Light-Enhanced Potassium Absorption by Corn Leaf Tissue

Abstract. *The rate of absorption of potassium by slices of corn leaf in the light was about twice the rate in the dark. When the light was turned on or off, changes in the rate of absorption took place some minutes after the change in illumination. Experiments with the antimetabolites, 2,4-dinitrophenol and cyanide, indicated that the source of energy for active accumulation of potassium by green tissue in the light was different from that in the dark. In the light, energy was closely linked to photosynthetic reactions; in the dark, it was linked to respiratory processes.*

Although roots are the primary organs in higher plants for the initial absorption of ions, cells of green leaves must also acquire essential mineral elements from their ambient solution—the solution delivered into the extracellular fluid (outer space) of the leaf by the xylem.

Hoagland and Davis (*1*) studied the possible connection between light and ion absorption in algae. Other investigators were also interested in the coupling of light and ion transport in various algae (*2*) and other aquatic plants (*3*). Generally, it was concluded that light provides energy for active ion transport by making available both respiratory substrates and high-energy intermediates. MacRobbie (*2*) concluded that the light-enhanced movement of potassium in *Nitella* was the result of the utilization of high-energy phosphate through photophosphorylation, while chloride transport was linked to the movement of electrons in photosynthetic reactions. Kylin (*4*) used pieces of leaves from various plants to investigate the effect of light on the uptake of sulfate and concluded that the transport of sulfate was mediated by two different energy sources in the light and in the dark.

Light-enhanced uptake of rubidium by cells enzymically isolated from tobacco leaves was observed only in the presence of bicarbonate (*5*). However, the effect of bicarbonate on respiration and organic acid synthesis was not studied in those experiments. No other experiments seem to have been done on the role of light in ion transport by the cells of leaves of terrestrial plants.

Smith and Epstein (*6*) developed a technique for experimenting on ion uptake by leaf cells. The process of this uptake closely resembled that in root tissue in all characteristics examined (*7*). With this method, variability resulting from changes in leaf temperature, stomatal opening, and transpiration can be minimized. This leaf-slice technique, which was extended to the mangrove *Avicennia marina* (*8*), has provided a method for precise experiments on the kinetics of ion transport by leaf cells of terrestrial higher plants (*6, 7*).

I studied the effect of light and dark on the absorption of potassium by corn leaf tissue, and the coupling between various energy sources and ion transport in light and in dark. Slices (400 μ wide) of leaf from corn *Zea mays*, DeKalb 805, gave maximum accumulation of potassium on a unit weight basis and were used in all experiments. On the day of the experiment, leaves were harvested from plants grown in the greenhouse. Leaf slices were placed in a solution and treated in light or dark for 60 minutes. The leaf tissue was then immersed in a solution containing 0.1 m*M* KCl labeled with rubidium-86 and 0.5 m*M* $CaSO_4$. The temperature of the solutions was maintained at 30° ± 1°C. At the end of the period of experiment, the samples were transferred for 30 minutes to a solution containing unlabeled 1 m*M* KCl and 0.5 m*M* $CaSO_4$, for removal of that fraction of labeled K associated with the cell wall (*9*). The light treatment was carried out either in the greenhouse or a growth chamber with the light intensity varying from 16,500 to 33,000 lumen/m^2. Light saturation for ion transport took place at low light intensities (approximately 1100 lumen/m^2).

The absorption of potassium as a function of time was studied in the presence and absence of light (Fig. 1). The uptake of potassium was a linear function of time in the light and in the dark. The rate of absorption in the light was about twice that in the dark.

The dark and light treatments were alternated along the time course (Fig. 2). For the first 60 minutes, potassium was absorbed in the dark at an essentially constant rate. After 60 minutes, the lights were turned on. In the first 15 to 20 minutes of the light period, there was no change; after this, the rate of absorption increased to a new, constant level. The lights were then turned off. The rate of absorption remained constant at the previous level for about 10 minutes. At the end of this time, the rate of potassium absorption increased even more for about 15 minutes and then declined to approximately that of the initial dark period. This experiment was repeated several times. The same general trend was observed each time, although the magnitude and the time period of the responses varied.

The effects of metabolic inhibitors on the rate of potassium absorption in light and dark were studied. The uncoupler, 2,4-dinitrophenol, at a concentration of 0.01 m*M*, reduced the rate of potassium absorption in the dark much more than in the light (to 15 percent of the control in the dark as opposed to 67 percent in the light). Dinitrophenol is a known uncoupler of oxidative phosphorylation (*10*), and it would appear that the contribution to potassium transport of adenosine triphosphate from respiration is much greater in the dark than in the light. The effect of cyanide on potassium absorption substantiates this con-

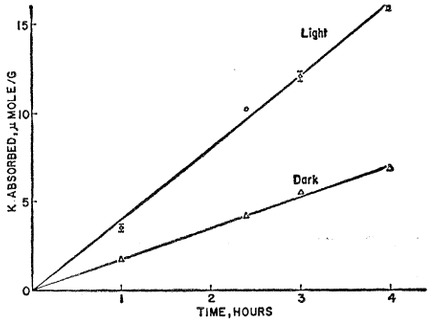

Fig. 1. Absorption of potassium by corn leaf tissue as a function of time in the light or dark. Potassium concentration, 0.1 m*M*; calcium concentration, 0.5 m*M*. Points are means of two values marked by horizontal lines. Where the lines are not indicated, the difference between the values was equal to or less than the diameter of the point.

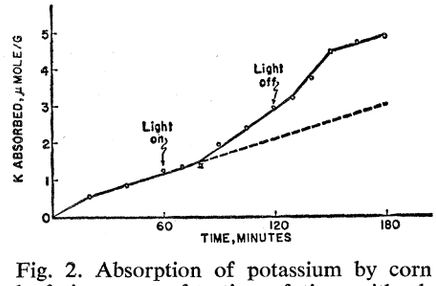

Fig. 2. Absorption of potassium by corn leaf tissue as a function of time with alternating periods of light or dark. All other conditions and conventions as in Fig. 1.

clusion; 0.01 m*M* NaCN reduced the rate in the dark to 60 percent of the control, but in the light it was 98 percent or more. Because cyanide inhibits the cytochrome system (*10*), it should decrease the supply of high-energy phosphate compounds more in dark than in the light due to the fact that in the light these compounds could be formed from light-dependent processes (photophosphorylation) (*4*). The absorption of potassium by corn leaf tissue in the light is closely coupled to the energy supplied by light-dependent processes, while in the dark the energy for active potassium accumulation is obtained through respiratory pathways, as in nonphotosynthetic tissue.

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Pulmonary Ventilation Measured from Body Surface Movements

Abstract. *Changes in anteroposterior diameters of the rib cage and abdomen are sensed with magnetometers and summed to give outputs which are very nearly linearly related to changes in lung volume. The volume events of breathing can be measured without recourse to a mouthpiece or face mask, other than for calibration, and with minimal encumbrance to the subject.*

Pulmonary ventilation is commonly measured directly, either as volumes of gas displaced in and out through the airways, or as volumes displaced by the body surface. Because direct methods involve mouthpieces, face masks, or neck seals, they are cumbersome and impractical for prolonged measurement. They also tend to make the subject aware that his breathing is being measured, which in itself influences breathing, and they limit the subject's range of activity. For these reasons indirect methods have been sought. These have included devices which sense movements or changes in electrical properties of the chest wall, or some combination of these (*1–3*). A difficulty has been that the chest wall not only changes volume with breathing, it also changes shape. The shape depends on such matters as the nature of the act of breathing—for example, whether or not the subject is talking—on restrictions offered by clothing, and on posture and activity. To compensate for changes in shape, measurements have been made at more than one site.

Recently Konno and Mead showed that, to a useful approximation, the changes in shape can be accounted for by treating the chest wall as a system with only two degrees of freedom, the volume change of the rib cage accounting for one and that of the abdomen for the other. They further demonstrated that the volume change of each was very nearly linearly related to changes in anteroposterior diameters (*4*). Here we describe an improved transducer system for recording these diameters, as well as a convenient way to mix the signals in order to give an output proportional to total change in lung volume.

Our approach has been to measure at one body surface the strength of a magnetic field generated at the opposite surface. Identical coils are used, both to generate and to sense the fields. Two pairs of coils are oriented with their long axes in the horizontal (transverse) plane and at right angles to the sagittal plane, at the midline at the level of the nipple and umbilicus, respectively. Since the axes of the coils remain parallel, and the magnetic field produced is dipolar, the voltage induced in the receiving coil is inversely proportional to the cube of the coil separation. Because the changes in diameter are small relative to the absolute diameters, the relationship between voltage change and diameter change may be reasonably approximated as linear during ordinary breathing.

Figure 1 gives the wiring diagram for the apparatus along with the coil specifications. The coils are held within rubber sleeves, glued to aluminum plates. The aluminum plates are fixed to the skin by means of flexible plastic discs with adhesive coatings on both surfaces. The coils are further supported either with strips of adhesive tape or by means of rubber straps such as are used to hold electrocardiographic electrodes in place. The pairs of coils are tuned and driven at their resonant frequencies of 600 and 1390 cycle/sec, respectively. At these frequencies the influence of tissue (or gas) on the magnetic field strength is negligible. Cross talk is reduced to acceptable levels with filters.

In use, the outputs of the two channels are summed and their relative gains adjusted so that when, at constant lung volume (nose clip in place and mouth closed), the subject voluntarily shifts volumes back and forth between rib cage and abdomen, the summed output remains constant. (This maneuver is most easily accomplished by alternately relaxing and contracting the muscles of the abdominal wall.) At constant lung volume, any volume change of the rib cage must be equal and opposite to that of the abdomen. Therefore, if the relative gains are adjusted so that the summed output remains constant during the iso-volume maneuver, each signal must bear the same relationship to volume change, and their sum must have a fixed relationship to the total volume change of

Table 1. Simultaneous measurements of minute ventilation (liter/min ATPS), estimated spirometrically (s) and from chest wall measurements (w) (see *5*).

Rest		Rebreathing		Exercise	
s	w	s	w	s	w
		Subject E.B.			
4.7	4.2	24.5	23.2		
		64.2	63.3		
		Subject J.B.			
10.4	9.8	17.8	17.2		
		52.8	54.0		
		Subject D.L.			
7.2	6.3	19.6	16.4		
		67.2	61.6		
		Subject J.M.			
6.6	6.4	13.8	12.8	18.8	17.5
		26.0	25.0	38.4	35.7
		Subject T.T.			
9.6	9.5	35.3	36.0	26.2	27.0
		55.0	59.5	40.1	45.5