1}$ ; Qc in  $\mu\text{mol g}^{-1} \text{fw h}^{-1}$ .

Each value mean of 4 replicates ± standard error of mean.

**Table 3. Net tracer fluxes and xylem fluxes in excised maize roots.**

		Temperature °C							
		10		15		20		25	
Control	ABA 10 <sup>-6</sup> M	Control	ABA 10 <sup>-6</sup> M	Control	ABA 10 <sup>-6</sup> M	Control	ABA 10 <sup>-6</sup> M	Control	ABA 10 <sup>-6</sup> M
0.15	0.17	0.20	0.41	0.58	0.43	0.43	0.34		
*0.18	0.16	0.48	0.31	0.23	0.89	1.45	2.75		

All fluxes in  $\mu\text{mol g}^{-1} \text{fw h}^{-1}$ .

Tracer net flux calculated as  $J_{oc} - J_{co}$  (Table 2).

\*Calculated from exudation experiments data on a weight basis.

The best test to establish whether ion transport is active or passive is the Ussing-Teorell flux ratio equation (Ussing, 1949; Teorell, 1949).

$$\text{Flux ratio} = \frac{J_{oc}}{J_{co}} = \frac{C_o}{C_i \exp ZFE/RT}$$

Where Z is the valency of ion;  $C_o$  and  $C_i$  are the ionic concentrations assumed to be equal to the activity of ion at either side of the membrane; F is the Faraday; R is the gas constant; T is the absolute temperature and E is the electrical potential difference across the membrane. A comparison of the observed and predicted flux ratios (Table 4.) indicates that K is actively pumped inwards, this has been recorded previously by Davis & Higinbotham (1976) for maize roots and by Pierce & Higinbotham (1970) for *Avena* coleoptyle cells. From these data the major active movement is predicted across the tonoplast into the vacuole. This is not in agreement with the data of Davis & Higinbotham (1976). A clear idea of what is happening will only be achieved when potential differences are measured and also accurate volume measurements are made. Nevertheless, it should be noted that ABA had little effect on flux ratio.

Working with barley excised roots Pitman *et al.*, (1974a) reported that ABA acts to inhibit  $J_{cx}$  and leave  $J_{oc}$  unaltered or slightly increased. Determining the unidirectional fluxes and transport in the exudate of the same plant species, Behl & Jeschke, (1981) reported that ABA strongly inhibited both K transport in the xylem exudate and the ion influx ( $J_{oc}$ ), as well as the cytoplasmic content ( $Q_c$ ) decreased. Such a response of ABA did not appear in the excised maize roots in our previous (Collins & Channa, 1983) and in the present investigation. Thus it can be seen that ABA stimulated fluxes across the plasmalemma and tonoplast and increased the cytoplasmic content (Table 2) over a temperature range from 15-25°C, and the stimulatory effect of ABA on K-accumulation remained fairly constant for the period of 24h (Fig. 3). In a separate experiment it was found that ABA stimulates K-transport into the exudate more between 20-25°C, in the experiment



**Table 4. Predicted and observed flux ratios for maize root cells.**

Temperature °C	Cytoplasm Observed(a)	Joc/Jco Predicted(b) Eco -105 mV	Vacuole Observed(a)	Jcv/Jvc Predicted(b) Evc + 10 mV
10				
Control	1.33	1.31	2.09	0.19
ABA 10 <sup>-6</sup> M	1.20	1.23	1.36	0.21
15				
Control	1.56	1.29	2.89	0.19
ABA 10 <sup>-6</sup> M	1.64	0.68	1.84	0.35
20				
Control	1.61	0.56	1.74	0.41
ABA 10 <sup>-6</sup> M	1.27	0.33	1.84	0.71
25				
Control	1.25	0.49	2.42	0.42
ABA 10 <sup>-6</sup> M	1.12	0.24	1.23	0.86

(a) Calculated from unidirectional fluxes given in Table 2.

(b) Calculated from Ussing-Teorell equation.

External K concentration 0.5 mM. Assuming a PD of -105 mV cytoplasm to outside, and a PD of +10 mV across the tonoplast (Davis and Hinginotham, 1976).

where the isotope was added to the external medium (Fig. 4 & 5). This suggests that the major effect of ABA is on entry into the symplasm. Similar findings have also been reported with sunflower and bean root systems (Karmoker & Van Steveninck, 1978; Glincka, 1980).

The major factor for the contradiction in the reports for barley and maize roots might be difference in the compartmentation, levels and distribution of ABA and its metabolites in these 2 plant species. Behl *et al.*, (1981) have reported that in barley roots, there are two compartments for ABA, one is identified as the cytoplasm and contains 3.62  $\mu$ M ABA and the second is the vacuole containing 0.30  $\mu$ M ABA, ABA concentration decreased rapidly towards the more basal segment (6-30 mm) of the root and ABA metabolites phaseic acid (PA) and dihydrophaseic acid (DPA), were distributed similarly to ABA. However in maize the highest content of ABA is reported to be the region of root apex (0-1mm), and the concentration was about 10 times lower than the concentration found in barley roots (Rivier & Pillet, 1981). The metabolites of ABA, PA and DPA and methyl ester (Me-ABA), have also been reported to be inhibitory by themselves or compete with ABA for receptor sites (Deshke, *et al.*, 1979; Collins & Channa, 1983).

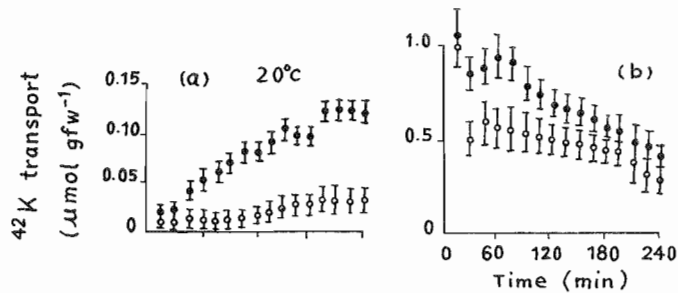


Fig. 4. Effect of ABA on  $\text{K}^{42}$  transport into the exudate at 20°C. (a) Isotope added to the bathing medium. Roots pretreated with ABA or DMSO for 2h prior to  $\text{K}^{42}$  addition. (b) Roots preloaded with  $\text{K}^{42}$  for 18h. Isotope absent from the bathing medium. Plants grown in the dark at 25°C. • — ABA o — Control.

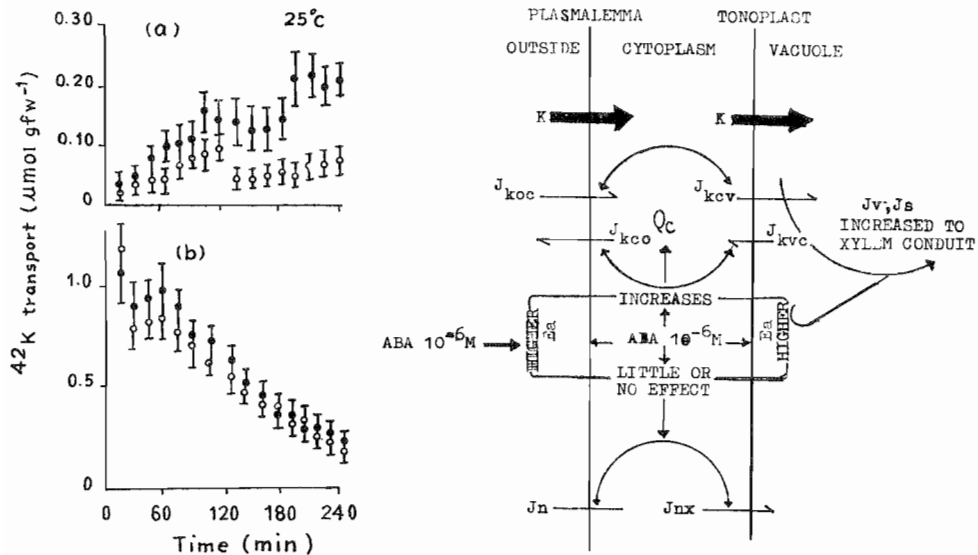


Fig. 5. Effect of ABA on  $\text{K}^{42}$  transport into the exudate at 25°C. (a) Isotope added to the bathing medium. Roots pretreated with ABA or DMSO for 2h prior to  $\text{K}^{42}$  addition. (b) Roots preloaded with  $\text{K}^{42}$  for 18h. Isotope absent from the bathing medium. Plants grown in the dark at 25°C. • — ABA o — Control.

Action of ABA on intercellular K flux in excised maize root. Serial two-compartment cell model (not including cell wall, and symplasm and endodermis together as a barrier for xylem conduit). Individual fluxes between the external solution and cytoplasm, and between the cytoplasm and vacuole, Q amount of ions in cytoplasm, Externally solution: Index O, Cytoplasm: Index C; Vacuole: Index V; Xylem: index X; Net tracer flux  $J_n$ ; Volume flow to xylem conduit:  $J_v$ ,  $J_s$ . Bold arrow indicates active transport across the plasmalemma and tonoplast. Light arrow indicates the direction of ion flux and effect of ABA on fluxes and its binding with cell membrane.  $E_a$  is the membrane activation energy for ion transport.

The increased K-accumulation, cytoplasmic content and fluxes across both the membranes (Fig. 3 and Table 1) and stimulated xylem fluxes (Table 3 and Fig. 4 & 5) indicates that it is the active K uptake which is affected by ABA.

Thus the evidence for the mechanism of ABA action in the maize root remains controversial. However, we have put forward a model for ABA action on the intercellular K fluxes. The salient features of this model are that the K is actively transported inwards in maize roots and externally applied ABA increases cytoplasmic contents (Qc) and fluxes from outside to cytoplasm (Joc) and from cytoplasm to vacuole (Jcv) i.e. increases the loading of symplasm. ABA has similar effect on the fluxes from vacuole to cytoplasm (Jvc) and from cytoplasm to outside (Jco), but does not alter tracer net flux of ions (Jn). Coupled with increased ion transport across the individual membrane ABA stimulates total volume flow (Jv, Js) to the xylem conduit.

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