

PLATE 12.—The coloured Plate.

Figs. 1-4 are all on the same scale of magnification, and represent characteristic views of the four ingredients described in this paper, as seen in micro-sections of untreated coal, showing their natural colours as seen under the microscope.

Fig. 1.—Section of fusain. At the top, note portion of a bright coloured spore from the adjacent durain. The bulk of the section is still recognisable or macerated wood fibres, the walls of which are quite black and opaque.

Fig. 2.—Section of durain. Numerous crushed and partly broken spore coats, ranging from gold to orange colour, and various small fragments are interspersed with the black granular matrix.

Fig. 3.—Section of clarain. Tissues of a stem, spores and more or less translucent bodies of various kinds, are mingled.

Fig. 4.—Section of vitrain. Showing its essential structureless condition. The various shades of colour depending upon the thickness of the section, which is never quite uniform.

Fig. 5.—Tubes showing the approximate colour and the proportion of *débris* from the four ingredients after the treatment described on page 477. F, fusain, D, durain, C, clarain, V, vitrain.

The Comparative Rate of Absorption of Various Salts by Plant Tissue.

By WALTER STILES, M.A., Lecturer in Botany in the University of Leeds, and
FRANKLIN KIDD, M.A., D.Sc., Fellow of St. John's College, Cambridge.

(Communicated by Prof. W. M. Bayliss, F.R.S. Received August 30, 1918.)

Introduction.

In a previous paper we have dealt with the intake by carrot and potato cells of single salts in different concentrations, and we there considered, especially, the dependence of the equilibrium attained in salt absorption on the concentration of the solution exterior to the tissue. In the course of these experiments dealing with the relation between concentration and intake, it was indicated that the rate of absorption and the position of equilibrium ultimately attained depended also upon the nature of the salt. As, however, experiments with different salts were made with different samples of tissue, we did not consider ourselves justified in laying much stress on the results obtained on account of the variability of different samples of tissue, a difficulty to which attention has previously been called. In the experiments recorded in this paper, we have therefore chosen one concentration and compared the conductivity changes produced in solutions of different salts by carrot and potato cells of the same sample.

2 Q 2

Method.

The method used is that described in a former paper (12). The experiments were carried out in triplicate. All the results compared with one another were obtained with the same sample of tissue and from experiments carried on contemporaneously.

The concentration selected throughout was N/50, as with this concentration of salts of "nutrient" or harmless metals exosmosis is likely to be small in comparison with the absorption, so that the results will give a near approximation to the relative rates of absorption from the various solutions. When exosmosis takes place to any great extent the tissue loses water and its turgidity. Carrot in solutions of nutrient or harmless metals of a concentration of N/50 remained turgid right up to the conclusion of the experiments.

In each series the salts employed had a common anion or kation, so that the influence of different ions on the rate of absorption is displayed. Four series with carrot and three with potato were carried out, the common ions in the carrot series being respectively chloride, sulphate, nitrate, and potassium. Chloride, sulphate, and nitrate series were carried out with potato.

Experimental Results.

1. *Chlorides*.—The chlorides used were those of potassium, sodium, lithium, and calcium. The changes in conductivity in the case of carrot are given in the accompanying Table, and are shown graphically in fig. 1.

Table I.—Carrot in Solutions of various Chlorides of Concentration N/50.

| Potassium chloride. | | Sodium chloride. | | Lithium chloride. | | Calcium chloride. | |
|---------------------|------------------------------------|------------------|------------------------------------|-------------------|------------------------------------|-------------------|------------------------------------|
| Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. |
| 0·5 | — 145 | | | 0·5 | — 64 | 0·25 | —101 |
| 1·0 | — 175 | 1·0 | — 80 | 1·0 | — 67 | 0·5 | —113 |
| | | 2·0 | — 117 | | | 1·0 | —113 |
| 6·38 | — 335 | 6·62 | — 222 | 6·12 | —119 | 6·20 | —143 |
| 18·28 | — 758 | 18·62 | — 560 | 18·0 | —257 | 18·0 | —176 |
| 28·75 | —1138 | 29·0 | — 896 | 28·5 | —374 | 28·5 | —230 |
| 43·25 | —1497 | 43·5 | —1228 | 43·0 | —449 | 43·0 | —341 |
| 49·25 | —1595 | 49·5 | —1329 | 49·0 | —489 | 49·0 | —371 |
| 91·25 | —2039 | 91·5 | —1677 | 91·0 | —599 | 91·0 | —628 |

From the Table and curves it will be observed that, in the first place, the apparent rate of absorption differs greatly with the different salts, and also that the initial rate does not depend on the position of equilibrium. There is little doubt that after 91 hours equilibrium is practically attained.

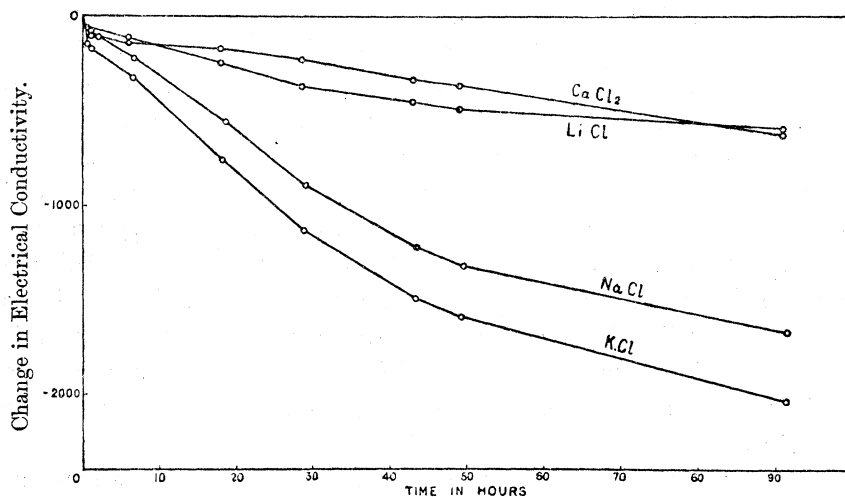


FIG. 1.—Carrot in Solutions of various Chlorides of Concentration N/50.

In N/50 solutions the four salts employed have almost identical ionic concentration, so that the difference in the rates of intake cannot be accounted for on the ground of differences in concentration. In Table II are given the degree of dissociation (which is proportional to the ionic concentration), and the mobility of the kation and the coefficients of diffusion in the case of the four salts. These physical constants are those given by Landolt and Börnstein (3).

Table II.—Absorption of Chlorides by Carrot. Mobility of Anion 65·4.

| Salt. | Degree of dissociation. | Mobility of kation. | Coefficient of diffusion. | Decrease in conductivity after 1 hour. | Decrease in conductivity after 18 hours. |
|----------------------|-------------------------|---------------------|---------------------------|--|--|
| Lithium chloride ... | 91 | 33·4 | 0·70 | 67 | 257 |
| Sodium chloride ... | 91 | 43·6 | 0·94 | 80 | 550 |
| Calcium chloride ... | 85 | 51·8 | 0·68 | 113 | 176 |
| Potassium chloride | 92 | 64·7 | 1·36 | 175 | 750 |

This Table suggests that the initial rate of salt absorption is dependent on the mobility of the kation. This result falls into line with the results obtained for hydrogen chloride(11). The mobility of the hydrogen ion is

very high, namely 315, and it is found that the hydrogen ion is very rapidly absorbed from hydrogen chloride, and indeed from all acids (2).

The total amount of absorption is, however, as one would suppose, not conditioned by ionic mobility, but by some other factor, for calcium chloride, which after one hour has been absorbed to a greater extent than any other chloride except that of potassium, after 18 hours has fallen well behind all the others, which, however, maintain their relative positions. The initial order of absorption of kations from the chlorides thus appears to be K, Ca, Na, Li, while as regards total quantity absorbed it is K, Na, Li, Ca. The relative positions of lithium and calcium are a little doubtful, as at the end of the experiment there is actually a little more apparent absorption from calcium than from lithium chloride. It must be remembered that the numbers are only approximate, as they neglect exosmosis. Although this is undoubtedly negligible in the case of non-toxic solutions, yet lithium is generally regarded as somewhat toxic, and it is possible that there is more exosmosis from the tissue in the case of lithium than with the other chlorides (11).

In regard to the general course of absorption the curves are approximately logarithmic after the first few hours. During the initial period, however, the rate of withdrawal of salt from the solution is more rapid than it would be if the same logarithmic relation between time and intake held from the beginning. This suggests that there is an initial process at work rapidly withdrawing salt from the solution, which is followed by a slow general process which continues for several days before equilibrium is reached. If the results are expressed in terms of the percentage of salt required to produce equilibrium, the parts of the curves where the general process predominates all follow the same approximate course, showing that absorption proceeds to equilibrium at the same rate. Thus, although the initial rates of intake may be dependent on the mobility of the ions, in regard to the general course of absorption, the differences in rate of intake appear to be directly due to the position of equilibrium.

The initial absorption from solutions of the same salts by potato is similar, but the absorption is soon masked by the exosmosis that supervenes in the case of this more sensitive tissue. The numbers obtained experimentally are shown in Table III, and these results are exhibited graphically in fig. 2. The initial order of absorption is K, Na, Ca, Li.

Table III.—Potato in Solutions of various Chlorides of Concentration N/50.

| Potassium chloride. | | Sodium chloride. | | Lithium chloride. | | Calcium chloride. | |
|---------------------|------------------------------------|------------------|------------------------------------|-------------------|------------------------------------|-------------------|------------------------------------|
| Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. |
| 0·5 | —116 | 0·5 | — 87 | 0·5 | — 33 | 0·5 | — 70 |
| 3·0 | —115 | 3·0 | — 61 | 3·0 | — 23 | 3·0 | — 45 |
| 24·25 | — 45 | 24·4 | + 66 | 24·5 | +150 | 24·12 | +136 |
| 45·25 | + 40 | 45·5 | +190 | 45·5 | +314 | 45·12 | +219 |

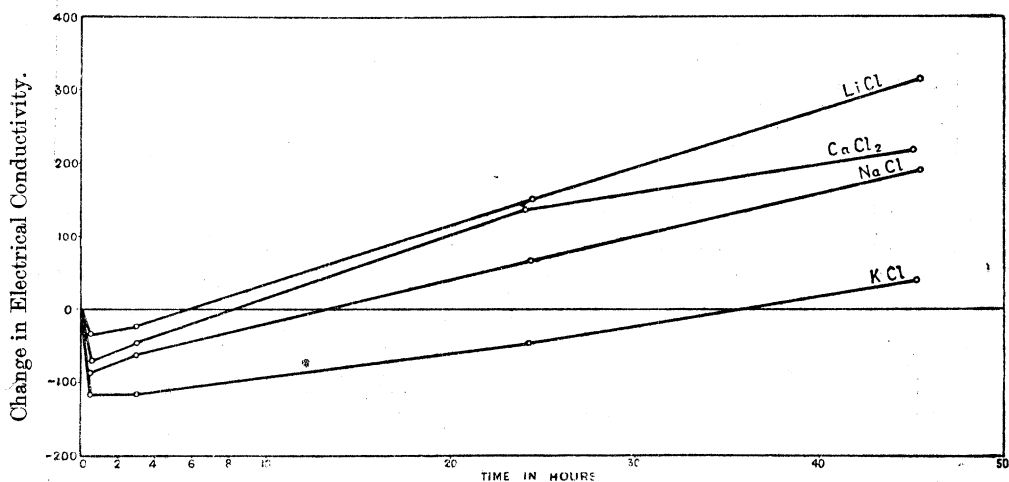


FIG. 2.—Potato in Solutions of various Chlorides of Concentration N/50.

2. *Sulphates*.—The salts employed in this series were the sulphates of potassium, sodium, magnesium, zinc, and aluminium. The first three are nutrient or harmless salts, zinc is generally regarded as a toxic element, while the anomalous behaviour of aluminium has been discussed in an earlier paper (12).

The results are such as might be expected. The greatest apparent absorption takes place with potassium sulphate, less with sodium sulphate, and still less with magnesium sulphate. With zinc and aluminium sulphates the electrical conductivity of the solution increases with continued immersion of carrot tissue in it. It will be observed that in the case of zinc sulphate a decrease in conductivity takes place during the first half hour corresponding to an absorption of the salt. Subsequently, the conductivity rises and continues to do so until the end of the experiment. This behaviour is completely explained on the basis of the absorption of the zinc; its toxic

action brings about exosmosis which causes the subsequent rise in conductivity. The loss of turgidity of the discs corresponds with this.

Table IV.—Carrot in Solutions of various Sulphates of Concentration N/50.

| Potassium sulphate. | | Sodium sulphate. | | Magnesium sulphate. | | Zinc sulphate. | | Aluminium sulphate. | |
|---------------------|------------------------------------|------------------|------------------------------------|---------------------|------------------------------------|----------------|------------------------------------|---------------------|------------------------------------|
| Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. |
| 0·5 | -176 | 0·5 | - 54 | 0·5 | -37 | 0·25 | - 13 | 0·25 | +102 |
| 1·0 | -183 | 1·0 | - 48 | 1·0 | -37 | 0·5 | - 20 | 0·5 | +139 |
| 14·25 | -205 | 14·5 | - 4 | 14·5 | -26 | 14·0 | +180 | 14·0 | +381 |
| 25·25 | -215 | 25·5 | - 34 | 25·0 | -26 | 25·0 | +368 | 25·0 | +451 |
| 43·0 | -208 | 43·25 | - 66 | 43·0 | -12 | 43·0 | +766 | 43·0 | +644 |
| 64·5 | -273 | 64·75 | -117 | 64·5 | -33 | 64·5 | +929 | 64·5 | +816 |

In the case of aluminium this explanation does not hold as the discs are perfectly healthy and turgid at the end of the experiment. We have suggested provisionally in a former paper that the aluminium ion is absorbed much more rapidly than the sulphate ion, and that the consequent replacement of the aluminium ion by one of a higher mobility, as, for instance, hydrogen, accounts for the increase of conductivity in this case. This point will be dealt with in more detail in a later section of this paper.

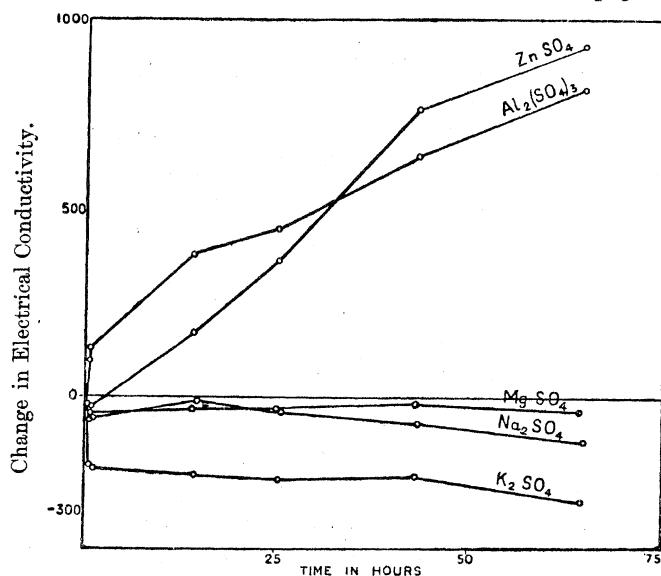


FIG. 3.—Carrot in Solutions of various Sulphates of Concentration N/50.

The initial rates of absorption indicated are in the order K, Na, Mg, Zn, and this order remains the same at the end of the experiment.

The figures given in Table IV, compared with those obtained for chlorides, show how much less is the apparent absorption from potassium and sodium sulphates than from the corresponding chlorides. The difference is so great that it can scarcely be referred to differences in the tissue used in the two series. Nevertheless, all the experiments in the sulphate series were repeated, and the same results obtained. A comparative series with anions given later confirmed this result.

The behaviour of potato in solutions of sulphates is very similar to its behaviour in solutions of chlorides. As before, the apparent initial absorption of the sodium salt is less than that of the potassium salt, but subsequent exosmosis prevents the obtaining of definite data as to the subsequent course of absorption by potato. The results obtained are shown in Table V, and graphically in fig. 4. They suggest the same order of absorption as with carrot. The order of the coefficients of diffusion of the four sulphates used is K, Na, Zn, Mg, while the order of absorption by carrot and potato is K, Na, Mg, Zn. There is thus a parallelism between the absorption and the coefficient of diffusion, although the position of zinc differs in the two series. It should be noted that the position of zinc in the absorption series is doubtful; as, on account of secondary changes resulting in exosmosis, more may be absorbed than appears from the observed results.

Table V.—Potato in Solutions of various Sulphates of Concentration N/50.

| Potassium sulphate. | | Sodium sulphate. | | Magnesium sulphate. | | Zinc sulphate. | | Aluminium sulphate. | |
|---------------------|------------------------------------|------------------|------------------------------------|---------------------|------------------------------------|----------------|------------------------------------|---------------------|------------------------------------|
| Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. |
| 0·5 | — 91 | 0·5 | — 79 | 0·5 | — 3 | 0·5 | + 15 | 0·5 | + 55 |
| 1·12 | — 91 | 1·13 | — 59 | | | | | | |
| 14·0 | — 25 | 14·0 | + 31 | 13·85 | + 101 | 14·3 | + 142 | 13·78 | + 200 |
| 20·0 | + 64 | 20·0 | + 101 | 19·87 | + 184 | 19·51 | + 170 | 19·28 | + 248 |
| 41·75 | + 225 | 41·75 | + 345 | 41·56 | + 336 | 41·28 | + 506 | 41·28 | + 643 |

3. *Nitrates*.—The nitrates of potassium, sodium, calcium, aluminium, and zinc were employed. The initial apparent absorption by carrot is very marked with potassium and sodium nitrates, less so with calcium and zinc nitrates, and slight but yet distinct with aluminium nitrate. With zinc

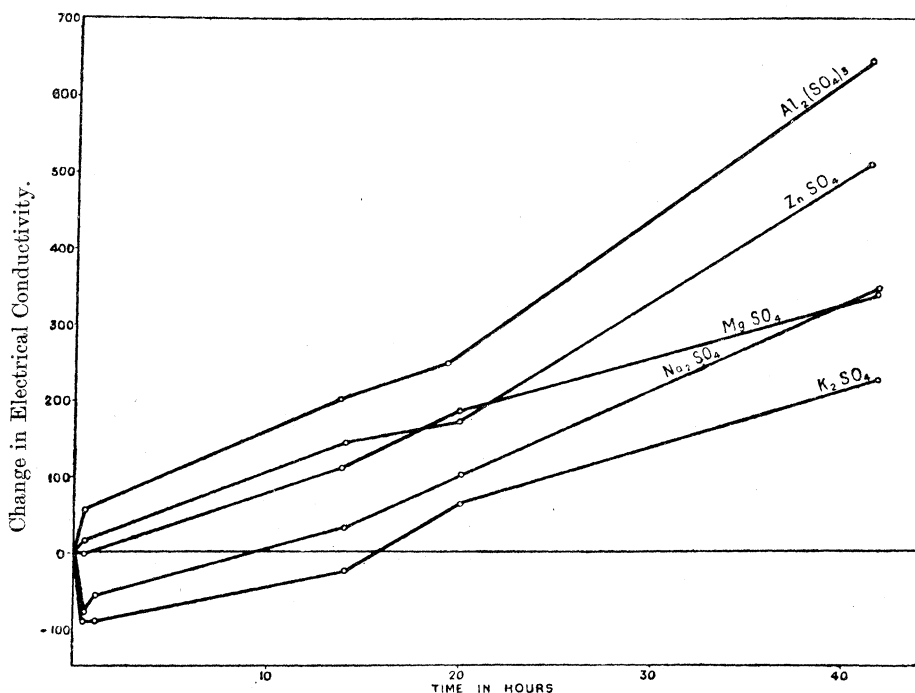


FIG. 4.—Potato in Solutions of various Sulphates of Concentration N/50.

nitrate the initial absorption is soon masked by exosmosis. The actual changes in conductivity observed are given in Table VI, and are shown graphically in fig. 5.

Table VI.—Carrot in Solutions of various Nitrates of Concentration N/50.

| Time in hours. | Changes in conductivity of solutions. | | | | |
|----------------|---------------------------------------|-----------------|------------------|---------------|--------------------|
| | Potassium nitrate. | Sodium nitrate. | Calcium nitrate. | Zinc nitrate. | Aluminium nitrate. |
| 0·5 | — 183 | — 89 | — 86 | — 57 | — 20 |
| 19·25 | — 891 | — 659 | — 215 | + 107 | — 135 |
| 71·50 | — 2023 | — 1360 | — 493 | + 540 | — 268 |

The relation of the initial absorption to the ionic mobilities and coefficients of diffusion is again suggested.

The subsequent decline in the rate of absorption of the calcium salt relative to the potassium and sodium is also in evidence. The toxic action of zinc is once more shown both by the subsequent rise in conductivity of the

external solution and the loss of turgidity of the tissue. The tissue discs in the other solutions remained turgid at the end of the experiment.

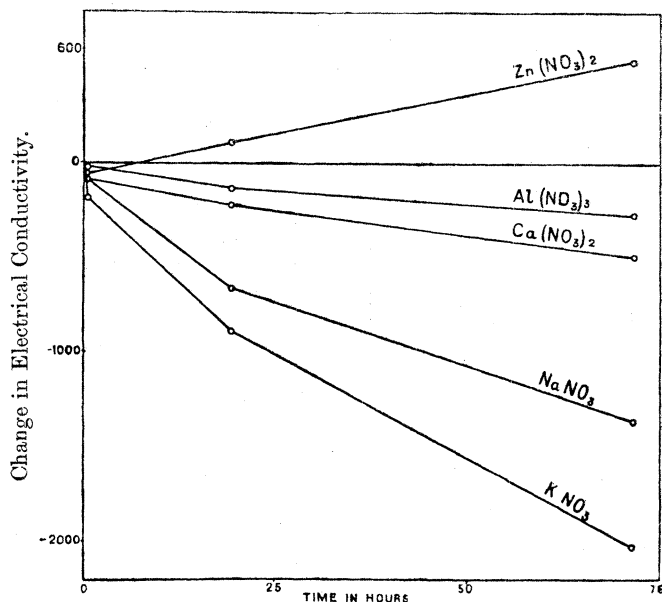


FIG. 5.—Carrot in Solutions of various Nitrates of Concentration N/50.

At the end of the experiment the reaction of the solution towards litmus was examined. The calcium and zinc nitrate solutions were neutral to litmus; whereas the potassium and sodium nitrate solutions were slightly acid, the aluminium nitrate was markedly acid.

The same series of nitrates were used with potato. As with other series, the same difference in the relation of absorption and exosmosis as compared with carrot is observable. The highest apparent exosmosis took place in the case of calcium nitrate. The results obtained are shown in Table VII and fig. 6.

The reactions of the solutions towards litmus at the end of the experiment were exactly the same as with carrot. The significance of this we shall discuss later.

4. *Potassium Salts.*—The results obtained with chlorides, sulphates, and nitrates indicate that the potassium ion is absorbed more rapidly than the other metallic ions used in these experiments. As, for the reasons we have given in a former paper, the values for absorption obtained by the conductivity method give approximately the intake of the less absorbed ion, in comparing the absorption of anions, we have chosen potassium salts, as the

Table VII.—Potato in Solutions of various Nitrates of Concentration N/50.

| Potassium nitrate. | | Sodium nitrate. | | Calcium nitrate. | | Zinc nitrate. | | Aluminium nitrate. | |
|--------------------|------------------------------------|-----------------|------------------------------------|------------------|------------------------------------|----------------|------------------------------------|--------------------|------------------------------------|
| Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. | Time in hours. | Change in electrical conductivity. |
| 0·75 | — 67 | 0·75 | — 7 | 0·45 | — 6 | 0·75 | — 27 | 0·45 | 0 |
| 14·12 | — 95 | 13·97 | + 4 | 14·0 | + 60 | 14·10 | + 23 | 13·50 | — 141 |
| 20·70 | — 44 | | | 20·18 | + 127 | | | 19·35 | — 155 |
| 42·45 | + 67 | 41·77 | + 285 | 42·18 | + 382 | 41·93 | + 210 | 42·5 | — 181 |

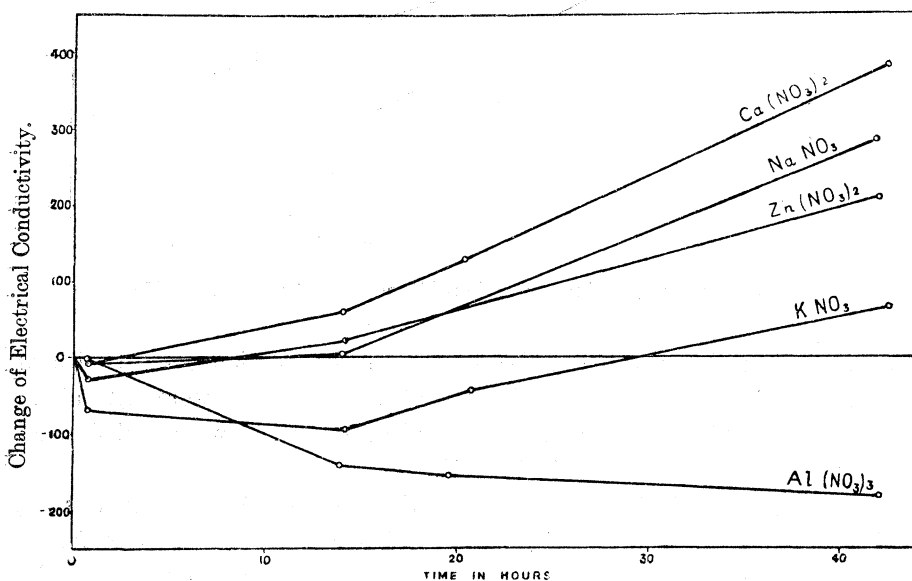


FIG. 6.—Potato in Solutions of various Nitrates of Concentration N/50.

measured decreases in conductivity should give approximate values for the intake of the anions.

The results obtained with carrot are shown in Table VIII and fig. 7.

These salts therefore produce the expected result. It will be observed that the original order of apparent absorption is potassium sulphate, potassium nitrate, and potassium chloride.

Nevertheless, the slowing down of the absorption from the sulphate solution due to the much smaller final absorption of sulphate (*cf.* the series with sulphates) later alters the order to potassium nitrate, potassium chloride, and potassium sulphate.

Table VIII.—Carrot in Solutions of various Potassium Salts in Concentration N/50.

| Time in hours. | Change in electrical conductivity. | | |
|----------------|------------------------------------|---------------------|--------------------|
| | Potassium chloride. | Potassium sulphate. | Potassium nitrate. |
| 0·25 | — 145 | —212 | — 197 |
| 2·25 | — 233 | —258 | — 214 |
| 19·0 | — 550 | —266 | — 625 |
| 42·0 | —1042 | —311 | —1152 |

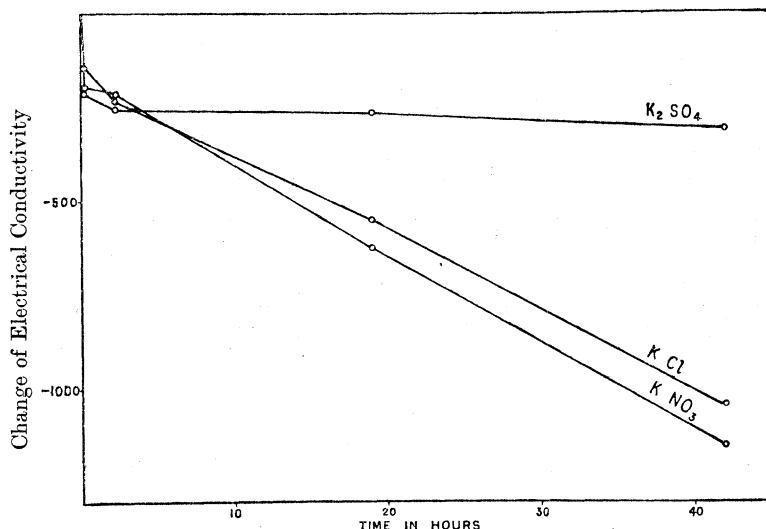
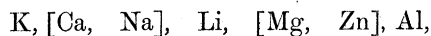


Fig. 7.—Carrot in Solutions of various Potassium Salts of Concentration N/50.

The difference between chloride and nitrate is small and no emphasis can be laid on it. The slight absorption of sulphate is very striking.

From these results it may be concluded that the order in which kations are absorbed at the beginning of the experiments is in general the following:—



although the nature of the anion may influence the order to some extent. The anions are absorbed initially in the order SO_4 , NO_3 , Cl . In both the case of kations and anions this order alters in the course of absorption, owing to the different position of equilibrium attained in the cases of the various salts. The following Table shows the influence of the nature of the salt on the value of the absorption ratio (*i.e.*, the ratio between internal to external concentration of the salt or ion) after the absorption has proceeded towards equilibrium

as far as the conditions of experiment allow. The most noteworthy fact brought out from this Table is the much smaller total absorption of calcium and magnesium than of potassium and sodium, and the much smaller total absorption of sulphate than of chloride and nitrate. Potassium is always absorbed to a slightly greater extent than sodium, while the indication is that nitrate is absorbed somewhat more than chloride. The results will now be discussed in the following section, where the results of some other workers will be compared with those here recorded.

Table IX.—Ratio of Salt Concentration in Tissue to that in External Solution after Intake of Salt from Solutions in N/50 Concentration having a common Kation or Anion.

| Salt, N/50. | Absorption ratio. | Salt, N/50. | Absorption ratio. |
|---------------------------------------|-------------------|---|-------------------|
| Chloride series, 91 hours— | | Nitrate series, 71·5 hours— | |
| KCl | 3·58 | KNO ₃ | 4·65 |
| NaCl | 3·49 | NaNO ₃ | 3·30 |
| LiCl | 1·16 | Ca(NO ₃) ₂ | 1·19 |
| CaCl ₂ | 1·09 | Al(NO ₃) ₃ | 0·53 |
| Sulphate series, 64·5 hours— | | Potassium series, 42 hours— | |
| K ₂ SO ₄ | 0·51 | KCl | 1·99 |
| Na ₂ SO ₄ | 0·46 | K ₂ SO ₄ | 0·55 |
| MgSO ₄ | 0·097 | KNO ₃ | 2·20 |

Discussion.

In an earlier paper we have shown that the rate of intake of salts by plant tissue depends on the concentration of the solution from which absorption takes place, and that the equilibrium reached in salt intake depends very greatly on the concentration, a relatively less proportion of the salt being absorbed with increasing concentration. In attempting to determine the relative rates of absorption of different salts or ions it is therefore essential that the salts compared should be presented to the tissue in equivalent concentration. The data recorded in these pages have been obtained with concentrations of N/50.

It is first necessary to discuss how far the results obtained by the conductivity method justify a comparison of the rates of intake of different salts.

If the salt is absorbed without exosmosis resulting, and if the two ions of the salt are absorbed in equivalent quantities, the decreases in conductivity will be very close measures of the absorption of the salt. The increase in the degree of dissociation resulting from dilution will be slight, and as all the salts compared are absorbed more or less, a slight increase in the degree of

dissociation will result from this in all the solutions, which reduces any slight error arising from changes in the degree of dissociation resulting from dilution. Moreover, the greatest increase in the degree of dissociation is to be expected in the solutions from which most salt is absorbed. Hence, with greater absorption, the decrease in conductivity tends to give a value for the absorption less than the true value, from which it follows that changes in the degree of ionisation consequent on absorption of salt and the resulting dilution of the solution will not affect the comparison of the rates of absorption of different salts, except to make the differences appear slightly less than they actually are.

A more serious complication arises from exosmosis. We have formerly given reasons why, in the case of carrot immersed in solutions of nutrient and harmless substances, this source of error is not of importance, whereas with potato it makes the drawing of conclusions much more difficult. Hence, our conclusions are based primarily on the results obtained with carrot; the data from experiments on potato are subsidiary to and confirmatory of those from experiments on carrot. Among the results with the latter the toxic action of zinc shows clearly the influence of exosmosis in obscuring the absorption.

A third difficulty arises if the two ions of a salt are not absorbed equally. Nathansohn (5, 6), Meurer (4), Ruhland (10), and Pantanelli (7) have shown by direct chemical analysis that the ions of a salt are not necessarily absorbed with equal rapidity. In the case of inequality of ionic absorption the excess of ion absorbed must be replaced by another ion of the same sign, which may be brought about either by exosmosis from the tissue or by hydrogen or hydroxyl ions. If the absorption of the two ions differs greatly, and if the replacing ion differs markedly in mobility from that of the ion absorbed in excess, the fall in conductivity will no longer give a measure of the absorption.

Among the experiments recorded in this paper, those with aluminium are probably to be explained on these grounds. It will be recalled that with aluminium sulphate, although the discs remain turgid and show no sign of injury, yet the conductivity of the solution rises, thus simulating the state of affairs in a toxic solution. Now, Rothert (8) and especially Meurer (4) have shown by direct analysis that the aluminium ion is absorbed to a very great extent from solutions of aluminium sulphate. The results of Pantanelli (7) with a variety of plants are equally striking. We have collected Pantanelli's results with regard to absorption of aluminium salts in the following Table, which show how widely distributed throughout the plant kingdom is the rapid absorption of the aluminium ion in comparison with the sulphate ion:—

The anions are absorbed initially in the order SO_4 , NO_3 , Cl , but this gives place later to the order NO_3 , Cl , SO_4 , owing to the slowing down of the rate of absorption of sulphate.

These conclusions agree well with the results of earlier workers. Ruhland (9) showed that potassium and sodium nitrates penetrate the protoplasm of *Spirogyra* more rapidly than calcium nitrate, and potassium and sodium chlorides more rapidly than calcium chloride. Potassium and sodium nitrates penetrate more rapidly than the corresponding chlorides. The (final) order of kation absorption by *Spirogyra*, according to Ruhland, is therefore $[\text{K}, \text{Na}]$, Ca , and the order of anions : NO_3 , Cl .

Fitting (1) has recently followed the rate of intake of salts by the epidermal cells of *Rhoeo discolor* by following the rate of deplasmolysis in hypertonic solutions. He records that potassium nitrate and chloride penetrate the protoplasm with ease, but the rate of penetration of potassium sulphate is much smaller. As regards kations, sodium nitrate and sodium chloride both penetrate the protoplasm, but lithium chloride and lithium nitrate are less permeable than potassium nitrate. Magnesium chloride, nitrate and sulphate are only permeable in small degree, while in regard to calcium chloride and calcium nitrate Fitting could observe no permeability. The same applies to barium salts.

The order found by Fitting is thus as follows : for kations $[\text{K}, \text{Na}]$, Li , Mg , $[\text{Ca}, \text{Ba}]$; for anions $[\text{NO}_3, \text{Cl}]$, SO_4 .

Troendle (13) using the same method as Fitting on roots of *Lupinus albus* and palisade cells of the leaves of *Acer platanoides* and *Salix babylonica*, finds various ions absorbed in the following order : kations, Rb , K , Na , Li , Mg , Ba , Sr , Ca ; anions, NO_3 , Cl , SO_4 .

Pantanelli's researches, to which reference has been made earlier, extend over a wide range of forms, including flowering plants (e.g., *Cicer arietinum*, *Vicia Faba*), green algae (*Valonia utricularis*, *Ulva lactuca*), and a yeast (Barbera Wine yeast). His results show that a considerable variation occurs in different forms. With higher plants, the absorption of calcium is markedly less than that of potassium, while the rapidity of the absorption of nitrate is clearly shown. With lower plants, on the other hand, calcium is readily absorbed. Pantanelli's results bring out clearly the different rates of absorption of the kation and anion of the same salt, but it is also clear from comparison of the absorption of the same ion from different salts, that the absorption of one ion is influenced by the other. For example, *Cicer arietinum* absorbed 0.35 mgrm. of potassium from a 0.025 N solution of potassium chloride, while from a solution of potassium nitrate of the same concentration 2.74 mgrm. of potassium were absorbed in the same time.

In general, therefore, it may be concluded that earlier work agrees with our own as to the relative degree of absorption of different ions. The remarkable thing is that the differences between different tissues in this respect are as small as they appear to be.

In general it would appear that the initial rate of absorption of kations is influenced very largely by the mobility of the ion or the coefficient of diffusion of the salt. Troendle, on the contrary, draws the conclusion that the rapidity of entrance of ions is not controlled by the force of diffusion of ions and molecules through the protoplasm into the vacuole. He draws this conclusion as a corollary to an earlier one which he reached, as we think (12) on insufficient grounds, that the rapidity of entrance of ions is independent of the concentration of the salt. We have already pointed out how our own results as to the influence of concentration contradict the conclusion of Troendle as to the influence of concentration, although we agree with him that the absorption of salt is not governed by Fick's law of diffusion. Troendle concludes that the rapidity of penetration of salts depends on the nature of the kation, and that the rapidity of entrance increases with the atomic weight of the kation in any one group of the periodic classification. This certainly appears to be the case with the alkali metals, but Troendle admits that magnesium contradicts his rule, as he found it was absorbed more rapidly than calcium. Our own numbers suggest that calcium is absorbed more rapidly than magnesium at first, a fact which would support Troendle's opinion, but how far this is a general phenomenon remains to be seen.

Troendle and earlier workers have not differentiated between the initial rate of absorption and the position of equilibrium which is finally attained. The results recorded in this paper show clearly that the initial order of absorption is not maintained. Thus, calcium and sulphate, which are initially absorbed at a rate equal to or greater than that of sodium and chloride respectively, are absorbed ultimately to only a third or a quarter of the extent to which these monovalent ions are taken in. How far this is a distinguishing feature of divalent as contrasted with monovalent ions cannot be said, although magnesium appears to behave like calcium. We know, however, that the trivalent aluminium ion is absorbed to a large extent, but this may be to a considerable extent, as Meurer supposes, by the cell wall and not by the cell interior, and so may be an exceptional case.

We would conclude, tentatively, that the initial rate of absorption of salts is dependent to a great extent on the mobility of the ions or the coefficient of diffusion of the salt, but that the total intake of salt depends on something other than this, as a result of which calcium, magnesium, and sulphate are

absorbed to a much less extent than potassium, sodium, chloride, and nitrate.

Summary.

1. The rate of absorption of various chlorides, sulphates, nitrates, and potassium salts from solutions of 0.02 N concentration was measured by the electrical conductivity method previously described.

2. After a brief initial period, lasting only a few hours, of rapid withdrawal of salt from solution, there follows a long period, lasting several days, during which absorption proceeds to an equilibrium. Over this period the curve follows an approximately logarithmic course.

3. Kations appear to be absorbed initially in the following order: K, [Ca, Na], Li, [Mg, Zn], Al. The position of ions enclosed within brackets may have to be reversed. This initial order of the rate of absorption does not indicate, however, the extent to which the ions are absorbed when equilibrium is approached; the order of absorption is then K, Na, Li, [Ca, Mg], the chief difference between this order and the initial order being in the position of Ca, which is absorbed to only a slight extent compared with K and Na.

4. Anions appear to be absorbed initially in the order SO_4 , NO_3 , Cl, which gives place later to the order NO_3 , Cl, SO_4 on account of the comparatively slight extent to which the sulphate ion is absorbed. The difference between nitrate and chloride is slight, and stress should not be laid on it.

5. These results agree in general with those of Ruhland, Fitting, Pantanelli, and Troendle, using different methods and different experimental material. These workers, however, did not distinguish between differences in the initial rates of absorption and differences in the position of equilibrium.

6. It seems clear that the rate and extent of intake of one ion of a salt may be influenced by the nature of the other ion.

7. The results obtained in regard to aluminium support the observations of Rothert and Meurer that this ion is rapidly absorbed from aluminium sulphate. This proceeds much more rapidly than the absorption of the anion.

8. Although Troendle's view that in any group of the periodic classification the metallic ions are absorbed more rapidly the higher the atomic weight, is not contradicted, yet the view that the initial rate of absorption is largely dependent upon the mobility of the ions or diffusibility of the salt is equally well supported, and can be put forward provisionally as a more reasonable hypothesis.

The position of equilibrium appears, however, to be governed by some quite different property, as to the nature of which it would be premature at

present to make a suggestion. Our results are that the divalent ions, Ca, Mg, and SO_4 , are at the final equilibrium absorbed to a much less extent than the monovalent ions, K, Na, Cl, and NO_3 .

LITERATURE CITED.

- (1) Fitting, H. "Untersuchungen über die Aufnahme von Salzen in die lebende Zelle." 'Jahrb. Wiss. Bot.,' vol. 56 (Pfeffer-Festschrift), pp. 1-64 (1915).
 - (2) Hind, M., "Studies in Permeability. III.—The Absorption of Acids by Plant Tissue," 'Ann. of Bot.,' vol. 30, pp. 223-228 (1916).
 - (3) Landolt, H., and Börnstein, R. "Physikalisch-chemische Tabellen," Berlin, 4. Aufl., 1912.
 - (4) Meurer, R. "Über die regulatorische Aufnahme anorganischen Stoffe durch die Wurzeln von *Beta vulgaris* und *Daucus carota*," 'Jahrb. Wiss. Bot.,' vol. 46, pp. 503-567 (1909).
 - (5) Nathansohn, A. "Ueber die Regulation der Aufnahme anorganischen Salze durch die Knollen von *Dahlia*," 'Jahrb. wiss. Bot.,' vol. 39, pp. 607-644 (1904).
 - (6) Nathansohn, A., "Weitere Mitteilungen über die Regulation der Stoffaufnahme," 'Jahrb. Wiss. Bot.,' vol. 40, pp. 403-442 (1904).
 - (7) Pantanelli, E. "Über Ionenaufnahme," 'Jahrb. Wiss. Bot.,' vol. 56 (Pfeffer-Festschrift), pp. 689-733 (1915).
 - (8) Rothert, W. "Das Verhalten der Pflanzen gegenüber Aluminium," 'Bot. Zeit.,' vol. 64, Abt. 1, pp. 43-52 (1906).
 - (9) Ruhland, W. "Beiträge zur Kenntnis der Permeabilität der Plasmahaut," 'Jahrb. Wiss. Bot.,' vol. 46, pp. 1-54 (1909).
 - (10) Ruhland, W. "Zur Frage der Ionenpermeabilität," 'Zeitschr. f. Bot.,' vol. 1, pp. 747-763 (1909).
 - (11) Stiles, W., and Jörgensen, I. "Studies in Permeability. I.—The Exosmosis of Electrolytes as a Criterion of Antagonistic Ion-Action," 'Ann. of Bot.,' vol. 29, pp. 349-367 (1915).
 - (12) Stiles, W., and Kidd, F. "The Influence of External Concentration on the Position of the Equilibrium attained in the Intake of Salts by Plant Cells." 'Roy. Soc. Proc.,' B, vol. 90, pp. 448-470 (1919).
 - (13) Troendle, A. "Sur la perméabilité du protoplasme vivant pour quelques sels." 'Arch. Sci. Phys. et Nat.,' 4^e Pér., vol. 45, pp. 38-54, 117-132 (1918).
-