Planta (Berl.) 116, 173—185 (1974)

The Effect of Abscisic Acid on the Uptake of Potassium and Chloride into *Avena* Coleoptile Sections

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Received May 26/November 19, 1973

Summary. The effect of abscisic acid (ABA) on uptake of potassium ($^{86}Rb^+$ or $^{42}K^+$) by *Avena sativa* L. coleoptile sections was investigated. ABA lowered the potassium uptake rate within 30 min after its application and inhibition reached a maximum (ca. 75%) after 2 h. The inhibition of K^+ uptake increased with ABA concentration over a range of 0.03 to 10 μg/ml ABA. At a higher K^+ concentration (20 mM) the percentage inhibition decreased. The percentage inhibition of K^+ uptake by ABA remained constant with external K^+ varied from 0.04 to 1.0 mM. After a loading period in 20 mM K^+ ($^{86}Rb^+$), apparent efflux of potassium was only slightly increased by ABA. Experiments in which growth was greatly reduced by mannitol or by omission of indole-3-acetic acid from the medium indicated there was no simple quantitative correspondence between ABA inhibition of coleoptile elongation and ABA inhibition of K^+ uptake. Chloride uptake was also inhibited by ABA but to a smaller degree than was K^+ uptake. No specificity for counterions was observed for K^+ uptake. Uptake of 3,0-methylglucose and proline were inhibited by ABA to a much smaller extent (14 and 11%) than that of K^+, a result which suggests that ABA acts on specific ion uptake mechanisms.

Introduction

Several types of findings have led us to explore the relationship between abscisic acid (ABA) and potassium uptake in a tissue in which ABA is an active inhibitor of growth. ABA inhibits auxin-induced elongation (Addicott *et al.*, 1964) and this inhibition is detectable within 5 min after ABA application (Rehm and Cline, 1973). On the other hand, research on control functions of ABA in stomatal activity seems to follow a line unrelated to growth. The accumulation of K^+ in guard cells is important in controlling stomatal opening in light (Fischer and Hsiao, 1968). The increased amount of K^+ in the guard cells was proved to be sufficient to produce the changes in guard cell volume and osmotic pressure associated with stomatal opening (Humble and Raschke, 1971; Sahwney and Zelitsch, 1969), and the flux in guard cells in relation to stomatal opening and closing has been demonstrated to be under the influence of ABA (Horton and Moran, 1972; Mansfield and Jones, 1971).

An effect of ABA on K^+ uptake was also demonstrated in other plant responses. It was reported that ABA inhibits K^+ uptake in slices from expanding *Vicia faba* leaves (Horton and Bruce, 1972) and in discs of expanded leaves of *Commelina communis* (Mansfield and Jones, 1971), although it was concluded in the case of *Commelina* that ABA had a much greater effect on ion uptake into guard cells than into the leaf tissue as a whole. In beet-root tissue discs, Van Steveninck (1972) reported that ABA delayed the development of the uptake capacity for Cl^-, Na^+ and K^+. Once the tissue had developed this capacity (more than 24 h after ABA application), however, ABA strongly stimulated the net uptake of these ions.

Older work (Cooil and Bonner, 1957) showed that addition of K^+ to the growth medium increased the growth of coleoptile sections. In view of the importance of K^+ in maintening elongation of *Avena* coleoptile sections, and of the inhibition of this elongation by ABA we set out to examine the way in which ABA might influence K^+ uptake into a tissue at a time when growth is being inhibited. Further we wished to make some initial assessment of the possibility that the two activities of ABA might be functionally related although the results thus far have not indicated a simple quantitative correspondence.

In this paper we report some characteristics of the influence of ABA on K^+ uptake in oat coleoptile sections. In estimating K^+ uptake, it was assumed that $^{86}Rb^+$ and K^+ moved identically as has been shown in other higher plant systems (Rains, 1968; Läuchli and Epstein, 1970). To substantiate the validity of this assumption we did a test using both ^{86}Rb and ^{42}K as tracers for potassium (K^+) uptake.

In addition, Cl^- uptake and uptake of two organic compounds, methylglucose and proline, and the effect of ABA on these were investigated.

Materials and Methods

Seeds of *Avena sativa* L. cv. California Red were soaked in running tap water for 2 h and planted in vermiculite in the dark at 24°. All manipulations thereafter were carried on in the dark or under dim, green light. Seedlings 80–90 h old were selected for uniformity. Leaves were removed and coleoptile sections of 4.7 mm were cut from 3 mm below the tip. About 35 sections (approximately 0.1 g fr. wt.) were floated on 5 ml uptake medium.

The standard uptake medium contained 5 mM tris-hydroxymethylaminomethane-citric acid (Tris-citrate) buffer, pH 4.8, and 0.5 mM $CaSO_4$. Indole-3-acetic acid (IAA) at 0.1 µg/ml and 2% sucrose were used in the uptake medium at all times except where indicated otherwise. The ABA used throughout the experiment is (RS)-(±)-abscisic acid obtained from Hoffman-LaRoche. At the end of incubation, the sections were tranferred to 50 ml of desorption solution at 0° for 30 min. The desorption solution contained 0.5 mM $CaSO_4$ plus 1 mM KCl (or higher concentration as indicated in results) in K^+ and Cl^- uptake studies, and 10 mM glucose for 3,0-methylglucose, or 0.1 mM L-proline for proline uptake studies. After desorption, the sections were blotted dry before radioassay procedures.

Radioactive rubidium (^{86}Rb) and potassium (^{42}K) were used as tracers for K^+ movement. Radioactive chloride (^{36}Cl), 3,0-methyl[^{14}C]D-glucose, and L-[^{14}C]-proline (uniform) were used for Cl^-, methylglucose and proline uptake studies, respectively.

After freezing and thawing of coleoptile sections, the nonexchangeable $^{86}Rb^+$ or $^{42}K^+$ was radioassayed by Cerenkov radiation in 15 ml of 2.5 mM aqueous 7-amino-1,3-naphthalene disulfonic acid (Läuchli, 1969). After $^{36}Cl^-$ uptake, the tissue sections in counting vials were ground into small fragments while frozen on dry ice. The capped vials, containing tissue and 1 ml distilled water, were incubated in a 50° bath for 30 min. Then radioactivity was counted in a Packard Tri-carb scintillation spectrometer with 15 ml toluene-dioxane-ethanol scintillation fluid added to each vial. For the assay of 3,0-methyl[^{14}C]glucose and [^{14}C]proline tissue, sections were processed the same as for the ^{36}Cl radioassay except that 1 ml of 95% ethanol instead of distilled water was added to the vial to extract methylglucose or proline. The quenching effects of tissue fragments were corrected for by internal standards.

In the efflux experiments, freshly cut coleoptile sections were allowed to take up K^+ ($^{86}Rb^+$-labeled) from uptake medium containing 20 mM KCl in the presence of 0.1 μg/ml IAA for 6 h. After this, sections were briefly rinsed in unlabeled uptake medium, blotted dry, and divided into two lots. One lot was transferred to 5 ml unlabeled uptake medium with IAA. The second lot was transferred to an equal volume of the same solution plus ABA (10 μg/ml). After varying time intervals the medium was withdrawn with a syringe and was replaced with 5 ml fresh medium. Aliquots of the withdrawn solutions were counted by Cerenkov radiation in the scintillation counter.

All data presented are the results of experiments performed at least 2 times.

Results

The Characteristics of the Effect of ABA on Potassium Flux

Time courses of K^+ uptake in the absence and presence of ABA over a period of 12 h from the time sections were cut and placed in solution are shown in Fig. 1. Without ABA a decrease in the K^+ uptake rate continued for the first hour and was followed by a lag phase or period of low uptake rate. The rate increased again to a maximum which remained constant after about 4 h of incubation. In the presence of ABA uptake was inhibited after 1 h, and the uptake rate was reduced up to 75% between 4 and 10 h incubation. In order to test the validity of using ^{86}Rb as a K label a time course of uptake experiment was run using both ^{86}Rb and ^{42}K simultaneously in 1.0 mM K^+. K^+ uptake determined by ^{86}Rb and by ^{42}K showed quantitative agreement within a few percent.

In order to test whether or not the strong reduction of the high uptake rate after 4 h by ABA could be due to inhibition of the development of an increased capacity to accumulate K^+, we preincubated sections in unlabeled solution for 4 h and then added $^{86}Rb^+$ and ABA. The results in Fig. 2 show that the linear phase of uptake had been reached. ABA inhibited the K^+ uptake within 30 min, and the inhibition reached a maximum of 75% after 2 h. It is obvious that the effect of ABA was to

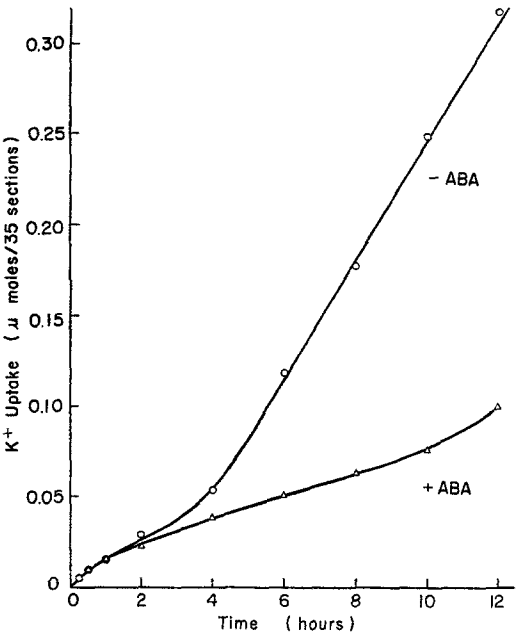

Fig. 1. Time course of potassium (^{86}Rb) uptake by freshly cut oat coleoptile sections in the presence and absence of 10 μg/ml ABA. The uptake medium contained 0.5 mM $CaSO_4$, 0.2 mM KCl, 2% sucrose and 0.1 μg/ml IAA in 5 ml Tris-citrate buffer, pH 4.8

reduce the high uptake rate which was already established, and not to prevent the development of that uptake capacity.

The relationships between ABA concentration, K^+ uptake and growth are shown in Fig. 3. The inhibition of K^+ uptake increased with ABA concentration over the range of 0.03 to 10 μg/ml. This was the same range of ABA concentration found to be effective in inhibiting coleoptile section growth as shown here and in Addicott *et al.* (1964).

To determine the extent to which the effect of ABA on K^+ uptake may be dependent on the inhibition of growth by ABA, the uptake was measured in the presence of 0.3 M mannitol which almost completely inhibited growth after 1 h. Growth was also reduced by omitting auxin from the incubation medium. The results in Table 1 showed that when growth was nearly stopped by mannitol, ABA inhibition of uptake was not changed. The inhibition by ABA was nearly as great in the absence of auxin-induced elongation as it was in its presence. Although the ion-uptake rate was higher in the presence of IAA, a large portion of the ABA inhibition of uptake remained under conditions in which growth

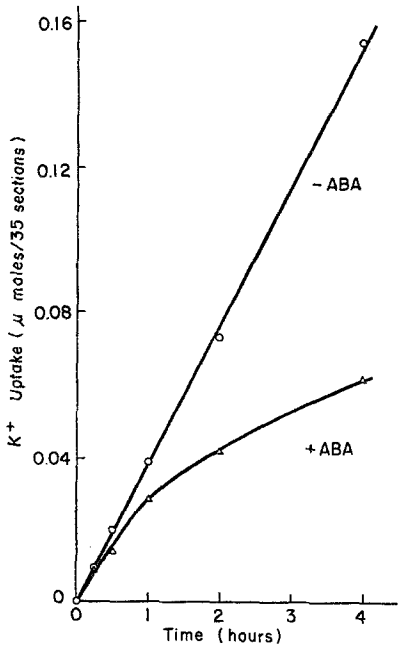

Fig. 2. Effect of ABA on potassium uptake by sections preincubated 4 h. Preincubation was in standard uptake medium with 0.2 mM KCl. ABA (10 μg/ml) and ^{86}Rb added at zero time

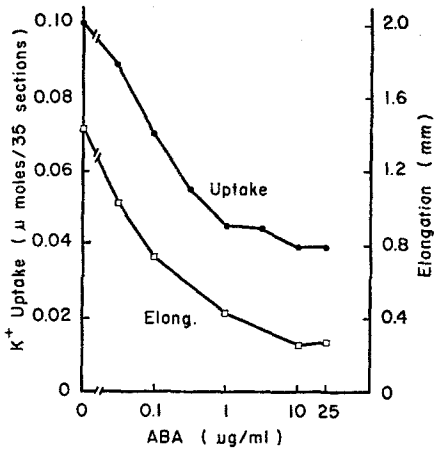

Fig. 3. The relationships between ABA concentration, and potassium uptake and growth of oat coleoptile sections. Elongation and uptake of K^+ ($^{86}Rb^+$) of freshly cut sections measured after 6 h in standard uptake medium containing 0.2 mM KCl and various concentrations of ABA

Table 1. Effect of growth inhibition on ABA inhibition of potassium uptake
Growth inhibited by 0.3 M mannitol or by withholding 0.1 μg/ml IAA. 6 h uptake period in 0.2 mM KCl (^{86}Rb labeled) uptake medium after preincubation in non-labeled uptake medium for 1 h. ABA at 10 μg/ml.

Treatment	K(^{86}Rb) uptake (μmol/35 sections)	ABA inhibition (%)	Elong. during uptake period (%)
+IAA, −ABA	0.12	58.2	28.2
+IAA, +ABA	0.05		5.1
+IAA, +mannitol, −ABA	0.124	62.2	3.3
+IAA, +mannitol, +ABA	0.047		2.9
−IAA, −ABA	0.086	50.2	8.0
−IAA, +ABA	0.043		1.9

was greatly reduced. It may be concluded that the inhibition of K^+ uptake by ABA is not dependent on ABA inhibition of growth.

The uptake of K^+ was measured over a range of external K^+ concentrations from 0.04 to 20 mM (in this case desorption solution contained 0.5 mM $CaSO_4$ and 10 mM KCl was used). As shown for high and low ranges of K^+ concentration in Fig. 4a and b, the uptake increased with concentration, and the percentage of uptake inhibition by ABA was essentially constant up to 1.0 mM external KCl concentration. The percentage of inhibition decreased at higher external K^+ concentration.

The amounts of uptake in 2 h measured by ^{86}Rb and ^{42}K as shown in Fig. 4 are essentially the same. Therefore, the conclusion of various authors (Rains, 1968; Läuchli and Epstein, 1970) that Rb^+ and K^+ are absorbed through a common carrier mechanism appears to be valid also for oat coleoptile sections.

The K^+ uptake in the presence and absence of ABA did not appear to be influenced by the species of inorganic anion accompanying K^+. As shown in Table 2, K^+ uptake was similar when Cl^- was either replaced with Br^-, NO_3^-, or SO_4^{2-}, or with citrate (KOH added).

The ABA-mediated differences in K^+ uptake reported here could result from modification of either influx or efflux rates. In order to evaluate the influence of efflux on the apparent influx rate, coleoptile sections were incubated in 20 mM K^+ with $^{86}Rb^+$ label for 6 h, and the loss of radioactivity to unlabeled solution was measured for 10 h thereafter. As shown in Fig. 5, efflux of K^+($^{86}Rb^+$) was slightly greater with ABA present from the start of wash-out than without it. Flame photometer assays indicated the concentration of K^+ in the tissue after the loading period was about 40 mM, and from this the additional loss K^+ from the tissue due to ABA was calculated to be 2.2 mM. In an experiment

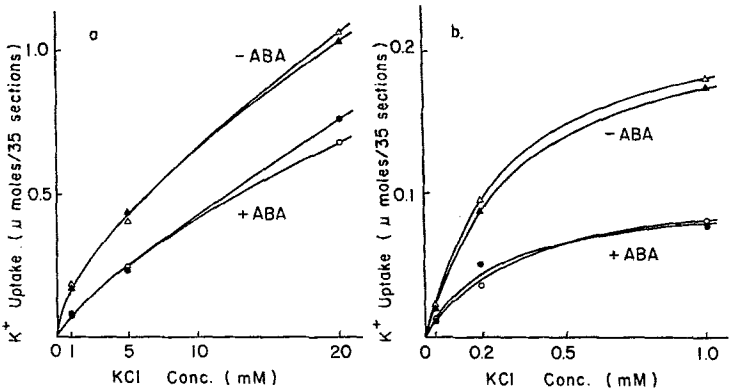

Fig. 4 a and b. Effect of potassium concentration on the uptake of K^+ in the presence and absence of 10 μg/ml ABA. $^{86}Rb^+$ (open symbols) and $^{42}K^+$ (closed symbols) were used as tracers for K^+. Uptake was measured in 2 h after 4 h of pre-incubation in uptake medium without radioactive label. The desorption solution contains 50 ml of 10 mM KCl and 0.5 mM $CaSO_4$. Both ^{86}Rb and ^{42}K were counted by Cerenkov radiation

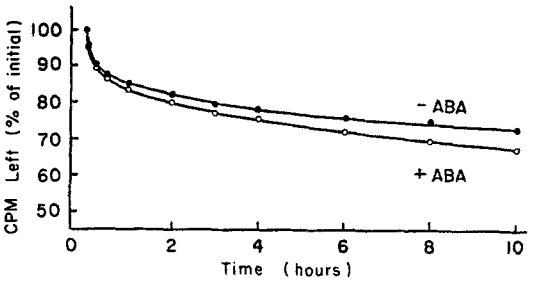

Fig. 5. Effect of abscisic acid on the efflux of potassium from coleoptile sections. Sections were pre-loaded for 6 hours in medium containing 20 mM KCl (^{86}Rb-labeled). ABA (10 μg/ml) and unlabeled medium added from the start of efflux measurement

measuring uptake from 20 mM$^+$($^{86}Rb^+$) over 10 h (data not shown) ABA was responsible for a K^+($^{86}Rb^+$) accumulation difference of 27 mM in the tissue. Since this uptake difference was more than 10 times the efflux difference, the ABA influence on K^+ accumulation cannot be a result of increased efflux under these conditions.

Experiments using 0.2 mM K^+ loading solutions with similar loading and efflux periods in 0.2 mM K^+ gave correspondingly small differences in efflux with and without ABA. Sections taken from plants germinated and grown in the presence of ^{86}Rb had similar minor differences in efflux rate in the presence and absence of ABA.

Table 2. Effect of ABA (10 μg/ml) on potassium uptake in the presence of various anions

Uptake of freshly cut sections for 6 h in uptake medium containing 0.5 mM $CaSO_4$, 2% sucrose, 0.1 μg/ml IAA and various potassium salts at K^+ concentration of 1 mM in Tris-citrate buffer.

Potassium source	K(^{86}Rb) uptake μmol/35 sections		Inhibition byABA (%)
	−ABA	+ABA	
KCl	0.326	0.234	28.3
KBr	0.365	0.228	37.5
KNO_3	0.342	0.216	36.8
KOH	0.388	0.212	45.4
K_2SO_4	0.319	0.201	37.0

Relation between ABA Inhibition of Growth and K^+-uptake Rate

To determine if the inhibition of K^+ uptake by ABA is responsible for the observed inhibition of growth by ABA, coleoptile sections were incubated with varying concentrations of K^+ in the medium in the presence or absence of ABA. This was done in order to test if variations of the K^+ uptake rate or of internal concentration produced by varying the external concentration would affect growth in a manner similar to variations produced by ABA inhibition. Table 3 shows the growth and K^+ uptake of sections incubated for 8 h with 0, 0.2 or 20 mM K^+ in the standard medium with and without 10 μg/ml ABA. In response to the change in external K^+ concentration the apparent K^+ uptake varied from 0 to 4.47 μmol while the growth increased by not more than 25%. ABA inhibition of growth was nearly the same at all K^+ concentrations or with no K^+ added. There does not appear to be a direct relationship between the K^+ uptake rate and the growth rate inhibition by ABA.

ABA Inhibition of Chloride Ion Uptake

Tests were conducted to determine if ABA influences the uptake of Cl^- by oat coleoptile sections. The uptake of ^{36}Cl into freshly cut sections measured during 6 h in media containing KCl or NaCl, and in the presence or absence of 10 μg/ml ABA, is shown in Table 4. ABA inhibition of Cl^- uptake is slightly less than that of K^+ uptake from 1 mM KCl. The data also indicate that Cl^- uptake at this concentration and its inhibition by ABA are not affected by having Na^+ replace K^+ as a cation. Again, the dependency of ABA inhibition of uptake on growth is ruled out since the ABA inhibition remained when growth was reduced by omitting IAA from the medium or nearly stopped by having 0.3 M mannitol in the medium.

Table 3. Relation between ABA inhibition of growth and K^+ uptake in 8 h
The K^+ uptake rate was varied by supplying different K^+ concentration in the medium. The incubation medium contained 0.5 mM $CaSO_4$, 2% sucrose, 0.1 µg/ml IAA and various KCl in 5 ml Tris-citrate buffer. The uptake and growth were from two different experiments.

K^+ in medium (mM)	Growth (mm)		Inhibition by ABA (%)	K^+ uptake (µmol/35 sections)		Inhibition by ABA (%)
	−ABA	+ABA		−ABA	+ABA	
0	1.39	0.30	78	0	0	0
0.2	1.46	0.33	77	0.194	0.073	63
20	1.09	0.28	74	4.47	2.69	40

Table 4. Effect of ABA (10 µg/ml) on chloride (^{36}Cl) uptake into freshly cut coleoptile sections in 6 h
Growth was limited by either 0.3 M mannitol or omitting IAA (0.1 µg/ml) in the medium.

	Control	ABA	Inhibition by ABA (%)
Cl^- uptake (cpm/35 sections)			
in 1 mM KCl			
+IAA	2785	2160	22.4
+IAA, +mannitol	3931	3324	15.4
−IAA	2495	2070	26.4
in 1 mM NaCl			
+IAA	2810	2080	26.0
+IAA, +mannitol	4020	3020	24.8
−IAA	3020	2230	26.2
K^+ uptake (µmol/35 sections)			
in 1 mM KCl, +IAA	0.318	0.198	34.0

Effect of ABA on Uptake of Organic Molecules

Studies on the uptake of 3,0-methylglucose have shown that a specific carrier mediates the transport of glucose and this glucose analogue (Gayler and Glasziou, 1972; Reinhold and Eshbar, 1968). Moreover, it is reported that this glucose analogue is not metabolized after being taken up (Reinhold and Eshbar, 1968), a characteristic which may be of special advantage for absorption studies with an organic compound. During an 8-h period oat coleoptile sections accumulated 3,0-methylglucose at a slowly decreasing rate as shown in Fig. 6. This is in contrast to the lag phase observed in the uptake of potassium (Fig. 1). The effect

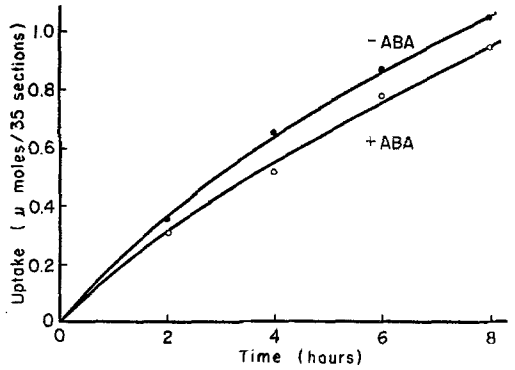

Fig. 6. Effect of ABA (10 μg/ml) on the uptake of methylglucose. Freshly cut coleoptile sections were allowed to take up methylglucose for various times in uptake medium containing 10 mM 3,0-methylglucose (^{14}C labeled) without sucrose

of ABA (10 μg/ml) on 3,0-methylglucose uptake was small, about 10% inhibition, and the influence on rate appeared to be constant throughout the period of measurement.

Since it appeared that the ABA inhibition of 3,0-methylglucose uptake could be due to the growth inhibition, the influence of ABA was tested in the presence of 0.3 M mannitol. Uptake of L-[^{14}C]proline was also measured in the same way. The results in Table 5 show that ABA inhibited methylglucose uptake to the same extent in mannitol as without. This indicates ABA can inhibit uptake of organic molecules independently from growth inhibition. L-Proline uptake was inhibited to a small degree (11%) without mannitol, but in the presence of mannitol there was essentially no ABA inhibition. This later effect may not be due entirely to smaller cell size when growth is inhibited, since proline metabolism is also modified by growth changes (Cleland, 1968).

Discussion

The uptake of potassium by oat coleoptile sections was found to be strongly inhibited by abscisic acid. This effect in *Avena* is similar to the ABA response reported for expanding *Vicia* leaves but not older non-expanding leaves (Horton and Bruce, 1972). Unpublished experiments of ours showed similar inhibition of K^+ uptake by ABA in coleoptile sections of ages 3.5 to 6.75 days, even though at the latter age the coleoptiles had stopped growing.

The influence of ABA on uptake is not entirely specific for potassium since chloride uptake also was inhibited, although to a smaller extent.

Table 5. Effect of growth on abscisic acid inhibition of methylglucose and proline uptake

Sucrose was not included in the uptake medium in methylglucose uptake study. Growth was limited by 0.3 M mannitol.

Substance accumulated	Uptake (nmol/35 sect.)		Inhibition by ABA (%)
	Control	ABA	
3,0-methylglucose-^{14}C (10 mM)			
−mannitol	851	730	14
+mannitol	831	670	19
L-*Proline-^{14}C (0.1 mM)*			
−mannitol	14.2	12.7	11
+mannitol	17.8	17.4	2

The effect does not appear to be a result of a general change in membrane permeability, however, since the uptake of organic molecules (Table 5) was influenced to a much smaller extent than that of K^+. K^+ efflux also was little affected, and this was in the direction of increasing efflux indicating increased permeability (Fig. 5). Therefore, the effect of ABA on K^+ and Cl^- uptake probably results from influence on specific ion uptake mechanisms.

Attention has been directed to the roles of ABA and K^+ in the regulation of stomatal opening in recent years (Kriedemann *et al.*, 1972; Horton and Moran, 1972). It is not very probable, however, that the uptake phenomena reported here can be attributed solely to the uptake of K^+ into guard cells. In this connection we measured the size of stomata in the coleoptile sections used. We then estimated that the total volume occupied by the guard cells was less than 0.5% of the volume of all cells in the coleoptile sections. Moreover, the stomata of these dark grown coleoptiles did not appear to be functional. They remained closed in darkness, after transfer to light for about 30 min, or after incubation of sections in 1 mM KCl for 6 h in light or in darkness. Thus it is very unlikely that guard cells take up K^+ differently from other cells of the coleoptiles and that the effect of ABA presented here is primarily the result of K^+ uptake into the guard cells.

The possibility that differences in K^+ uptake were due to differences in growth can be discarded (Table 1). The alternative that differences in K^+ uptake were in some way responsible for differences in growth, or the possibility that the two processes were unrelated may be considered from the point of view of either the kinds of evidence which indicate close parallels or those data which indicate no close parallels. When one considers K^+ uptake in terms of its contribution to the osmotic

properties of the system there appear to be no close parallels; for whether the absolute amount of change in K^+ uptake induced by ABA was large or small (depending on the external K^+ concentration) or negligible (in the absence of added inorganic cations), ABA was effective as an inhibitor of elongation (Table 3). When one considers the close parallels between the effect of varying ABA concentrations on K^+ uptake rate and on growth rate (Fig. 3) and the similarity in the initial response curve after ABA application (Fig. 2, and Rehm and Cline, 1973) a common ground might be sought at the level of activities in the membrane. Membrane-bound carrier systems for K^+ (interacting also with H^+, Na^+ and indirectly with Cl^-) and membrane-associated systems altering cell-wall properties may well have something in common.

It has been proposed (Hager *et al.*, 1971) that auxin action in cell elongation involves stimulation of a plasmalemma-bound, directional ATPase or proton pump that secretes protons into the cell wall to cause wall loosening. It was envisaged that compensating inward flow of cations or outward flow of anions would accompany the proton flux. The results reported here could well be related to an ABA interference at some point with a proton-excretion process or the related charge-balancing ion movements.

The possible influence of ABA on membrane-bound K-Na-stimulated ATPase is under investigation.

References

Addicott, F.T., Carns, H.R., Lyon, J.L., Smith, O.E., McMeans, J.L.: On the physiology of abscisins. In: Régulateurs Naturels de la Croissance Végétale, p. 687–703. Paris: CNRS 1964

Cleland, R.: Hydroxyproline formation and its relation to auxin-induced cell elongation in the *Avena* coleoptile. Plant Physiol. **43**, 1625–1630 (1968)

Cooil, B., Bonner, J.: The nature of growth inhibition by calcium in the *Avena* coleoptiles. Planta (Berl.) **48**, 696–723 (1957)

Fischer, R.A., Hsiao, T.C.: Stomatal opening in isolated epidermal strips of *Vicia faba*. II. Responses to KCl concentration and the role of potassium absorption. Plant Physiol. **43**, 1953–1958 (1968)

Gayler, K.R., Glasziou, K.T.: Sugar accumulation in sugarcane-Carrier-mediated active transport of glucose. Plant Physiol. **49**, 563–568 (1972)

Hager, A., Menzel, H., Kraus, A.: Versuche und Hypothese zur Primärwirkung des Auxins beim Streckungswachstum. Planta (Berl.) **100**, 47–75 (1971)

Horton, R.F., Bruce, K.R.: Inhibition by abscisic acid of the light and dark uptake of potassium by slices of *Vicia faba* leaves. Canad. J. Bot. **50**, 1915–1917 (1972)

Horton, R.F., Moran, L.: Abscisic acid inhibition of potassium influx into stomatal guard cells. Z. Pflanzenphysiol. **66**, 193–196 (1972)

Kriedemann, P.E., Loveys, B.R., Fuller, G.L., Leopold, A.C.: Abscisic acid and stomatal regulation. Plant Physiol. **49**, 842–847 (1972)

Humble, G.D., Raschke, J.: Stomatal opening quantitatively related to potassium transport: evidence from electron probe analysis. Plant Physiol. **48**, 447–453 (1971)

Läuchli, A.: Radioassay for β-emitters in biological materials using Cerenkov radiation. Int. J. Appl. Radiat. Isotop. **20**, 265–270 (1969)

Läuchli, A., Epstein, E.: Transport of potassium and rubidium in plant roots. The significance of calcium. Plant Physiol. **45**, 639–641 (1970)

Mansfield, T.A., Jones, R.J.: Effects of abscisic acid on potassium uptake and starch content of stomatal guard cells. Planta (Berl.) **101**, 147–158 (1971)

Purves, W.K.: Monovalent cations and growth regulation. I. Growth responses in cucumber hypocotyl segments. Plant Physiol. **41**, 230–233 (1966)

Rains, D.W.: Kinetics and energetics of light-enhanced potassium absorption by corn leaf tissue. Plant Physiol. **43**, 394–400 (1968)

Rehm, M.M., Cline, M.G.: Rapid growth inhibition of *Avena* coleoptile segments by abscisic acid. Plant Physiol. **51**, 93–96 (1973)

Reinhold, L., Eshbar, Z.: Transport of 3-0-methylglucose into and out of storage cells of *Daucus carota*. Plant Physiol. **43**, 1023–1030 (1968)

Sawhney, B.L., Zelitch, I.: Direct determination of potassium ion accumulation in guard cells in relation to stomatal opening in light. Plant Physiol. **44**, 1350–1354 (1969)

Van Steveninck, R.F.M.: Abscisic acid stimulation of ion transport and alternation in K^+/Na^+ selectivity. Z. Pflanzenphysiol. **67**, 282–286 (1972)