CONDUCTIVITY AND PERMEABILITY.

By W. J. V. OSTERHOUT.

(From the Laboratory of Plant Physiology, Harvard University, Cambridge.)

(Received for publication, July 19, 1921.)

When an electrical current passes from a salt solution into a living cell, ions must enter the protoplasm. An increase in the permeability of the protoplasm to ions must decrease its electrical resistance, and *vice versa*. The electrical resistance of the protoplasm may therefore be regarded as a measure of its permeability to ions.

If we attempt to measure the electrical resistance of the protoplasm we must first consider the structure of the tissue. For example, we find in the case of *Laminaria* that the protoplasm of each cell forms a thin layer which surrounds a large central vacuole filled with cell sap. Since experiments have shown that the cell sap has about the same electrical resistance as the solution which bathes the cell, it is evident that when the electrical resistance of the cell increases, on transferring it from sea water to another solution of the same conductivity, the change must be due to an increase in the resistance of the thin layer of protoplasm which bounds the cell. This has led the writer to assume that the resistance is proportional to a substance, M, at the surface of the cell; if M forms a layer at the surface it is obvious that an increase in the thickness of this layer will increase the resistance, and *vice versa*. It is therefore assumed that the resistance depends upon the amount of M which is present in the surface.\(^1\)

In *Laminaria* the protoplasmic masses (cells) are separated from each other by a thin layer of gelatinous substance (cell wall). In passing through the tissue a part of the current goes through the protoplasm and another part passes between the protoplasmic masses,

\(^1\) This assumption is simple and facilitates quantitative treatment. It is recognized that changes in resistance might depend upon other properties of this layer, and that the layer need not necessarily be continuous.
in the substance of the cell wall. Consequently when we employ the electrical method we must ascertain whether we are investigating the permeability of the protoplasm or merely that of the cell wall.

Obviously the best method of attacking this problem is to kill the tissue by such means (e.g., partial drying, heating to 35°C., weak alcohol, etc.) as can not alter the cell wall, and then investigate its behavior under the influence of various reagents. We find that all of these methods produce the same result. After death the tissue no longer shows the changes in resistance which are observed when living tissue is subjected to the influence of reagents. It is therefore evident that the changes are due to the living protoplasm.

The cell wall appears in all cases to have practically the same conductivity as the surrounding solution. If we subject living tissue to solutions of the same conductivity, but of different chemical composition, the resistance of the cell wall remains unaltered while that of the protoplasm undergoes great variations. If, for example, living tissue is placed in a solution of NaCl or CaCl₂ (of the same conductivity as sea water) its behavior differs. In NaCl the resistance falls; in CaCl₂ it rapidly rises and later falls to a minimum. We infer that the permeability of the protoplasm increases in NaCl; and that in CaCl₂ there is a decrease followed by an increase.

This is in complete agreement with results obtained when permeability is measured by such methods as plasmolysis, specific gravity, tissue tension, exosmosis, and diffusion through living tissue. This agreement indicates that the electrical method measures the permeability of the protoplasm. It is however desirable to go further, if possible, and analyze the factors involved in electrical resistance.

As explained in a former paper (Osterhout, W. J. V., J. Biol. Chem., 1918, xxxvi, 485) the fact that a part of the current passes through the protoplasm is shown by the fact that CaCl₂ raises the resistance of living tissue and by the fact that the temperature coefficient of electrical conductivity differs in living and dead tissue.


If we consider the behavior of the current from this point of view, it is evident that in the simplest cases, where the plant is a membrane only one cell thick (as in Porphyra and Monostroma) and the current passes through this membrane at right angles to its surface, we need consider only a single cell and its adjacent cell wall, as shown in Fig. 1, A. The part of the current which goes through the protoplasm may be designated as $C_p$, while that which traverses the cell may be called $C_w$.

Experiments show that the resistance of the living tissue is much greater than that of tissue which has been carefully killed with all possible precautions to prevent any alteration of the cell wall. We therefore feel confident that the conductivity of the living protoplasm is less than that of the cell wall.

If we neglect these we may say that in traversing a cell the current passes through a thin layer of cell wall and then one of protoplasm (in both cases at right angles to the plane of the layer), then through the cell sap, and finally through a layer of cell wall and one of protoplasm (at right angles to their planes). It is evident that in this case we may neglect the effect of the cell wall and of the cell sap since their resistance is very small in comparison with
the points X and Y in the wire P may be called $C_P$; that in the other wire $C_W$. The total current, $C$, flowing between X and Y will be the sum of the partial currents, or,

$$C = C_P + C_W$$

We may consider the current (conductance) as equal to the reciprocal of the resistance and write

$$\frac{1}{R} = \frac{1}{R_P} + \frac{1}{R_W}$$

in which $R$ is the total resistance between X and Y, $R_P$ is the resistance of the wire P, and $R_W$, that of W. Applying this equation to Laminaria* (and expressing the resistance in the usual way as the per cent of the normal) we may calculate the values of $C_W$, $C_P$, $R_W$, and $R_P$.

Under normal conditions in sea water, the resistance is taken as 100 and therefore $C = 1 + 100$ but in certain solutions (having the same conductivity as sea water) the resistance may rise to 300 or more; and in this case $C$ would equal $1 + 300 = .0033$ (or less), and since some of it must flow in the protoplasm the amount which traverses the cell wall must be less than this. We are therefore safe in putting it as low as $1 + 350 = .002857$.

All the experiments hitherto made indicate that the conductivity of cell the wall remains unaltered in spite of changes in the chemical that of the protoplasm and is in series with it. We may therefore consider the protoplasm to be replaced by a single wire having a resistance equal to that of the two layers of protoplasm which are traversed by the current in a direction at right angles to their planes.

*So far we have considered only the simplest case, when the plant is only one cell thick. But it is evident that these considerations also apply when several membranes are placed together, forming a mass comparable to the tissue of Laminaria. The only difference is in that case the current would traverse a very thin layer of cell wall in passing from one protoplasmic mass to the next, so that what we have spoken of as the resistance of the protoplasm would be composed in part of the resistance of these cell walls. When the protoplasm is dead the total resistance is only 10.29 and the resistance of these cell walls must be only a small fraction of this. Consequently their resistance in the living tissue of Laminaria is undoubtedly less than 1 when that of the protoplasm is 140. The resistance of these cell walls may therefore be neglected.
character of the solution, provided the conductivity of the solution remains the same. We may therefore take .002857 as the fixed value of $C_w$.

Let us now consider what values $C_p$ assumes as the resistance changes. In sea water we have $R = 100$ and

$$C = \frac{1}{100} = .002857 + C_p$$

whence $C_p = .007143$ and $R_p = 1 - C_p = 140$. In the same manner we find that when $R = 90$, $R_p = 121.15$, and when $R = 10$, $R_p = 10.29$.

The changes in resistance thus far discussed have been treated as though they occurred in sea water; in this case the experiments indicate that the conductivity of the cell sap remains practically constant and hence need not be taken into account in our calculations. We may now ask whether this is also the case when the changes in resistance occur in other solutions. In order to investigate this, experiments were made with solutions of NaCl and CaCl$_2$ (of the same conductivity as sea water). The tissue was placed in these solutions and removed after various intervals of exposure. It was cut into small bits and ground (so as to open the cells) and the conductivity of the expressed juice was compared with that of sea water. As no significant difference was found we may consider that the conductivity of the cell sap does not change sufficiently in these solutions to alter our calculations.

Let us now consider the changes in protoplasmic resistance which occur in toxic solutions. When tissue is placed in NaCl 0.52 M the net resistance falls rapidly. The death curve may be obtained by means of the formula

$$\text{Resistance} = 2700 \left( \frac{K_A}{K_M - K_A} \right) \left( e^{-K_A T} - e^{-K_M T} \right) + 90 e^{-K_M T} + 10$$

9 The total conductance of the protoplasm is greater than that of the cell walls, but the protoplasm occupies a much greater fraction of the conducting cross-section than the cell walls, so that the actual conductivity of the protoplasm is much less than that of the cell wall.

in which $T$ is the time of exposure, $K_A$ and $K_M$ are constants, and $e$ is the basis of natural logarithms. We find by means of this formula that in a solution\$11 of NaCl 0.52 M (for which $K_A = 0.018$ and $K_M = 0.540$) the net resistance after 10 minutes is 87.76 per cent of the normal; after 30 minutes it is 64.26, and after 60 minutes it is 41.62. Knowing the net resistance we can calculate the protoplasmic resistance, as explained above. After 10 minutes the protoplasmic resistance is 117.12 per cent (corresponding to the net resistance of 87.76 per cent). Since it is desirable to express all resistances as per cent of the resistance in sea water we divide 117.12 by 140 (which is the protoplasmic resistance in sea water) and obtain 83.66 per cent. Proceeding in this way we find that after 30 minutes the protoplasmic resistance is 56.22 per cent and after 60 minutes 33.74 per cent. In order to fit the formula to these values we must change the constants, putting $K_{AP} = 0.0234$ (in place of $K_A = 0.018$) and $K_{MP} = 0.702$ (in place of $K_M = 0.54$). It is therefore evident that in changing from net resistance to protoplasmic resistance we merely shift the value of the constants. The question arises whether this affects the general conclusions drawn from the study of net resistance. In order to decide this question the constants for CaCl$_2$ and

---

**TABLE I.**

Velocity Constants at 15°C.

<table>
<thead>
<tr>
<th>CaCl$_2$ in solution</th>
<th>CaCl$_2$ in surface</th>
<th>$K_A$</th>
<th>$K_M$</th>
<th>$K_{AP}$</th>
<th>$K_{MP}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>per cent</td>
<td>per cent</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0</td>
<td>0.018</td>
<td>0.540</td>
<td>0.0234</td>
<td>0.702</td>
</tr>
<tr>
<td>1.41</td>
<td>12.5</td>
<td>0.000222</td>
<td>0.00666</td>
<td>0.000293</td>
<td>0.00878</td>
</tr>
<tr>
<td>2.44</td>
<td>20.0</td>
<td>0.000187</td>
<td>0.00546</td>
<td>0.000237</td>
<td>0.00708</td>
</tr>
<tr>
<td>4.76</td>
<td>33.33</td>
<td>0.000245</td>
<td>0.00590</td>
<td>0.00032</td>
<td>0.007136</td>
</tr>
<tr>
<td>15.0</td>
<td>63.73</td>
<td>0.000364</td>
<td>0.0073</td>
<td>0.0005035</td>
<td>0.00855</td>
</tr>
<tr>
<td>35.0</td>
<td>84.34</td>
<td>0.000481</td>
<td>0.00859</td>
<td>0.000678</td>
<td>0.00955</td>
</tr>
<tr>
<td>62.0</td>
<td>94.22</td>
<td>0.000533</td>
<td>0.009</td>
<td>0.000761</td>
<td>0.00989</td>
</tr>
<tr>
<td>100.0</td>
<td>100.0</td>
<td>0.0018</td>
<td>0.0295</td>
<td>0.002685</td>
<td>0.0323</td>
</tr>
</tbody>
</table>

for various mixtures of NaCl and CaCl₂ were ascertained; these are given in Table I.\textsuperscript{12}

There are two points of principal importance in the consideration of these constants: (1) It was shown in a former paper\textsuperscript{13} (which dealt with net resistance only) that the value of \( K_A + K_M \) increases regularly as the per cent of CaCl₂ in the surface of the cell increases. That this is also true in the case of protoplasmic resistance is evident from Fig. 2. (2) It was also pointed out that as the per cent of CaCl₂ in the solution decreases from 62 to 1.41 per cent the value of \( K_M \) first decreases (reaching a minimum at 4.76 per cent) and then increases. It was found that the amount of decrease corresponds to

\[
\begin{align*}
\text{x} &= \text{Increase in } K_A + K_M \\
\text{K_A} &= \text{Increase in } K_{AP} + K_{MP}
\end{align*}
\]

Fig. 2. Ordinates represent the increase in value of \( K_A + K_M \) and of \( K_{AP} + K_{MP} \). In each case the value given represents the increase over the corresponding value in the solution containing 1.41 per cent CaCl₂ (the corresponding per cent in the surface being 12.5). Abscissae represent per cent of CaCl₂ in the surface. In order to facilitate comparison the values of \( K_{AP} + K_{MP} \) have been divided by 1.685.

\textsuperscript{12} These are approximate values, obtained graphically. The constants of the curves of protoplasmic resistance are designated as \( K_{AP} \) (corresponding to \( K_A \)) and \( K_{MP} \) (corresponding to \( K_M \)). The curves of protoplasmic resistance may show less inhibition at the start than those of net resistance.

\textsuperscript{13} Osterhout, W. J. V., \textit{J. Gen. Physiol.}, 1920–21, iii, 415.
Fig. 3. Ordinates represent the amount of Na₄XC₄ and also the decrease in the value of $K_M(\Delta)$ and of $K_{MP}(\odot)$ as compared with the corresponding value in the solution containing 62 per cent CaCl₂. Abscissæ represent per cent of CaCl₂ in the solution. In order to facilitate comparison the values of $K_M$ have been multiplied by 0.251 and those of $K_{MP}$ by 0.321.
the amount of a hypothetical salt compound (Na₄XCa). This is also true in the case of protoplasmic resistance, as shown in Fig. 3.¹⁴

It would therefore appear that we arrive at the same conclusions whether we study net resistance or protoplasmic resistance. When the solution is changed the constants change in a corresponding manner in both cases, the only difference being in their absolute values, but it is evident that in this case differences in absolute values are of no importance.

It should be emphasized that this general conclusion would remain valid in case it should be found that the values given in this paper for $C_P$ and $C_W$ are incorrect. There seems to be no doubt that the value of $C_W$ is constant under the conditions of these experiments and as long as this is true the conclusions drawn from the study of net resistance apply also to protoplasmic resistance.

**SUMMARY.**

An electrical current passing through a living plant flows partly through the cell wall and partly through the protoplasm. The relative amounts of these two portions of the current can be calculated.

The outcome of such calculations shows that the conclusions drawn from the study of the resistance of the tissue as a whole apply also to the resistance of the protoplasm, and consequently to the permeability of the protoplasm to ions.

¹⁴ A rough calculation shows that this is also true of $K_{NP}$ and $K_{OP}$ (corresponding to the $K_N$ and $K_O$ mentioned in the former paper¹⁵).