

early phase of interaction facilitation is shown to be succeeded by a prolonged phase of interaction depression. A similar result is obtained if the test shock is applied to the homolateral nerve, and the conditioning shock to the contralateral nerve.

These results indicate that there is interaction between the separate cell layers (A and B) of the contralateral eye and layer (A<sub>1</sub>) of the homolateral eye in the dorsal nucleus of the lateral geniculate body of the cat, and not between the presynaptic fibers to these layers.

Possible explanations for these findings are: (1) The presynaptic fiber endings synapse on the cells in the layer or layers of the other side. The anatomical evidence is clearly to the contrary. (2) Flows of current associated with the activity of one cell layer pass through and affect cells in the adjacent layer or layers of the other side.

That flows of current associated with the activity of cells and fibers may influence the excitability of adjacent normal resting cells and fibers is now a well-attested experimental finding (6), but the situations in which this phenomenon has been studied in the central nervous system have usually involved techniques such as antidromic activation, which make the assessment of the findings in terms of normal function somewhat uncertain. If the explanation suggested above is accepted, interaction in the geniculate is an example of the probable importance in normal function of flows of current in determining excitability at a distance. It may well be that the layering in the geniculate, a feature which is carefully preserved through the vicissitudes of phylogenetic development, is of importance in allowing these flows of current to

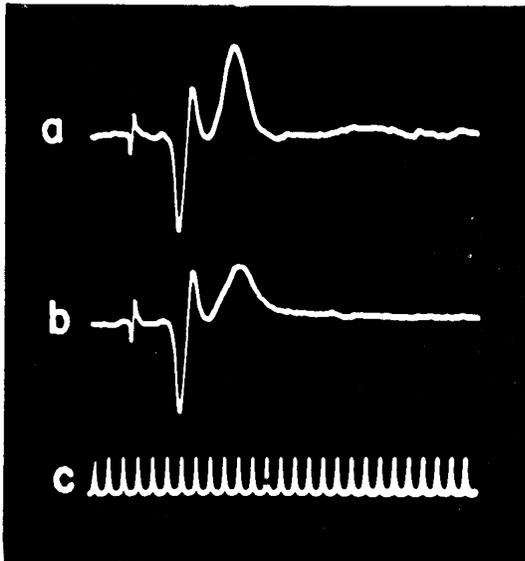


FIG. 2. *a* and *b*: responses recorded in lateral geniculate to stimulation of large diameter fibers in contralateral optic nerve; *a*, before, and *b*, after, a stimulus to the homolateral optical nerve similar in strength to that applied to the contralateral nerve. *c*: time intervals 0.2 msec.

assume an influence that they possibly would not have in a more random arrangement of nervous elements. This phenomenon may also be of importance within a particular layer of cells. The early phase of facilitation which is seen in the recovery cycle of geniculate cells following unilateral conditioning and testing has been explained (4) on the basis of reciprocal overlap of optic tract fiber endings. It is possible, however, that some of this facilitation may be due to flows of current within the layer where the stimulated fibers actually terminate. The relationship of the phenomenon of interaction to the excitability cycle and to the after-potentials of the geniculate cells has also been studied and these and other findings will be published in detail later.

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Manuscript received April 8, 1953.

## Stimulation of Rubidium Absorption by Auxins

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Among the more immediate and direct effects of auxins on plant cells are their stimulation of water uptake (cell enlargement) and of respiration (1). The effects of auxins on ion uptake are less clear, owing to the fact that both stimulation and depression have been found. The present report<sup>2</sup> definitely confirms the important conclusion of Commoner and Mazia (2, 3) that auxin may stimulate ion uptake in excised tissues. The results reported here outline more clearly the conditions associated with auxin-induced ion uptake and indicate some correlation between respiration and absorption of both ions and water. The conclusion that the mechanism of auxin action lies in stimulating water uptake through increased osmotic salt concentration in the cell sap (2, 3) has been previously criticized (4-6) on the basis that auxin-induced water uptake does not require the presence of salts in the external solution, and that auxin results in lowering the osmotic concentration in the cell, rather than increasing it. The present results also do not support the conclusion that the

<sup>1</sup>This study was supported by the Atomic Energy Commission under contract No. AT(45-1)-421. Additional support was provided by the Committee on Research, State College of Washington. The assistance of John Hanson and Mrs. Marie L. (Ehrman) Farr is appreciated.

<sup>2</sup>More detailed manuscripts of these studies are in preparation for publication elsewhere.

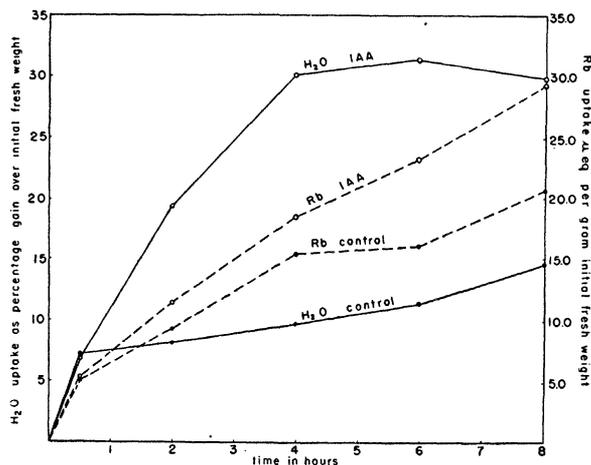


FIG. 1. Percentage increase in fresh weight and increase of Rb absorption by pea epicotyl segments in presence and absence of 1 ppm indoleacetic acid. RbCl concentration 5 meq/ml.

water uptake is induced by osmotic phenomena, rather they indicate a stimulation of both water and mineral ion uptake mediated through respiration.

The effect of auxins in stimulating ion uptake in excised tissue appears to be distinctly at variance with responses of intact plants (7). However, the present results seem consistent with the reports that auxin may induce greater uptake by seedlings of water and of salts (8), and that auxin-induced tumors have higher amounts of salts than other portions of the plant (9).

ously aerated either in 100 ml of solution in an Erlenmeyer flask or in a manometer vessel of a Warburg respirometer. Flasks were maintained at 25° C by use of a water bath in an undarkened laboratory. A minimum of 10 epicotyl segments or disks was used in each experimental flask. These generally were run in duplicate. The auxins used were  $\beta$ -indoleacetic acid (IAA) and  $\alpha$ -naphthalene acetic acid (NAA).

The pea epicotyl segments respond to IAA within 2 hr as shown both by increased fresh weight and greater Rb absorption (Fig. 1). This stimulation by IAA is apparent throughout the first 8 hr. Experiments extended over longer intervals (in a lighted laboratory) show that most of the response to IAA is attained during the first 8 hr for both water uptake and salt absorption. In fact, at 48 and 72 hr there appears to be a tendency for the controls to catch up in Rb absorption with the IAA-treated segments despite that fact that the differential in fresh weight persists at the levels attained within the first 24 hr.

In contrast with pea epicotyl segments, rutabaga (Table 1) and potato showed a much slower response to auxin in absorption of both water and Rb. Significant differences due to auxin did not appear before the 3rd or 4th day, but then both water and Rb uptake were greater than in the controls. It should be noted that auxin-induced water uptake in general is less when tissue is submerged than when floating (10); however, maximum ion absorption requires vigorous circulation of the external solution so that the experimental conditions reported here were not ideal from the standpoint of both water absorption and ion ab-

TABLE 1  
EFFECT OF IAA ON RUBIDIUM AND WATER UPTAKE BY DISKS OF RUTABAGA TISSUE

Treatment	Water uptake		Rubidium uptake by disks						
	gain in fresh wt (%)	meq/sample		Initial wt		Final wt		Dry wt	
			meq/g (%)	meq/g (%)	meq/g (%)	meq/g (%)	meq/g (%)	meq/g (%)	meq/g (%)
2 days									
0.0 ppm IAA	15	59	100	23	100	20	100	269	100
1.0 ppm IAA	26	58	98	23	100	18	90	267	99
10.0 ppm IAA	25	58	98	23	100	18	90	262	97
4 days									
0.0 ppm IAA	21	86	100	33	100	28	100	388	100
1.0 ppm IAA	49	108	126	43	130	29	103	535	138
10.0 ppm IAA	49	107	125	41	124	28	100	542	139

In the present work radioactive rubidium,  $Rb^{86}$ , was used as a tracer in RbCl solution to follow cation uptake. The tissues used were 5-mm segments of the 3rd internode of epicotyls from 7-day Alaska pea seedlings grown in the dark, disks of rutabaga tissue, and disks of potato tuber tissue (Katahdin var.). Rubidium absorption was measured by counting wet-ashed samples using a 2.5 mg/cm<sup>2</sup> mica window Geiger tube, a standard scaling circuit, and an automatic register. The tissues in each case were submerged and vigor-

sorption. Also as shown with rutabaga tissue in Table 1, increased Rb absorption was not necessarily reflected by the Rb concentration per unit final fresh weight. Generally, however, the increase in absolute amount, or in equivalents per unit of original fresh weight or dry weight was substantial. Thus it may be concluded that stimulation of growth as revealed by increase in fresh weight may be accompanied by an increased uptake of cations.

The question naturally arises as to whether Rb and

water move separately or together during the interval in which the absorption of both is stimulated by auxin. The evidence here, as in general, indicates a marked independence of rates in the two processes. Furthermore, a test with pea epicotyl segments in various osmotic concentrations of mannitol shows clearly that large changes in water uptake, or loss, may occur with no significant effect on Rb absorption (Fig. 2). It seems clear, therefore, that net water movement is not directly related to Rb absorption.

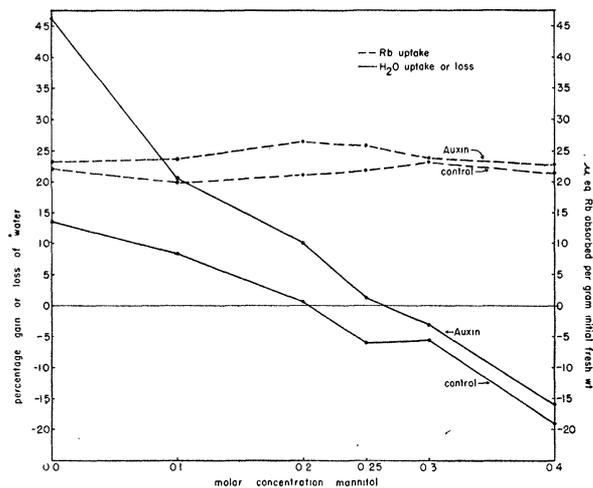


FIG. 2. Effect of 0.1 ppm IAA on Rb uptake by pea epicotyl segments during uptake or loss of water in various osmotic concentrations of mannitol. RbCl concentration 5 meq/ml.

The fact that rates or net movements of water and ions may differ markedly is not conclusive evidence that there is no relation between the two processes. In fact, it is now well known that, in addition to the passive phases of uptake, the accumulation and retention—above external concentrations—of both water and salt may be regulated by oxidative respiratory activity. Whether the metabolic mechanism responsible for active water absorption is different from that for salt accumulation is not known. This would require knowledge of the flux of each—water and salt—at the cell boundary and of the amounts of respiratory energy required for retaining each at given states. Preliminary tests measuring respiration of pea epicotyl segments do show that the stimulation by IAA does, as expected, include oxidative respiration as well as water and salt uptake (Fig. 3). The increase in amounts of Rb and  $O_2$  absorbed over that of the controls is within the same order of magnitude percentage-wise. No doubt the most important relation here is the increase in oxidative respiration which directly or indirectly supplies the driving force for both water and Rb accumulation.

The proportions of energy channeled into water uptake as opposed to that for Rb absorption are, of course, not readily measurable. However, it may be concluded from the results of the osmotic concentration tests that major reductions in the potential dif-

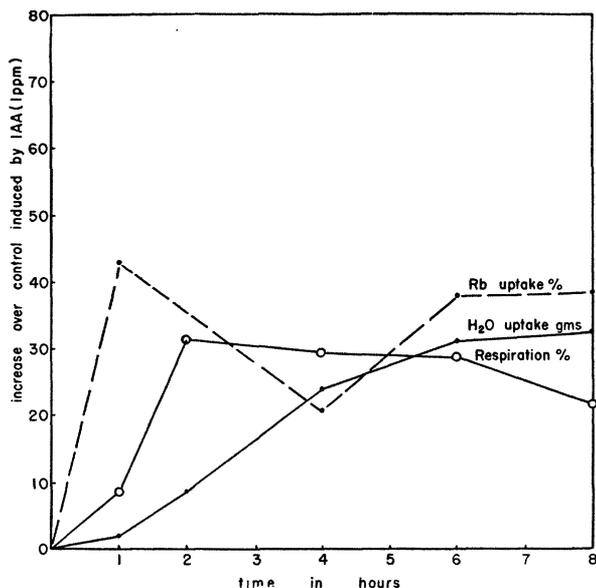


FIG. 3. Effect of 1 ppm IAA on the increase over the control of oxidative respiration, water uptake and Rb uptake. Pea epicotyl segments in 5 meq RbCl/ml.

fusion of water (with increased mannitol concentration) had no appreciable influence on Rb uptake (Fig. 2). It might be inferred that the imposition of a concentration gradient favoring withdrawal of water from the cell might result in channeling more energy into the process of water absorption or retention (perhaps at the sacrifice of energy for cation uptake). While the results of the pea segment test (Fig. 2) show some increase in Rb uptake in the range near isotonicity, it seems clear that a great stress (resulting in partial plasmolysis) on water retention fails to halt Rb accumulation. In this range of mannitol concentration, 0.3 M–0.4 M, IAA failed to induce either a significantly higher absorption of Rb or a significantly greater water retention. It would appear, therefore, that whereas active water uptake and Rb absorption share some effect of auxin in common, this effect does not consist primarily in the direct competition of the two processes for respiratory energy. In similar experiments with potato disks there is evidence suggesting some competitive effect between water and salt on the basis of relatively greater Rb absorption in the isotonic range.

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Manuscript received February 9, 1953.