

A COMPARISON OF PERMEABILITY IN PLANT AND ANIMAL CELLS.

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In a study of the fundamental characteristics of protoplasm it is desirable to compare the behavior of plants and animals under conditions which are as similar as possible. The experiments here described were undertaken from this point of view. Their object was to discover whether the behavior of animals and plants is essentially similar with regard to certain aspects of permeability, injury, recovery, and death.

The method consisted in measuring the electrical conductivity of the tissues. Under the conditions of the experiment the electrical conductivity of the tissue may be regarded as a measure of its permeability to ions.

The plant chiefly employed was *Laminaria*, although other material was used for comparison.¹ The tissue was cut into disks and packed together to form a cylinder whose electrical resistance was measured as previously described.²

The animal tissue used for comparison was the skin of the frog (*Rana pipiens*), taken from the animal immediately after killing³ and placed at once in the apparatus for measuring electrical resistance. Inasmuch as the skin has not sufficient mechanical rigidity to permit the same kind of manipulation which is possible in *Laminaria*, it was necessary to fasten each piece between two thin hard rubber disks (or between a rubber disk and one of thin celluloid), the disks being tied together by means of projections at the edges and the space between

¹ Osterhout, W. J. V., *J. Gen. Physiol.*, 1918-19, i, 299.

² Osterhout, W. J. V., *J. Biol. Chem.*, 1918, xxxvi, 557.

³ The animals were killed by decapitation. The use of anesthetics must be avoided as they may injure the skin.

them being partially filled with vaseline.⁴ The disks thus prepared were used in the same way as the disks of *Laminaria*. The conditions were therefore strictly comparable. In order to make this doubly sure, pieces of *Laminaria* of the same size as the pieces of frog skin were fastened between disks of hard rubber in the same manner and used for comparison. The resistance of a pair of disks containing frog skin was in the neighborhood of three times that of a pair of disks containing *Laminaria*. Usually five pairs of disks with frog skin were placed together to form a cylinder whose resistance was measured:⁵

The measurement of the resistance of the frog skin was less accurate than that of *Laminaria*. The point of minimum sound in the telephone was more indefinite (especially with live tissue). The resistance of the control was not constant as in the case of *Laminaria*. The controls of frog skin were placed in sea water + four volumes of distilled water, which was taken as approximately isotonic (for convenience this will be called 0.2 sea water). In this solution the resistance sometimes remained constant for some time, but more often it rose somewhat and finally became constant for a time or else began slowly to fall.⁶ Increasing or diminishing the proportion of distilled water did not help. Soaking the frog in the solution for an hour before removing the skin made no decided difference. In spite of these difficulties it was possible to select from several lots of material some whose resistance did not change much in 0.2 sea water, and thus to obtain consistent results. It was found desirable to express all the net resistances as per cent of the controls.⁷

⁴ Cf. Osterhout, W. J. V., *J. Biol. Chem.*, 1918, xxxvi, 557. The method shown in Fig. 7 was usually employed. The apparatus described as type B was also used and gave similar results.

⁵ Five pairs of disks containing *Laminaria* had about the same resistance as a cylinder of *Laminaria* tissue consisting of 80 pieces with only one rubber disk at each end.

⁶ Regarding changes in the conductivity of frog skin, under various conditions, see Höber, R., *Physikalische Chemie der Zelle und der Gewebe*, Leipzig, 4th edition, 1915, 441.

⁷ For example, a piece of frog skin was placed in NaCl and after a given time the resistance was measured; this was divided by the resistance of a control in 0.2 sea water measured at the same time (both lots having been placed in the solution at the same moment). In 0.2 sea water the skin remained alive for several hours.

One of the most striking results observed in studying the electrical resistance of *Laminaria* is the fact that some substances (as CaCl_2) decrease permeability while others (as NaCl) increase it. It is of interest to see whether animal tissue behaves in the same manner.

When *Laminaria* is placed in a solution of CaCl_2 (of the same conductivity as the sea water) the resistance⁸ rapidly rises, often as much as 65 per cent; in LaNO_3 it rises even higher (90 per cent or more),⁹ while in MgCl_2 the rise is less (up to 10 per cent). The rise is succeeded by a fall, which continues until death. The resistance has then dropped to about 10 per cent of the normal resistance.¹⁰

When frog skin is placed in CaCl_2 of the same conductivity as 0.2 sea water (about 0.056 M CaCl_2), the resistance rises rapidly, just as in the case of *Laminaria*, though not as high (up to 40 per cent). It then begins to fall, and continues to do so until the death point is reached¹¹ at about 10 per cent of the normal resistance. In LaNO_3 the rise is greater (up to 90 per cent), and in MgCl_2 it is less (up to 10 per cent). It will be seen that the behavior of frog skin toward these agents closely resembles that of *Laminaria*.

Acid (HCl) causes a rapid rise of resistance in *Laminaria*,¹² followed by a rapid fall. This is also the case with frog skin placed in a solution of HCl of the same conductivity as 0.2 sea water (about 0.024 M HCl) or in this solution diluted with 0.2 sea water. The use of HCl is attended by some complications which will be discussed in a later paper.

There is another group of substances, such as NaCl and KCl , which produce no rise in the resistance of *Laminaria*. On transferring tissue from sea water to solutions of these substances (of the same conductivity as sea water) there is a fall of resistance which continues until the death point is reached. The same is true of frog skin (using 0.2 sea water) except that the fall of resistance is much slower than in the case of *Laminaria*. It is, however, completely paralleled by the slow fall of resistance found in some other plant tissues, such as those of the dulse (*Rhodymenia palmata*).¹

⁸ Osterhout, W. J. V., *Bot. Gaz.*, 1915, lix, 317.

⁹ Osterhout, W. J. V., *Bot. Gaz.*, 1915, lix, 464.

¹⁰ The resistance of the apparatus is subtracted in all cases.

¹¹ The death point is not so well defined as with *Laminaria*.

¹² Cf. Osterhout, W. J. V., *J. Biol. Chem.*, 1914, xix, 493.

In mixtures of NaCl and CaCl₂ in suitable proportions¹³ *Laminaria* remains alive longer than in pure NaCl or in pure CaCl₂. This is also true of frog skin, although the result is not as marked as in the case of *Laminaria*; this is perhaps due to the fact that NaCl is less toxic to frog skin.

Of special interest is the behavior of anesthetics. In the case of *Laminaria* they produce two effects, a reversible (anesthetic) action consisting in a decrease of permeability and an irreversible (toxic) action consisting in an increase of permeability.¹⁴ On placing tissue in sea water containing suitable amounts of ether (1 per cent), chloroform (0.1 per cent), or chloral hydrate (0.1 per cent), the resistance rises and this condition is maintained for some time. With increasing concentration a point is soon reached at which the resistance rises rapidly to a maximum and then falls rather rapidly. When it has fallen below the normal there is little or no recovery on replacing it in sea water. With alcohol such recovery is possible.

The same is true of frog skin (using 0.2 sea water) but the effect is even more striking, the rise of resistance being greater and occurring at lower concentrations. In respect to recovery we find the same difference between ether, chloroform, and chloral hydrate on the one hand and alcohol on the other.

The method of measuring electrical resistance enables us to study the dynamics of the death process. It has been shown that when *Laminaria* dies in a solution of NaCl the process follows more or less closely the curve of a monomolecular reaction.¹⁵ The same is true of frog skin. In both cases we are led to the assumption that the process of death is one which is always going on during the normal life of the cell and that it is accelerated by the toxic agent. It is also found, in both *Laminaria* and frog skin, that if the death process has not proceeded too far a complete or partial recovery is possible when the tissues are removed from the toxic solution and returned to sea water (or 0.2 sea water).

In both cases it appears that permeability is a delicate and accurate index of the vitality¹⁶ of the protoplasm and that agents which pro-

¹³ Osterhout, W. J. V., *Proc. Am. Phil. Soc.*, 1916, lv, 533.

¹⁴ Osterhout, W. J. V., *Bot. Gaz.*, 1916, lxi, 148.

¹⁵ Osterhout, W. J. V., *J. Biol. Chem.*, 1917, xxxi, 585.

¹⁶ Osterhout, W. J. V., *Science*, 1914, xl, 488.

duce injury increase permeability. The amount of increase may be regarded as a measure of the amount of injury. A quantitative basis is thereby furnished for such conceptions as death, injury, recovery, and vitality.

The striking agreement between the behavior of frog skin and that of *Laminaria*, as well as of other plants previously studied,¹ strongly confirms the idea that the ideas which have been developed from the study of *Laminaria* are of general application. These ideas have been tested by the use of diverse methods.¹⁷

The general outcome of these studies reveals a marked amount of agreement, and it would seem that the physiological characteristics which they bring to light belong to the fundamental properties of protoplasm.

SUMMARY.

Quantitative studies show a striking agreement between frog skin and plant tissues in respect to certain important aspects of permeability, antagonism, injury, recovery, and death.

¹⁷ Osterhout, W. J. V., *Science*, 1917, xlv, 97; *J. Biol. Chem.*, 1918, xxxvi, 485.