A COMPARATIVE STUDY OF PERMEABILITY IN PLANTS.

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The writer has arrived at certain general conclusions concerning the behavior of protoplasm, which are based largely on the study of a single plant. To ascertain whether they have general validity it is necessary to study other plants as well as animals. The following paper gives a brief résumé of results obtained with a red alga (*Rhodymenia palmata*), a green alga (*Ulva rigida*), and a flowering plant (*Zostera marina*). These forms were chosen because they differ greatly from the brown alga *Laminaria Agardhii* (which furnished the material for the experiments hitherto described), not only in the chemical composition of the cell wall[1] but also in the structure of their tissues.

The experiments on *Laminaria* were made by cutting disks from the fronds and packing them in a cylinder, the electrical resistance of which was determined as previously described.[2]

The experiments with *Rhodymenia palmata* (the common dulse of the Atlantic coast) were carried out in precisely the same manner as those on *Laminaria*. This was possible because *Rhodymenia* forms thin sheets of tissue, large enough to be cut by a cork borer into disks 13 mm. in diameter. The disks were packed together, like a roll of coins, to form a cylinder, the electrical conductivity of which was measured as previously described.[2] *Rhodymenia* is much more difficult to keep in good condition than *Laminaria*, and on this account is not so well suited to investigations of this kind. It demands a low temperature and thorough aeration, and even with these does not live so long as *Laminaria*.

[1] Regarding the composition of the cell wall in algæ see Czapek, F., Biochemie der Pflanzen, Jena, 2nd edition, 1913, i, 640 ff.

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

In *Ulva* the structure of the frond is much simpler than in the other plants studied. It consists of two layers of similar cells, forming a membrane about 0.078 mm. in thickness. The cell walls are thin and consist of cellulose.[3] As it is not sufficiently stiff to be treated like *Laminaria*, pieces were cut out and supported between disks of hard rubber and celluloid as described in a previous paper.[4]

The leaves of *Zostera* have a very simple structure. The fibrovascular bundles are poorly developed. There are intercellular spaces, but it is possible to find leaves in which there is very little gas in these spaces. In such material the amount and position of the gas seems to remain unchanged during the experiment. The cell walls are of cellulose.

As the leaves are not wide enough to furnish disks such as were used in other experiments, a different procedure was adopted. A number of pieces were held in a horizontal position (parallel and a little separated) by means of two parallel celluloid combs placed at right angles to the length of the leaves. The electrode carriers moved between the combs, forcing the leaves together when measurements were made. The electrode carriers were held in frames as in the case of *Laminaria*, but the two upper glass rods were removed and a special form of hard rubber plate was placed at each end.

In some of the experiments pieces of the leaf were placed between disks of hard rubber and celluloid, just as in the case of *Ulva*.

In all cases the resistance was first determined in sea water, which was then replaced by another solution of the same conductivity. All readings were made at the same temperature or, if necessary, corrected to the proper temperature.

Experiments on *Laminaria* have shown that it is possible to follow the progress of death in the same manner as the progress of chemical reactions *in vitro*. For the most part the process follows more or less closely a monomolecular course. For *Laminaria* placed in NaCl 0.52 M, the velocity constant of the reaction at 15°C. was found (as the average of eight experiments) to be 0.00723. For *Rhodymenia* the same number of experiments (at the same temperature) gave K = 0.0009. Hence the rate appears to be about eight times as great

[3] The wall contains a methyl pentosan yielding rhamnose. Cf. Czapek,[1] 641.

[4] Osterhout, *J. Biol. Chem.*, 1918, xxxvi, 563, fig. 3.

in the case of *Laminaria*. In *Ulva* the rate is slower than in *Rhodymenia*, but *Zostera* is in this respect intermediate between *Laminaria* and *Rhodymenia*.

Up to a certain point the death process in *Laminaria* is reversible. Thus tissue remaining in NaCl 0.52 M until it has lost 10 per cent of its resistance will recover if replaced in sea water. This is also true of *Ulva*, *Rhodymenia*, and *Zostera*.

According to their effect upon *Laminaria* substances may be divided into two classes: (1) those which (like NaCl) cause only a fall in resistance, and (2) those which (like $CaCl_2$) cause a rise of resistance followed by a fall. There are great differences among these substances in respect to the effects which they produce, but as far as the experiments have gone these differences are similar in all the plants studied. Thus it is found that the amount of rise in resistance and its duration are much less in the case of Mg than of Ca and this applies to all the plants mentioned.

Rhodymenia agrees with *Laminaria* in showing a rise in resistance[5] in $CaCl_2$, $BaCl_2$, $SrCl_2$, $MnCl_2$, $NiCl_2$, and a greater rise in alum, $Ce(NO_3)_3$, and $La(NO_3)_3$.

Ether produced a rise in *Laminaria* and *Ulva* (*Zostera* was not studied). In *Rhodymenia* ether (2.5, 3, 5, and 5.5 per cent by volume), chloroform (0.02, 0.03, and 0.05 per cent by volume), and alcohol (1, 3.5, 7, 8 per cent by volume) added to the sea water produced little or no rise. This is not surprising in view of the fact that these substances always produce less rise in *Laminaria* than does Ca and that even Ca produces very little rise in *Rhodymenia* (Fig. 1). In respect to recovery from the injury caused by these substances *Rhodymenia* agrees with *Laminaria* in that recovery is practically complete in alcohol (if the fall in resistance has not gone too far), but is almost entirely absent in ether and chloroform.[6]

In general it was found that substances of one class antagonize those of the other, not only in the experiments on *Laminaria*,[7] but also in the cases of the other plants mentioned. As was to be expected, the most favorable proportions were not always the same for

[5] Osterhout, *Bot. Gaz.*, 1915, lix, 317, 464.

[6] Osterhout, *Bot. Gaz.*, 1916, lxi, 148.

[7] Osterhout, *Science*, 1915, xli, 255.

the different plants. Thus it was found that in the case of *Rhodymenia* it required more Ca to antagonize Na than it did in the case of *Laminaria*. It was also observed that in the case of *Rhodymenia* (Fig. 2) the antagonism was not so great as in *Laminaria* and this appears to be correlated with the fact that less decrease of permeability is produced by Ca in *Rhodymenia* (Fig. 1). In other words, the effect of such a substance as Ca upon permeability not only indicates

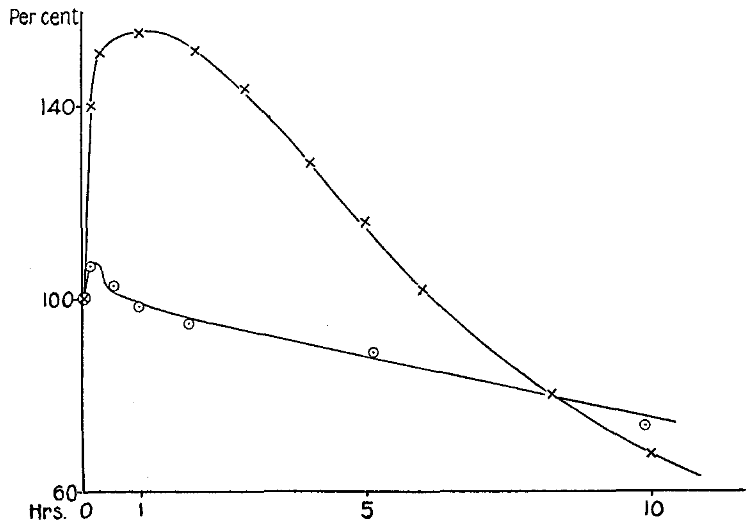

FIG. 1. Curves showing the effect of $CaCl_2$ 0.278 M on the electrical resistance of *Laminaria* (upper curve) and of *Rhodymenia* (lower curve). The ordinates denote net electrical resistance expressed as per cent of the normal resistance in sea water (which is taken as 100 per cent). Temperature 17° ± 2°C. Average of six experiments. Probable error less than 3 per cent of the mean.

what substances it will antagonize, but also, to some degree at least, the amount of antagonism.

It may be added that *Rhodymenia* affords an interesting confirmation of the value of the electrical method in measuring antagonism since the plants begin to change color soon after injury occurs. It was found that the relative rates of death as indicated by color changes in NaCl, $CaCl_2$, and the various mixtures corresponded with the results obtained by determining conductivity.

One of the most interesting experiments on *Laminaria* consists in placing it first in NaCl (causing a fall in resistance) and then in $CaCl_2$, causing a rise. In this way rapid changes of permeability may be produced and the alternation may be continued for a considerable

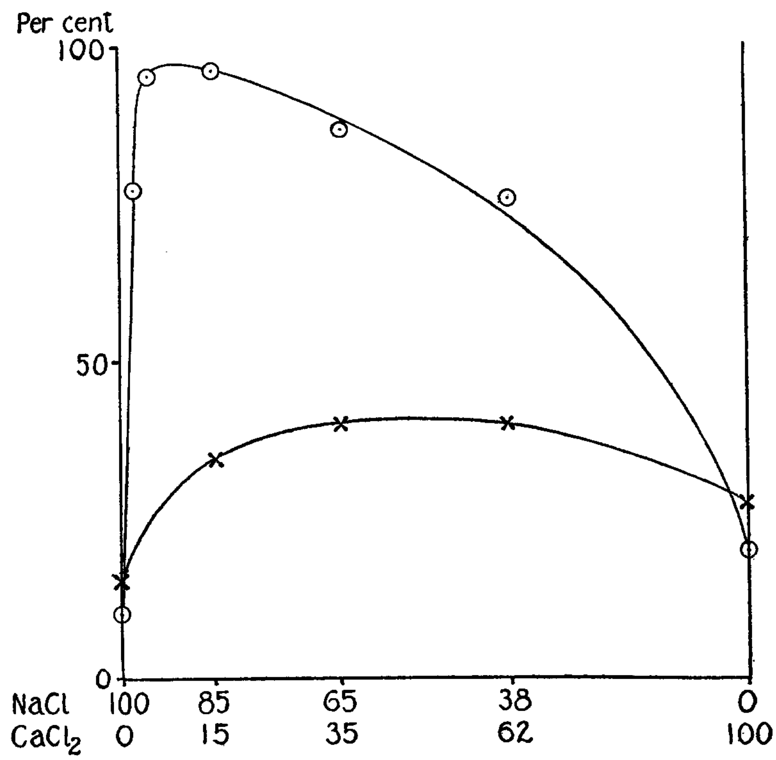

FIG. 2. Curves showing antagonism (after an exposure of 24 hours) between NaCl 0.52 M and $CaCl_2$ 0.278 M in *Laminaria* (upper curve) and *Rhodymenia* (lower curve). The ordinates denote net electrical resistance expressed as per cent of the normal resistance in sea water (which is taken as 100 per cent). The abscissæ denote molecular proportions of the solutions (all the solutions having the conductivity of sea water). Thus NaCl 85, $CaCl_2$ 15 signifies a mixture of 75 cc. NaCl 0.52 M + 25 cc. $CaCl_2$ 0.278 M in which the molecular proportions of Na to Ca are as 85 to 15. Temperature 17.5° ± 5°C. During the 24 hours the resistance of *Laminaria* in sea water remained practically unaltered while that of *Rhodymenia* fell to 84.5 per cent. Average of six experiments. Probable error less than 5.2 per cent of the mean.

period without any bad after effects.[8] This is also the case with the other plants studied.

It appears that in all the plants investigated there is a striking agreement in essentials, though there is considerable diversity in details. It is therefore evident that the conclusions drawn from the study of *Laminaria* are of general validity for all the plants investigated. It is hoped that similar studies on animals may be presented in the near future.

SUMMARY.

Quantitative studies on *Laminaria* (a brown alga), *Ulva* (a green alga), *Rhodymenia* (a red alga), and *Zostera* (a flowering plant) show that the behavior of these plants, in respect to changes in permeability, is essentially alike in all cases.

[8] Osterhout, *Bot. Gaz.*, 1915, lix, 242.