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PERMEABILITY

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CHAPTER X

THE INFLUENCE OF EXTERNAL CONDITIONS ON THE INTAKE AND EXCRETION OF WATER BY PLANT CELLS AND TISSUES

THE discussion of the water relations of the plant cell in Chapter IX involved a consideration of the internal conditions which may influence the rate of passage of water through the cell wall and protoplasm. These conditions are the concentration and nature of the substance dissolved in the cell sap which between them determine the osmotic pressure of the cell. The permeability of the protoplasm to solutes will also influence the rate of intake of water, inasmuch as the passage of solutes into or out from the cell will tend respectively to raise or to lower the osmotic concentration of the cell sap and hence the rate of intake of water through the protoplasm and cell wall. Lepeschkin (1908*a*) appears to suggest that the osmotic pressure of a solution is a function of the permeability of the membrane, but the error of this view is obvious and has already been indicated by Brooks (1917*a*), Höfler (1920) and V. H. Blackman (1921). Apart from electrical effects, the osmotic pressure which can be developed with a permeable membrane must continually fall with time until equilibrium of the penetrating solute on the two sides of the membrane is attained.

External conditions which are known to influence the rate of passage of water into and out from the cell are temperature and the composition of the external medium. It has to be noted that changes in the rate of passage of water into and out from the cell are not necessarily to be attributed to changes in the permeability of the protoplasm. For, neglecting the possible effect of limiting plasma-membranes, the rate of intake or excretion of water is the resultant

of (1) effects attributable to purely osmotic relations of the cell, (2) effects due to the entrance or exosmosis of dissolved substances which alter the osmotic relations, (3) effects on the capacity for imbibitional swelling of cell wall, protoplasm and vacuole, and (4) effects resulting from any influence on the permeability of the cell wall and protoplasm. It may not always be possible to distinguish with certainty which of these various effects is or are mainly responsible for observed behaviour. It will therefore be most satisfactory first to describe the results obtained experimentally, and then to discuss how far these observed results are to be correlated with protoplasmic permeability or with other phenomena indicated above.

Temperature

A number of earlier observations have suggested that the rate of intake of water by, or its excretion from, plant cells and tissues, is considerably influenced by temperature. Among these may be mentioned those of Vesque (1877) on the absorption of water by forest trees, Wieler (1893) on the bleeding of cut stems of a number of plants, and Lepeschkin (1906) on the exudation of water by the sporangiophores of *Pilobolus*. As these results, suggestive as they are, do not provide us with exact data for our analysis, we may pass at once to a consideration of those researches in which exact measurements of the effect of temperature on water intake or excretion have been attempted.

DETERMINATIONS BY THE PLASMOLYTIC METHOD

Systematic attempts to determine the influence of temperature on the rate of passage of water through the cell membranes were made by Krabbe (1896) and van Rysselberghe (1901). The former measured the time required for complete contraction of cylinders of turgid pith when plasmolysed at different temperatures and concluded that the rate of excretion and absorption of water rises with increase of temperature.

Van Rysselberghe used cylinders of elder pith, epidermal cells of *Tradescantia* and *Begonia*, *Lemna*, *Spirogyra* and other plants. The cylinders of pith were plasmolysed at different temperatures in strong sucrose solutions (0.731 *M*) and the amount of shrinkage measured at different times over a period of 24 hours. The temperature effect was determined by comparing the amount of shrinkage after two hours at the different temperatures. But obviously this

could only give a correct indication of the temperature effect if the relative amounts of shrinkage at the different temperatures were the same at all times during the experiment, which was not the case. Had he chosen to compare the shrinkage after three or four hours instead of after two, he would have obtained a quite different set of values for the relation between temperature and rate of passage of water through the cell membranes. The only way to obtain correct information on the influence of temperature in these experiments is to compare the *rate* of passage of water out of the tissues at different temperatures, but under otherwise exactly the same conditions. This is to be accomplished, as pointed out by Miss Delf (1916), by constructing the time-shrinkage curves for the different temperatures and then comparing the rate of shrinkage *at the same stage of shrinkage*, as given by the value of $\tan \alpha$, where α is the angle made by the tangent to the curve with the time axis.

The data of van Rysselberghe have been subjected to this treatment by Miss Delf, when they indicate an increase in the rate of passage of water through the cell membranes with increasing temperature up to about 20° C., but between this and 30° C. the effect of temperature is negligible. Miss Delf found that such a result is obtainable only when a very strong plasmolysing solution is used, the reason being apparently that there is an "upper limit to the rate at which the mechanical tissue system of cells can collapse and shrink," so that with the strong solutions used by van Rysselberghe a great part of the contraction curves obtainable from his data represent a contraction of the cell wall system over which permeability has no control.

Other experiments of van Rysselberghe, in which only the times taken for cells to plasmolyse or deplasmolyse are given, are obviously open to still greater objection, both on the grounds already stated in the case of the experiments with pith, and also on account of the difficulty of carrying out such experiments with exactitude. Further, it is doubtful whether sufficient account has been taken of the great variability of plant tissue from different individuals of the same species, so that it is not certain whether van Rysselberghe's results could be accepted as expressing more than approximately the relation between temperature and rate of intake or excretion of water, even if they were not open to grave objection on other grounds. No further consideration will therefore be given to the results of Krabbe and van Rysselberghe in this place.

DETERMINATIONS OF THE EFFECT OF TEMPERATURE BY THE METHOD OF THE RATE OF LINEAR SHRINKAGE OF TURGID TISSUES

The first critical research on the influence of temperature on cell permeability to water is that of Miss Delf (1916). Her method was similar in principle to that used by van Rysselberghe, but was considerably more sensitive. By means of the optical lever, which had already been introduced into plant physiology by Bose (1906) to record small movements in plants, changes in length of short strips of tissue could be observed under a magnification of 350 diameters. The apparatus devised by F. F. Blackman and used by Miss Delf is directly applicable only to the investigation of hollow cylindrical structures, those used by Miss Delf being onion leaves and dandelion scapes.

The essentials of the method are as follows. The lower end of the plant cylinder is firmly fixed by means of cotton to a glass tube of narrow bore which passes through a cork held immovable by a metal clamp. The upper end of the cylinder is pierced by a fine glass hook attached to a loop of very fine waxed cotton which at its upper end is itself attached to the projecting wire arm of the optical lever, which carries a small mirror reflecting the image of an illuminated cross wire on to a millimetre scale. Contraction of the cylinder can thus be very accurately measured by the movement of the image of the cross wire on the scale. For details of the apparatus and procedure, including the method adopted for obtaining different constant temperatures, reference must be made to the original paper.

The material selected for investigation already noted above was chosen because the inner surface of the hollow cylinders of which it is composed is lined entirely with cells possessing thin cellulose walls. Solutions of cane sugar in various concentrations (0.18, 0.3, 0.5 and 0.731 weight-molecular solutions) were allowed to flow through the hollow cylinders of plant tissue and the contraction resulting followed by the optical lever arrangement. The total contraction produced by these solutions varies somewhat with the age of the material, but very greatly with the concentration of the solution. Thus dandelion scapes in 0.30 *M* sucrose contracted to the extent of 0.2 to 0.4 per cent. of the original length, while in 0.731 *M* sucrose the contraction was as much as 2 to 2.5 per cent. of the original length. Similarly, onion leaves in 0.18 *M* sucrose contracted 0.3 to 0.5 per cent. and in 0.731 *M* sucrose 3 per cent.

of the initial length. Although greater contractions were obtained in the stronger sucrose solutions, it was found almost impossible to decide how much of this was to be attributed to plasmolysis, and how much to the after-shrinkage of the cell walls. On this account weaker solutions, "subtonic," that is, diluter than isotonic, were used for the crucial experiments, the actual concentrations chosen being such that the contractions produced after the tissue had been allowed to swell to equilibrium in pure water were sufficiently large to be measured satisfactorily with the apparatus employed, while a definite end-point was reached in about two hours. The solutions which fulfilled these conditions were 0.18 *M* sucrose for onion leaves and 0.3 *M* for dandelion scapes.

With the subtonic solutions employed the shrinkage was found to follow an approximately logarithmic course. Miss Delf states that "with great care in the choice of material and in repeating the same experimental conditions, there was a certain amount of variation in the rate of plasmolysis at the same temperature. At medium temperatures, therefore, it was usual to perform several experiments under the same conditions, and to select the ones which gave the curve of approximately logarithmic form." This selection of certain curves appears a weakness in Miss Delf's work, for as the rejected experiments were conducted with the same care and under the same conditions as the selected experiments, the form of the time-shrinkage curves does not seem an adequate ground for selecting some and rejecting others.

At temperatures above that of the laboratory complications occur. These are (1) a contraction resulting from the effect of prolonged high temperature, probably on account of the escape of water from the cells as a result of increased exosmosis of solutes from the cell sap at high temperatures, and (2) an expansion resulting probably from the entry of sucrose into the cell. Up to 35° C. in the case of the dandelion scape, and up to 36° C. in the onion leaf, it was found to be unnecessary to apply any correction on account of these complications, but above this temperature the shrinkage due simply to the presence of the subtonic solution at the higher temperature was obtained by subtracting the shrinkage resulting in distilled water at the higher temperature from the total shrinkage actually observed.

From the shrinkage-time curves obtained by Miss Delf the rates of contraction at 30, 50 and 70 per cent. of the total contraction were calculated for the temperatures employed in the experiments, and the rates for temperatures between 5° and 40° C. found by inter-

polation. The relative values for the rate of linear shrinkage of the tissue at the stage of half-contraction are shown in Table XXVII, the values for 25° C. being taken as unity.

TABLE XXVII

Relative rates of linear contraction of onion leaves and dandelion scapes in subtonic solutions of sucrose at different temperatures.

(Data from Miss Delf)

Temperature in centigrade degrees	Relative rate of linear contraction	
	Onion leaves in 0.18 <i>M</i> sucrose	Dandelion scapes in 0.3 <i>M</i> sucrose
5	0.36	—
10	0.44	0.22
15	0.50	0.30
20	0.66	0.50
25	1.0	1.0
30	1.7	1.9
35	2.9	3.0
40	5.0	5.0

From these numbers the temperature coefficients (Q_{10} , see Chapter III, p. 101) for a rise of 10° C. were calculated, with the results given in Table XXVIII.

TABLE XXVIII

Temperature coefficients for rate of linear shrinkage of onion leaves and dandelion scapes in subtonic sucrose solutions.

(Data from Miss Delf)

Range of temperature in centigrade degrees	Temperature coefficient (Q_{10})	
	Onion leaves	Dandelion scapes
5-15	1.4	—
10-20	1.5	2.3
15-25	2.0	3.3
20-30	2.6	3.8
25-35	2.9	3.0
30-40	3.0	2.6

It is particularly interesting to consider how far these temperature effects are to be regarded as effects of temperature on permeability of the protoplasm, as they are assumed to be by Miss Delf.

If the permeability of the cell or tissue to water is defined as the quantity of water passing through unit area of the cell membranes (cell wall + protoplasm) in unit time under unit difference of pressure we have the equation

$$\frac{dw}{dt} = \zeta (P_e - P + T) A,$$

where $\frac{dw}{dt}$ is the rate of passage of water out of the cell or tissue, ζ is the permeability, P_e and P are the osmotic pressures of the external solution and the cell sap respectively, T the turgor pressure (cf. Chapter IX), and A is the area of the cell surface through which water passes.

Now the rate at which water is lost by the tissue is proportional to the rate of volume shrinkage, and if c.g.s. units are employed may be taken as equal to it. Let us suppose that in a small time interval δt the length l of the cylinder contracts by a small length δl , and that in the same time the contraction in width is δa , the original diameter of the cylinder being r and the thickness of the tissue a . Let us further suppose the water loss in the same time is δw . The change in volume in the time δt is then

$$\pi a l (2r - a) - \pi (a - \delta a) (l - \delta l) \{2(r - \delta a) - (a - \delta a)\}$$

$$\text{or } \pi [a (2r - a) \delta l + 2rl \delta a] - (l \delta a + 2r \delta l + \delta a \delta l) \delta a.$$

Hence, using c.g.s. units, we have in the limit the rate of water loss by the tissue given by

$$\frac{dw}{dt} = \pi a (2r - a) \frac{dl}{dt} + 2\pi r l \frac{da}{dt}.$$

$$\text{Whence } \zeta = \frac{\pi}{P_e - P + T} \left\{ a (2r - a) \frac{dl}{dt} + r l \frac{da}{dt} \right\} \frac{1}{A}.$$

Thus, if it is assumed (1) that differences in imbibitional swelling at different temperatures are negligible, (2) that the value of the exudation pressure $P_e - P + T$ at the same stage of shrinkage is practically constant for temperatures over the range 5° to 42° C., and (3) that the cylinders shrink only in a longitudinal direction, the above equation may be written

$$\zeta = K \frac{dl}{dt},$$

where K is a constant since A is the same for all cylinders in the same stage of shrinkage. If, on the other hand, there should be a shrinkage in a transverse direction proportional to the longitudinal shrinkage, the equation connecting permeability and shrinkage may be written

$$\zeta = K l^2 \cdot \frac{dl}{dt},$$

K again being a constant.

Now the first two assumptions are very reasonable, and it is probable that the actual shrinkage would approximate to one of the two cases considered under (3). In the first of these cases the

permeability is proportional to the rate of linear shrinkage, in the second to the rate of linear shrinkage multiplied by the square of the length. Hence if comparisons are only made, as in the case of Miss Delf's experiments, with cylinders in the same stage of shrinkage, l^2 will be the same in all cases compared with one another and the permeability will similarly be proportional to the rate of linear shrinkage.

The values obtained by Miss Delf may then legitimately be regarded as measures of the permeability of the cell membranes (cell wall + protoplasm) to water. Miss Delf speaks of them as measures of the permeability of the protoplasm, but as the effects of cell wall and protoplasm are not separated, they are better regarded as measures of the permeability of the cell. It will be noted that errors arising from exosmosis of dissolved substances and intake of salt are allowed for in the experimental procedure, and need not therefore be further considered.

DETERMINATIONS OF THE INFLUENCE OF TEMPERATURE ON THE RATE OF INTAKE OF WATER BY THE CHANGE IN WEIGHT METHOD

Storage Tissues. The influence of temperature on the intake of water by storage tissues, potato tuber and carrot root, has been investigated by Stiles and Jørgensen (1917 *b*). In the method employed by them, the course of absorption of water at different temperatures is followed by immersing the tissue of known weight in water and weighing the tissue at intervals. The change in weight may be fairly attributed to gain or loss of water only, as the weight of dissolved substance which diffuses out from the tissue during the period of the experiment is negligible in comparison with the weight of water involved.

In order to eliminate errors due to the variability of tissue in different samples, a variability which may be very large, and to ensure equality of surface and weight of tissue in all comparative experiments, the following procedure was adopted. Cylinders of tissue were cut from the tubers or roots by means of a cork-borer 1.8 cms. in diameter. These cylinders were then cut into disks of a uniform thickness of 0.2 cm. by means of a hand microtome. For any series of experiments performed for comparative results all the disks required were cut at once, well mixed together and weighed in sets of 20. In this way samples of the material, each sample consisting of 20 disks, were obtained having approximately

the same weight and surface. The experiments at any one temperature were all conducted in triplicate or quadruplicate, so that for a comparison of the rate of water intake at four different temperatures, 12 or 16 sets of 20 disks were required, 3 or 4 at each temperature. The probable error of the determinations was calculated so that some idea of the degree of reliability of the results might be obtained. The temperatures were maintained constant by means of thermostat baths provided with gas-mercury-toluene regulators.

Fig. 7. Curves illustrating the influence of temperature on the absorption of water by potato tuber. (After Stiles and Jørgensen.)

The course of water absorption at different temperatures by potato and carrot is shown in Figs. 7 and 8. From these absorption-time curves the rate of swelling of the tissue has been determined in the same way as the rate of shrinkage in Miss Delf's experiments, that is, by measuring the tangent of the angle made with the time axis by the tangent to the curve at any particular stage of swelling. By comparing the rate of intake of water at different temperatures at the same stage of swelling, the following temperature coefficients for the rate of intake of water are obtained.

Fig. 8. Curves illustrating the influence of temperature on the absorption of water by carrot root. (After Stiles and Jørgensen.)

TABLE XXIX

Temperature coefficients of the rate of intake of water by storage tissues. (Data from Stiles and Jørgensen)

Temperature range in centigrade degrees	Temperature coefficient (Q_{10})	
	Potato tuber	Carrot root
10-20	3.0	1.3
15-25	2.75	1.4
20-30	2.7	1.6

Two points deserve special notice in regard to the results of Stiles and Jørgensen. In the first place, the rate of swelling of carrot was found to be considerably greater than that of potato. Thus at 10° C. the rate of swelling of carrot was about nine times that of potato under apparently the same conditions with regard to degree of swelling, while at 30° C., in spite of the lower temperature coefficient in the case of carrot, the rate of swelling was still a little

more than twice as great in carrot as in potato. This is probably due in part to the higher suction pressure observed in the carrot tissue used (cf. Chapter IX), but as there is no evidence that the tissues were in the same absolute stage of swelling, too much stress must not be laid on the difference between the two tissues.

In the second place a phenomenon noted by Miss Delf in onion and dandelion appears also in carrot and potato tissue, namely, the contraction and loss in weight of the tissues at temperatures above 30° C., which probably corresponds to a rapid exosmosis of solutes from the cell. This breaking down of the semi-permeability of the protoplasm requires some time to become obvious, so that, as the curves for 40° C. show in both potato and carrot, there is first an initial period of rapid absorption of water followed by exudation. This phenomenon has also been observed in other storage tissues, such as red beetroot and artichoke tubers (*Helianthus tuberosus*).

Confining attention only to the curves where this complication is not present, and using the same notation as in the preceding section, we have the relation

$$\frac{dw}{dt} = \zeta (P - T) A,$$

where it is assumed as before that the effect of temperature on imbibitional swelling is negligible. If it is also assumed as before that $P - T$ is approximately constant over the range of temperature in question, the temperature coefficients given above may be accepted as those of the permeability of the cells of the tissues to water.

Seeds. The influence of temperature on the absorption of water by barley grains was investigated by A. J. Brown and Worley (1912) by means of the change in weight method. Known weights of grains were immersed in water kept at temperatures of 3.8° C., 21.1° C. and 34.6° C., and the increase in weight determined after various intervals of time. From the absorption-time curves so obtained the rate of water intake at different stages of absorption was measured for the three temperatures employed. The values obtained indicated that the rate of water absorption at 21.1° is about 3.40 times the rate of absorption at 3.8°, while the rate at 34.6° is about 2.44 times that at 21.1°. These numbers give a mean value for the temperature coefficient (Q_{10}) of about 2 (actually 1.99), a value characteristic of a number of chemical reactions. Somewhat lower values were obtained by Shull (1920) in a series of carefully conducted

experiments with seeds of *Xanthium pennsylvanicum* and small Scotch yellow split pea, the values for Q_{10} between 5° and 35° C. found for *Xanthium* being 1.55 in one case, and 1.83 in another, and for pea 1.6. Very similar, though on the whole lower values, were obtained by Denny (1917 *a*) for the temperature coefficient of the rate of passage of water through the detached seed coat of *Arachis hypogaea* (1.34 to 1.64).

Brown and Tinker (1916 *a*) regard the rate of entry of water into barley grains as given by the equation

$$\frac{dy}{dt} = k(a - y),$$

or, integrating,

$$\log \frac{a}{a - y} = kt,$$

where y is the quantity of water absorbed in a time t , and a and k are constants. Shull, however, holds that both his own experimental results and those of Brown and Worley are better expressed by the equation

$$y = a \log_{10} (bt + 1) + c,$$

where y is the quantity of water absorbed, t the time of immersion and a , b and c are constants. For the whole course of water intake the time-absorption curves can, in some cases at any rate, best be represented by three such equations representing the early, middle and late stage of water absorption. Apart from their value in enabling the temperature coefficients to be calculated with exactitude, these equations do not help us much in explaining the processes of water intake.

In the case of seeds, where the percentage of water is comparatively low and the percentage of colloidal substances susceptible to imbibitional swelling very high, it is clearly impossible to describe the temperature coefficient of water absorption as a temperature coefficient of the cell membranes. To determine the effect of temperature on the different processes involved in the water intake by seeds, further experimental work is necessary. Denny's work with seed coats separated from the seeds suggests a way in which this might be attempted. Sufficient data are, however, at present lacking.

ON THE VALUES OF THE TEMPERATURE COEFFICIENT OF THE
PERMEABILITY OF THE CELL TO WATER

Three points deserve special mention in regard to the temperature coefficient of the cell membranes to water.

1. The permeability to water increases continuously from the lowest to the highest temperatures investigated. This means that, other factors being equal, water absorption or excretion increases continuously with rise of temperature. Above 30° C. a "time factor" (F. F. Blackman, 1905) appears, inasmuch as with prolonged immersion in water at such higher temperatures the initial absorption is followed by excretion of water; this has been observed in onion leaves, dandelion scapes, tubers of potato and artichoke, and roots of carrot and red beet.

2. The temperature coefficients vary considerably for different tissues and over different temperature intervals in the case of the same tissue, the lowest observed being for carrot root and the highest for dandelion scapes.

3. The temperature coefficients are higher, and often considerably higher, than those found for a physical process such as diffusion of solutes in water, which are generally between 1.2 and 1.3, and approach instead more closely those characteristic of chemical processes. Yet there is no ground for supposing that we have to do here with a chemical rather than a physical process. The results rather suggest the necessity for caution in drawing conclusions with regard to the nature of a process from the value of the temperature coefficient.

Brown and Worley point out that an exponential increase in the value of a physical property is very rare, but that vapour pressure of water is an exception. The general equation

$$v = ae^{k\theta}$$

gives both the relation between vapour pressure and temperature and that between water absorption by barley grains and temperature. Shull, however, does not agree that the rate of intake of water by seeds is determined by vapour pressure. He is no doubt correct in supposing that in the case of seeds the rate of water intake is determined by a number of factors, among which chemical changes in the colloids of the seed coat may not be unimportant. Denny also, on account of the values of the temperature coefficient found by him, disagrees with Brown and Worley in regard to vapour pressure of water determining the rate of entrance of water into seeds.

Dissolved Substances

The investigation of the influence of dissolved substances on the intake and exosmosis of water by plant tissue (potato tuber and carrot root) has also been investigated by Stiles and Jørgensen (1917 *b*) using the change in weight method. Some further observations have been made by Thoday (1918 *a*) using the same method in a cruder form. As the results obtained show that the influence of all dissolved substances is not the same, it will be convenient to consider the different cases separately.

Fig. 9. Curves illustrating the absorption of water by potato tuber immersed in distilled water and sucrose of various concentrations (0.2 *M* to 0.4 *M*). (After Stiles and Jørgensen.)

I. SUCROSE

Experiments were conducted on potato tissue at 20° C. with the same technique as that already described. Sucrose solutions of various concentrations were employed, the absorption-time curves for the tissue in the different concentrations of sucrose being shown in Fig. 9. It will be observed that with increasing concentration of sucrose both the rate of water intake and the total amount of water absorbed are reduced, and that in a solution of about $M/4$ concentration the intake of water is approximately zero. With higher concentrations of the sugar exosmosis of water takes place, both the

rate of exosmosis and the quantity of water exuded increasing with increase of sugar concentration.

Since, as we have already noted, the rate of intake of water is proportional both to the permeability and to the net suction pressure, so that

$$\frac{dw}{dt} = \zeta (P - P_e - T) A,$$

Fig. 10. Curves illustrating the absorption of water by potato tuber immersed in distilled water (*D.W.*) and sodium chloride solutions of various concentrations ($\frac{N}{5}$ to $\frac{N}{12}$). (After Stiles and Jørgensen.)

and as with increase in the concentration of the sugar P_e increases, and consequently $P - P_e - T$ decreases, the observed results can be explained on account of the reduction of the net suction pressure with increasing concentration of the external sugar solution; there

is no evidence from existing data that the presence of the sugar has any influence on the permeability of the cell membranes to water, nor is there any evidence of an appreciable entrance of the sugar nor of exosmosis of solutes from the cell sap. Similar results with potato in sucrose solutions were obtained by Thoday (1918 *a*).

2. SODIUM CHLORIDE

Similar experiments with sodium chloride showed that this salt behaved to potato tissue in the same way as sucrose, but that the solution in which the tissue neither gained nor lost in weight possessed a concentration slightly higher than $N/8$. This lower concentration is to be expected from theoretical considerations as the ionisation of the sodium chloride in solution almost doubles its osmotic pressure. The absorption-time curves for the tissue in different concentrations of the salt are shown in Fig. 10.

Similar experiments with carrot tissue showed that in a solution of $N/3$ concentration this tissue neither gained nor lost in weight.

3. ETHYL ALCOHOL, OCTYL ALCOHOL, CHLOROFORM AND MERCURIC CYANIDE

The results obtained with ethyl alcohol were quite different from those with sucrose and sodium chloride. The results with potato tissue are shown graphically in Fig. 11. With lower concentrations (up to molecular) absorption at first takes place as in dilute solutions of sucrose. But it will be observed that if ethyl alcohol behaved similarly to sucrose, we should expect the potato to undergo neither gain nor loss in weight in a solution having a concentration of about $M/4$, whereas swelling even takes place initially in solutions having as high a concentration as $2M$. But in concentrations M and $2M$ this swelling reaches a maximum, after which the solution loses water. With $M/2$ alcohol the maximum was not reached even after 16 hours, but the swelling was lower than in distilled water; in M alcohol the maximum intake of water is reached in about 7 or 8 hours, while in $2M$ alcohol in about half an hour. With concentrations of alcohol higher than $2M$ any preliminary period of water intake was not detected by the method, the excretion of water being rapid, the more so the higher the concentration of the external solution. The observation of Overton (1895) that ethyl alcohol may enter the cell so rapidly from hypertonic solutions that plasmolysis does not take place is in agreement with the behaviour noted here.

The behaviour of a secondary octyl alcohol was similar, and the curves given by Thoday for chloroform and mercuric cyanide leave little doubt that these substances behave on the whole similarly to the alcohols examined.

These results are simply explained. It is clear that these substances bring about an increase in the permeability of the cell to substances dissolved in the cell sap (Czapek, 1910 *a*; Stiles and Jørgensen, 1917 *a*), while at the same time it is to be supposed that the solute in the external liquid is itself capable of entering the cell.

Fig. 11. Curves illustrating the influence of ethyl alcohol in concentrations 10 *M* to 0.5 *M* on the absorption of water by potato tissue. (After Stiles and Jørgensen.)

In the first stage of the experiment there will thus occur a rise in the osmotic pressure of the cell-sap on account of the addition to it of alcohol or other substance. If the permeability of the cell membranes remained unaltered we may suppose that the swelling in the most concentrated of the alcoholic solutions would be the same as that in distilled water at equilibrium, but the rendering permeable of the cell to the solutes in the cell sap brings about a diminution of osmotic pressure within the cell which accordingly loses water on account of this. Thus to the first stage of excessive swelling there follows a

stage of water loss as the membranes are rendered more permeable. The exact shape of the absorption-time curve in any particular case must depend on the concentration of the external solution, the permeability of the cell to the external solute and the rate at which the solute acts on the cell membranes in rendering them permeable to the solutes of the cell sap. Thus it is not to be expected that the behaviour of the tissue in regard to water gain or loss will be the same with different toxic substances, nor is this the case.

4. SULPHURIC ACID, OSMIC ACID AND MERCURIC CHLORIDE

These substances influence the swelling of potato rather similarly to those just discussed, that is, there is a preliminary period of

Fig. 12. Curves illustrating the influence of sulphuric acid on the absorption of water by potato tuber. (After Stiles and Jørgensen.)

swelling followed by a period of shrinkage. There is no doubt that acids are absorbed by plant tissue, the evidence for which will be discussed in a subsequent chapter. The results obtained for sulphuric acid are shown in Fig. 12. It will be observed that in a concentration of $N/50$ the intake of water reaches a maximum in about an hour, while in a concentration as low as $N/2000$ the swelling gives place to shrinkage after 4 or 5 hours. Even in $N/5000$ sulphuric acid shrinkage supervened before the lapse of 24 hours while in distilled water the tissue was still undergoing slow swelling after this lapse of time.

A curious phenomenon noted in the case of sulphuric acid is that in the lower concentrations the tissue actually absorbed water at more rapid a rate at first than in distilled water. Calculation of the probable error of experiment left no doubt that this is not to be accounted for on account of the variability of different samples of tissue. This phenomenon is rather difficult to account for, since as the concentration of acid external to the tissue is so low, the penetration of it into the cell sap could scarcely increase the osmotic pressure of the latter sufficiently to account for the increased rate of water absorption. It is possible that this increased swelling may be referred to the increased absorption of water by proteins and other colloidal systems in acid solutions as compared with distilled water, but definite evidence confirmatory of such a view is wanting.

Thoday (1918 *a*) has shown that a similar increase of rate of water absorption in lower concentrations of the solute as compared with that in distilled water is to be observed in the case of osmic acid and mercuric chloride. It may be significant that mercuric chloride undergoes partial hydrolysis in solution so that the solution contains a small quantity of hydrochloric acid.

5. ETHYLIC ACETATE AND PHENOLS

The absorption of ethylic acetate by grains of barley was examined by Brown and Worley (1912). Ethylic acetate enters the grain, but the rate of water intake is more rapid than from pure water. This was regarded by Brown and Worley at the time as possibly due to a simplification of the water molecule in presence of this ester. Later Brown and Tinker (1916 *a*) observed a similar phenomenon in the case of various phenolic solutions. Barley grains absorbed various solutions of phenol of different concentrations the more rapidly the more concentrated the solution. With a number of different phenols in half-normal concentration the rate of absorption was in this order: phenol, catechol, resorcinol, pyrogallol. The last entered at the same rate as water. Since variations in osmotic pressure, vapour pressure and viscosity of these various solutions are slight, while the rate of absorption is in inverse order to the surface tensions of the solutions (Worley, 1914), Brown and Worley conclude that surface tension is also a factor in determining the rate of entrance of solutions into barley grains.