THE KINETICS OF EXOSMOSIS OF WATER FROM LIVING CELLS.

By MORTON McCUTCHEON AND BALDWIN LUCKE.

(*From the Laboratory of Pathology, School of Medicine, University of Pennsylvania, and the Marine Biological Laboratory, Woods Hole.*)

(Accepted for publication, February 17, 1927.)

In previous communications data were presented on the rate with which water enters living cells (the unfertilized egg of *Arbacia punctulata*) under the driving force of osmotic pressure (1, 2). The present paper is concerned with the reverse process—exosmosis of water.

The material and technic of the experiments were the same as formerly employed.

The Kinetics of Exosmosis.

The first point was to determine whether exosmosis follows the same diffusion equation as does endosmosis, namely $\frac{dx}{dt} = k\,(a - x)$, where a is the total volume of water that will cross the membrane before equilibrium is established, x the amount that has already crossed at time t, and k is the velocity constant. For this purpose, eggs were placed in a dish containing 60 per cent sea water (sea water 60 parts, and distilled water, 40 parts). In this hypotonic solution, eggs were allowed to swell until osmotic equilibrium was attained. A number of eggs were then transferred to a second dish containing full strength sea water (100 per cent sea water). Three cells were measured with an ocular screw micrometer at minute intervals, until they had again reached osmotic equilibrium. Duplicate observations were usually made by the two observers. The mean volumes of 6 or more cells were plotted against times, and a curve obtained, as is shown in Fig. 1. In the same graph, $\log \frac{a}{a - x}$ is plotted against times. This plot is found to give a straight line, the slope of which is k, the velocity constant.

It is evident from this relation that the process of exosmosis follows the same equation as was previously found to fit endosmosis. This result was invariably obtained in scores of experiments at various temperatures.

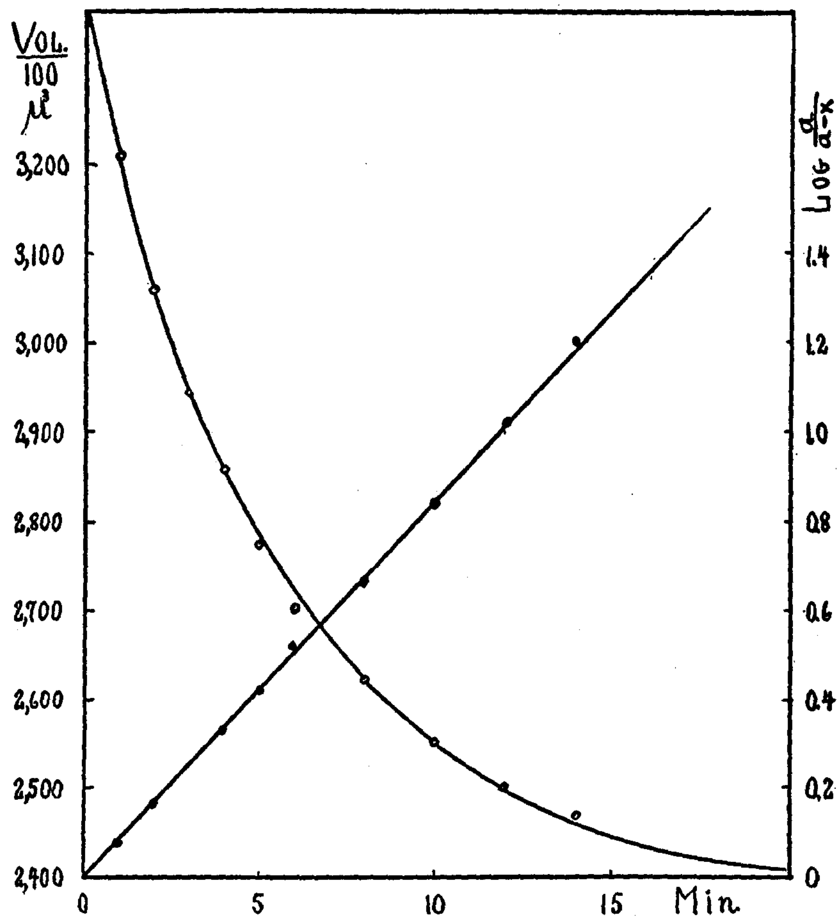

FIG. 1. A typical exosmosis experiment. Cells previously swollen in 60 per cent sea water were caused to shrink by placing them in 100 per cent sea water at 15°C. The curve represents the decrease of volume with time (open circles). The graph of $\log \frac{a}{a-x}$ against time (solid circles) is a straight line, the slope of which gives the value of k ($= 0.085$). This graph shows that the process follows the equation $kt = ln \frac{a}{a-x}$. (Each point represents the mean of 10 cells.)

Relative Rates of Exosmosis and Endosmosis.

The second point was to determine whether the *rates* of exosmosis and of endosmosis are the same. For this purpose eggs were placed in 60 per cent sea water, and velocity constants of swelling determined at several temperatures, as previously described (1). Eggs from the same animal were then returned from 60 per cent sea water to 100 per cent and the constants for the reverse process obtained. The results of

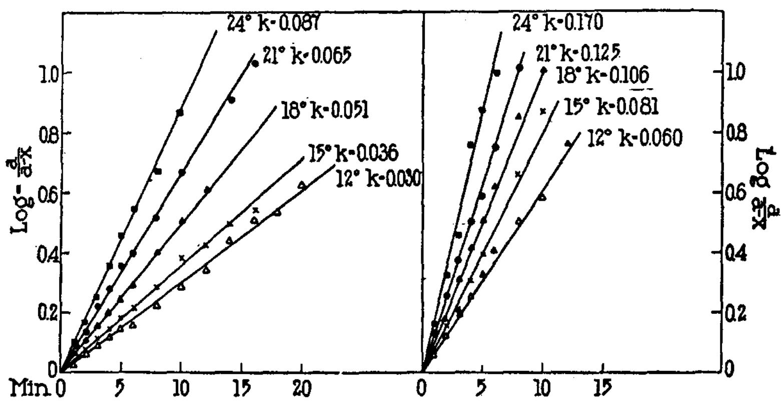

FIG. 2. The relative rates of exosmosis and endosmosis, at several temperatures. Log $\frac{a}{a-x}$ is plotted against time. The resulting graph is for each temperature a straight line, the slope of which gives the value of k, the velocity constant.

The graphs on the left represent *endosmosis* (swelling in 60 per cent sea water); the graphs on the right, *exosmosis* (shrinking after return to 100 per cent sea water). Under these conditions the values of k are, at each temperature, approximately twice as great in the latter process (contrast with Fig. 3). (Each point represents the mean of six cells.)

a typical experiment are shown in Fig. 2, in which log $\frac{a}{a-x}$ is plotted against times, for both endosmosis and exosmosis. It is seen that at a given temperature, the velocity constant of exosmosis is greater than that of endosmosis.

This experiment was repeated a number of times. While the values of k varied with different lots of eggs, essentially similar results were practically always obtained: the eggs shrank faster than they had swollen.

Subsequent experiments, however, showed that this difference in rate between exosmosis and endosmosis was not an essential one, that it existed only under special conditions. In the experiments just reported 60 per cent sea water was used to produce swelling of cells, but another concentration—100 per cent—to produce shrinking. Might this fact, rather than essential dissimilarities between endosmosis and exosmosis, be responsible for the differences in velocity con-

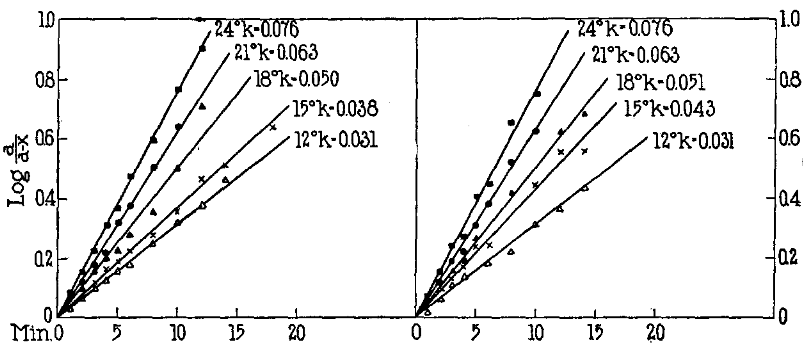

FIG. 3. The relative rates of exosmosis and endosmosis, at several temperatures, in media of the *same* osmotic pressure. The graph on the left represents *endosmosis* (swelling in 60 per cent sea water); the graph on the right *exosmosis* (shrinking in 60 per cent sea water after previous swelling in 50 per cent sea water). The medium is therefore of the same concentration in both processes; under these conditions the values of k are almost identical in exosmosis and endosmosis at each temperature (contrast with Fig. 2). (Each point represents the mean of six cells.)

stants? If swelling and shrinking could be produced in solutions of the *same* concentration, it seemed possible that equal values of k would be obtained.

Accordingly, eggs were placed in 60 per cent sea water at various temperatures and the several velocity constants determined for swelling. Other eggs were placed in a *more* hypotonic solution—50 per cent sea water. After having attained constant volume they were transferred to a 60 per cent solution and allowed to shrink, values of k being obtained as before. The results of this experiment are shown in Fig. 3. It is seen that the slope of the lines is the same for shrinking as for swelling, indicating that the velocity constants for the two processes, at each temperature, are the same.

Similar results were obtained where cells were allowed to swell in 70 or 80 per cent sea water, and other cells were allowed to shrink in solutions of the same concentration. In every experiment, practically identical values of k were obtained for swelling and shrinking at a given temperature, providing that the concentration of the medium was the same.

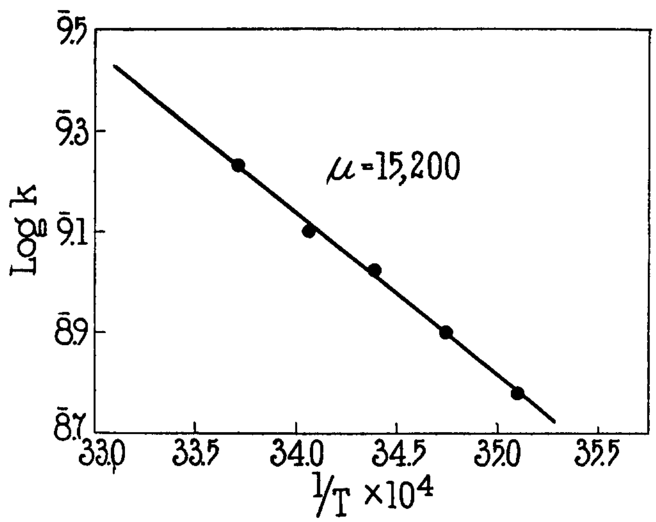

FIG. 4. The effect of temperature on exosmosis. The logarithms of the velocity constants of the experiment shown in Fig. 2 (graphs on the right) are plotted against the reciprocals of the absolute temperature. The slope of the line gives the value of μ (= 15,200).

Effect of Temperature on Exosmosis.

It follows from this as a corollary that exosmosis is affected by temperature just as is endosmosis (1), that is, there is a marked increase in rate with rise in temperature. Fig. 4 shows that the Arrhenius equation holds, the value of the temperature characteristic in this case being 15,200 (data were taken from Fig. 3). The value of μ varied in different experiments much as in endosmosis, but was always high.

These experiments therefore appear to indicate that the kinetics of exosmosis and endosmosis of water in this material are identical. The only difference in the processes is that the direction of the driving force of osmotic pressure is reversed. Both processes are affected in the same way by the external factors of temperature and concentration of sea water.

SUMMARY.

1. The rate of exosmosis of water was studied in unfertilized *Arbacia* eggs, in order to bring out possible differences between the kinetics of exosmosis and endosmosis.

2. Exosmosis, like endosmosis, is found to follow the equation $\frac{dx}{dt} = k\,(a - x)$, in which a is the total volume of water that will leave the cell before osmotic equilibrium is attained, x is the volume that has already left the cell at time t, and k is the velocity constant.

3. The velocity constants of the two processes are equal, provided the salt concentration of the medium is the same.

4. The temperature characteristic of exosmosis, as of endomosis, is high.

5. It is concluded that the kinetics of exosmosis and endosmosis of water in these cells are identical, the only difference in the processes being in the direction of the driving force of osmotic pressure.

BIBLIOGRAPHY.

1. McCutcheon, M., and Lucke, B., *J. Gen. Physiol.*, 1925–26, ix, 697.
2. Lucke, B., and McCutcheon, M., *Arch. Path. and Lab. Med.*, 1926, ii, 846.