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THE EXCHANGE OF IONS BETWEEN THE ROOTS OF LUPINUS ALBUS AND CULTURE SOLUTIONS CON- TAINING ONE NUTRIENT SALT¹

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Former work by one of us² has shown that the roots of *Lupinus albus* excrete electrolytes when grown in distilled water. From river water, on the contrary, the roots actively absorb electrolytes. There is a decided difference in root growth in the two cases. As compared with river water, the distilled water causes a decided inhibition of growth which is doubtless correlated with the loss of necessary salts from the roots to the distilled water. When quantities of certain calcium or sodium salts equal osmotically to the total salt content of Potomac River water are added to distilled water the loss of ions from the roots is found to be checked by the presence of calcium salts, but not by the presence of the sodium salts. Growth in the calcium solutions is found to equal that in river water checks; that in NaCl solutions being only slightly and temporarily better than in distilled water. The writers³ have made a study of the concentration relations of dilute solutions of calcium and magnesium nitrates to the roots of *Pisum sativum*, and have found that for each of these salts or for a mixture of the two, there is a fairly definite concentration at which excretion

¹ Published by permission of the Secretary of Agriculture.

² True, Rodney H., The Harmful Action of Distilled Water. Amer. Journ. Bot. 1: 255-274. 1914.

³ True, R. H., and Bartlett, H. H., Absorption and Excretion of Salts by Roots, as Influenced by Concentration and Composition of Culture Solutions. I. Concentration Relations of Dilute Solutions of Calcium and Magnesium Nitrates to Pea Roots. Bulletin 231, Bureau of Plant Industry, U. S. Department of Agriculture, Washington, D. C., 1912.

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of salts by the roots is equalled by absorption. This equilibrium concentration is lower for calcium nitrate than for magnesium nitrate, and lower for an equimolecular mixture of the two than for either alone. In the latter case it is about a hundred-thousandth molecular. If the initial concentration of the culture solution is less than the equilibrium concentration, excretion from the roots predominates over absorption and brings about a net rise in the concentration. Conversely, if the concentration of the solution is initially above the equilibrium point, the roots absorb more salts than they excrete and the concentration becomes less. The results with peas showed, furthermore, that with a culture solution of appropriate concentration and composition, absorption may take place until the solution becomes almost as free of electrolytes as distilled water. In such a case, excretion is obviously a negligible factor, and the net change in concentration of the solution must be ascribed to absorption alone. Absorption was found to be greatest in solutions containing calcium and magnesium nitrates in equimolecular proportions, but root growth was found to be equally good in any solution which did not contain less than one molecule of the calcium salt to nine of magnesium. In the more dilute solutions an even lower ratio of calcium to magnesium, 1 : 99, was found to completely overcome the deleterious effect exerted by magnesium alone. In other words absorption and growth appear to be more or less independent phenomena.

The present paper extends the same line of investigation to other salts and to a different plant. *Lupinus albus* L. has been studied in a considerable range of concentrations of $\text{Ca}(\text{NO}_3)_2$, CaSO_4 , $\text{Mg}(\text{NO}_3)_2$, MgSO_4 , KNO_3 , K_2SO_4 , KH_2PO_4 , KCl and NaCl . Future articles will deal with the effect of various mixtures of these salts in pairs and in threes on the same plant.

METHODS

The methods used were in general those described in our former article on peas (1. c.). Carefully selected seeds of *Lupinus albus* were germinated in moist sphagnum and used when the primary root was about 50 mm. long. Four roots were used in each 500 c.c. culture. Readings were made daily until it became apparent from the appearance of the plants that they were approaching exhaustion. This stage was marked by the withering of the foliage leaves, the partial dying of the edges of the cotyledons, the frequent failure of the hypocotyls and by the loss of electrolytes from the roots.

Jena glass beakers were chosen as containers, after preliminary experiments had shown that any difference between Jena glass and opaque quartz or paraffined glass due to the solubility of the former was much less than the experimental error from other causes. For example the diffusion of carbon dioxide from freshly distilled water is often sufficient to increase the electrical resistance of water left standing in any one of these three types of containers, thus offsetting any change in the opposite direction due to the solubility of the container. In fact, a common method of improving distilled water for use in conductivity determinations is to pass through it a stream of air, free of carbon dioxide. The loss of carbon dioxide from distilled water left standing in contact with the air is sufficient to lower its conductivity very appreciably. The water used for distillation was moderately "hard," *i. e.*, it contained bicarbonates which liberated carbon dioxide during the process of distillation. The fresh distilled water therefore contained more carbon dioxide than it did later after standing in contact with the air. It is self evident that water which is to be used for culture solutions should not be freed from carbon dioxide, in case it is wished to study the excretion or absorption of other electrolytes than carbonic acid from the roots. Since there must be a considerable lag in the attainment of CO_2 equilibrium between air and a solution to which CO_2 is supplied continuously, it follows that the electrolytic method shows, as the first effect of placing roots in distilled water, an increase in conductivity due to the excretion of CO_2 . It follows that if CO_2 constantly diffuses into the air from the solution, increase in conductivity on account of excretion of CO_2 from the roots must reach a maximum and thereafter remain reasonably constant as long as the roots continue to supply CO_2 . The maximum conductance due to CO_2 will be reached when the rate of diffusion of CO_2 from the solution into the air equals the rate at which CO_2 is supplied by the roots. The error in the conductance of a solution due to CO_2 can not be less than the conductance of water in equilibrium with air containing 3 parts in 10,000 of CO_2 . This lower limit of error is about equivalent to the conductance of half-millionth molecular NaCl. The upper limit of error can be approximately estimated as equivalent to the conductance of 16 millionths molecular NaCl. This estimate is based upon the measurement of absorption from solutions which show almost perfect absorption of the salt content by the roots. In reality the error is not as great as this figure, for probably no culture

solution is ever so completely depleted of ions that none remain except those resulting from the dissociation of carbonic acid.

Stock solutions (from which the culture solutions were made by dilution with distilled water) were accurately prepared from Merck's best "blue label" reagents.

In our experiments a range of concentrations was used comparable to the range from distilled water to the less concentrated soil solutions. The more concentrated culture solutions, for example, contained less mineral matter than the water from the Potomac River, but more than the water of the Great Dismal Swamp of Virginia. In the case of the simple salts the range of concentration in the culture solutions was greater than the range of the same single constituent among average soil solutions. In other words, we made an endeavor to study the reaction of the plant toward solutions similar in concentration to those which it might encounter under natural conditions.

It will be seen from the accounts of the particular experiments that the cultures were not kept at constant temperature. In order to avoid the deleterious effect of illuminating gas on the cultures, they were set up in a dark cabinet at the greenhouse. Although danger from gas leakage was thus avoided, it was found impossible, with the means at our disposal, to eliminate a considerable temperature fluctuation. The temperature of each culture was read daily when the conductivity was determined. It will be seen that the temperature curves, which are plotted parallel with the concentration curves for each experiment, show no consistent influence of temperature upon absorption or excretion. As a matter of fact, the most perfectly executed experiments, such as those charted in figs. 1 and 2, show no temperature effect whatever. Possibly this interesting fact may be correlated with certain observations made by Eckerson.⁴ This investigator has found, for example, that the primary roots of *Phaseolus* show no increase in permeability from 13° to 25° C. Similar phenomena were observed with other plants.

In our experiments concentrations were determined in the following manner. On the day that a series of cultures was prepared, the conductivity of each solution was determined at room temperature before the roots were placed in it. As long as the experiment lasted, the conductivity was read daily, each time at room temperature. It was impracticable to bring the culture solutions to constant temperature

⁴ Eckerson, Sophia, Thermotropism of Roots. *Bot. Gaz.* 58: 254-263. 1914.

before reading them, however desirable such a procedure might have been. It is well known that the temperature coefficients of conductivity for very dilute salt solutions, in which carbon dioxide exists in considerable concentration, are not the same as the coefficients for concentrated, relatively uncontaminated solutions. It was within the limits of accuracy of our work to use for all the dilute salt solutions the coefficient 0.20. All conductivities are referred to 18° C. Since in conductivity work with solutions of even $M/50$ concentration the impurity of the water may require a correction of 0.1 per cent., it is quite obvious that in some of our more dilute culture solutions the concentration increment between contiguous cultures was less than the initial concentration of impurities in the water. It was found, however, that the effect on conductivity of adding small increments of salt to distilled water was additive. Consequently we have assumed that the changes in conductivity of the solutions during the period of the experiment were likewise due to addition or subtraction of electrolytes. In the presentation of our results we have translated the changes brought about by the roots in the conductivity of the culture solutions into terms of change in concentration of the particular salt used in each experiment. All concentrations were determined with reference to the conductivities of the culture solutions as originally prepared, before the roots had been placed in them. As already remarked, at least part of the initial rise in concentration of most culture solutions after the roots are placed in them may be ascribed to carbon dioxide. Presumably the absorption of salt from all solutions was greater than the figures show, by the amount of this initial rise in the CO_2 concentration. As we have already pointed out, the error from this source can never have been as great as would correspond to a change in concentration of $14M \times 10^{-6}$, in the case of a salt like NaCl.

In connection with the fact that not only absorption but also excretion was measured in terms of the original salt used in spite of the fact that we know nothing in regard to what the roots may actually have excreted, it may be stated that most of the commoner electrolytes have nearly enough the same equivalent conductance so that little error would enter into our results on this account. At the close of each experiment the following measurements were taken for each plant: The length of the primary root, the length of several of the longer lateral roots, the length of the hypocotyl, and the length of the first internode above the cotyledons. It was found that only a very

loose relation existed between the length of the first internode and the length of the hypocotyl on the one hand, and either the development of the root system or composition of the medium, on the other. A much closer relation seemed to hold between the length of the primary root and the composition of the medium; consequently, in this paper the length of the primary root only is correlated with the chemical and physical data.

Throughout this paper concentrations are expressed as multiples of $M \times 10^{-6}$. M has its usual significance; it indicates a solution containing the gram-molecular weight of a compound in one liter of water. A solution whose concentration is $M \times 10^{-6}$ is therefore of one one-millionth molecular concentration, and a solution ten times as strong, for example, has the concentration $10M \times 10^{-6}$. In our work the least difference in concentration between adjacent cultures of a series containing only univalent ions was $6M \times 10^{-6}$; the greatest was $32M \times 10^{-6}$.

The reader will of course understand that two solutions of the same gram-molecular concentration are not necessarily chemically equivalent. A molecular solution of $\text{Ca}(\text{NO}_3)_2$, for example, is electrolytically equivalent to a twice molecular KNO_3 solution. This fact should be kept constantly in mind in order to avoid confusion in comparing the curves for the different experiments. It will be noticed that the distilled water curve is much flatter in the case of the bivalent salts than in the case of the univalent salts. This is due to the fact that the concentration of electrolytes excreted by the roots is in the one case expressed in terms of a bivalent salt, in the other case in terms of a univalent salt. In the case of all the univalent salts which we used except KH_2PO_4 , the conductance of equimolecular solutions was about the same for all, and roughly half the conductance of the bivalent salts. KH_2PO_4 is exceptional, as may be seen from the curves. It dissociates for the most part as a univalent salt into K^+ and H_2PO_4^- ions, but has a much lower conductance than other univalent salts. The curves are therefore very steep in the figures which deal with KH_2PO_4 , and in view of the fact that this salt induced excretion, the shape of the curves can not be regarded as very significant.

There is no reason to doubt that absorption and excretion of electrolytes take place simultaneously in all culture solutions. The figures accompanying this paper indicate of course only the net result of the two processes at any particular time. It would be very desir-

able to determine the composition of the culture solutions at the close of each experiment, in order to learn the magnitude of excretion into solutions from which there had been a net absorption, and *vice versa*. Thus far, however, we have been unable to make analyses of residual solutions. For the sake of simplicity, we have used the unmodified terms absorption and excretion in the detailed accounts of our experiments, but it should not be assumed that we have ever considered either process to have taken place to the exclusion of the other. Some of the results do indeed indicate that in certain cases the magnitude of excretion is negligible, for at the close of the absorption phase the residual culture solutions have been nearly exhausted of ions.

If a culture solution is of such concentration and composition that absorption by the roots exceeds excretion, the concentration of the solution diminishes from day to day, as long as the vigor of the seedlings remains unimpaired. The length of time that they can live in the dark is, however, conditioned by the reserve materials in the seed. As these materials are depleted the vigor of the seedlings diminishes. After about ten to fourteen days, in the case of *Lupinus albus*, the seedlings weaken, and the absorption phase is succeeded by an excretion phase. The roots rapidly give up their salts to the culture solution and the plants die.

CALCIUM NITRATE. EXPERIMENTS 1 AND 2

In experiment 1 solutions of $\text{Ca}(\text{NO}_3)_2$ ranging in concentration from 20 to $260M \times 10^{-6}$ were used. The difference in concentration between neighboring cultures of the series was $20M \times 10^{-6}$. The cultures were under observation 15 days.

Data covering the concentration changes are shown in figure 1. The units on the axis of abscissas indicate duration in days. The ordinates show the concentrations in gram molecules per 10^{-6} liters of distilled water. The course of the curved lines shows concentration changes calculated in gram molecules of $\text{Ca}(\text{NO}_3)_2$ dissolved in 10^{-6} liters of distilled water. The reader, therefore, can ascertain approximately the concentration of any solution at any time during the experiment and therefore the magnitude of change. The corresponding values of the control experiment in distilled water are represented by the line beginning at zero on the axis of ordinates. It appears that in these solutions of $\text{Ca}(\text{NO}_3)_2$ the roots of *Lupinus albus* lost electrolytes to the medium during the first day regardless of original con-

centration, the loss being in general greater in the weaker solutions than in those more concentrated. The increased CO_2 content of the solutions probably accounts in large part for the apparent loss of salts from the roots. The period of apparent loss to the solution was

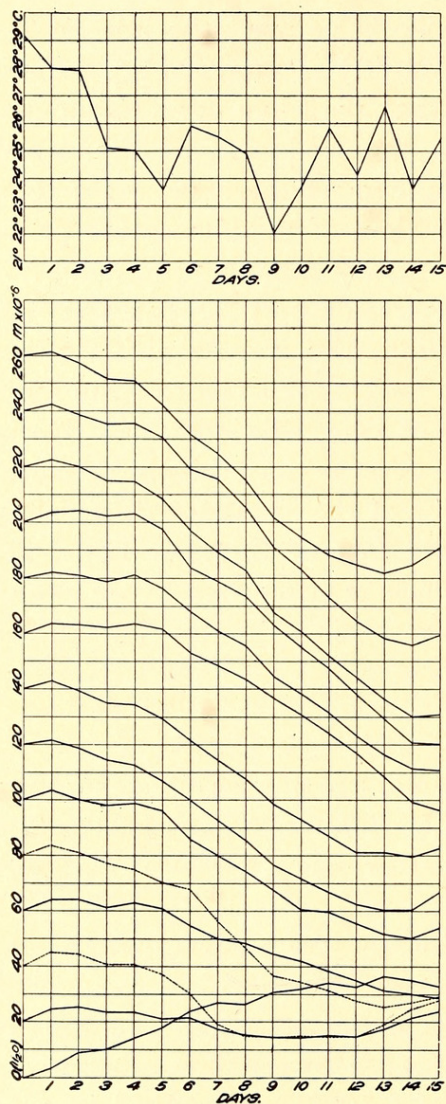


FIG. 1. Curves showing the changes in concentration of the $\text{Ca}(\text{NO}_3)_2$ solutions used in experiment I.

solutions which had concentrations of 40 and $80M \times 10^{-6}$ respectively the roots were able to absorb actively after a period of delay decreasing in length with the increasing concentration of the solutions. After two weeks of absorption both reached a concentration similar to that

followed in the less concentrated cultures (20 to $60M \times 10^{-6}$) by a day during which no clear change took place. In the medium and stronger concentrations (80 to $260M \times 10^{-6}$) absorption proceeded at a gradually increasing rate. Beginning at about the fifth day in a majority of the cultures absorption proceeded at a relatively uniform rate until about the twelfth or fourteenth day, when the conductivities indicated either a slackening of absorption or a predominant loss of ions from the roots to the solution. The loss of electrolytes was probably due to the changes in the cells of the roots caused by approaching exhaustion from a lack of available food. The root system showed little evidence of deterioration but a withering of the etiolated foliage leaves and even of the edges of the cotyledons took place. The hypocotyl sometimes also broke down.

The record of the weaker solutions (20 to $80M \times 10^{-6}$) offers an interesting point. In the most dilute solution ($20M \times 10^{-6}$) the roots seemed to be unable to absorb actively at any time leaving the solution little changed in its net ion concentration. In the

seen in the weakest solution, which may perhaps represent the concentration at which $\text{Ca}(\text{NO}_3)_2$ becomes unavailable to the plants under the given conditions.

The behavior of the distilled water check showed a striking contrast to that seen in the calcium cultures. The roots lost ions with approximate regularity for about 7 days after which the rate of loss decreased for the remaining time. At the close of the experiment the distilled water was equal in its ion content to over $30M \times 10^{-6}$, that is, it was richer in ions than the final concentration of any $\text{Ca}(\text{NO}_3)_2$ solution which had had an original concentration less than $100M \times 10^{-6}$. It will be seen that in general the net absorption in $\text{Ca}(\text{NO}_3)_2$ solutions was considerably greater in the stronger solutions than in the more dilute members of the series, due probably to the fact that there was more material present to be absorbed. The maximum absorption in comparison with the amount of $\text{Ca}(\text{NO}_3)_2$ offered was, as might be expected, highest in the more dilute solutions (20 to $40M \times 10^{-6}$). It seems necessary, if active absorption is to take place, that at least $40M \times 10^{-6}$ $\text{Ca}(\text{NO}_3)_2$ should be present in the solution, and it is much better if two or three times that concentration is present.

Measurements of various dimensions of the seedlings used were made at the close of the experiment, but only the growth of the primary root seemed to show any perceptible relation to modification of the medium. The growth made in distilled water was distinctly poorer than that seen in any of the calcium solutions and in a general way the total growth in length made by the roots was greater as the salt content of the medium increased. In some cases this was not true, but in view of the small number of plants in each culture there is good reason to believe that these departures were due in considerable part to the individual variation of the plants.

In view of the results seen in the experiment summarized in figure 1, it was thought desirable to ascertain the effect of further dilution of the salt and at the same time repeat the observations as far as the lesser concentrations were concerned. Accordingly in experiment 2 a series of thirteen solutions was made up ranging from 8 to $104M \times 10^{-6}$ with a constant interval of $8M \times 10^{-6}$ between adjacent members of the series. The experiment ran seventeen days, and is summarized in figure 2.

The record of these solutions shows the same general features seen in the foregoing experiment. The lupine roots were always

able to make some absorption, leaving even the weakest solution poorer in ions than it was at the beginning of the experiment. In general, net absorption increased with the increase of the original salt content up to a concentration of $40M \times 10^{-6}$. In this and in the more concentrated solutions the maximum absorption varied somewhat but did not advance with the increasing salt content. This seems to mean that the demand for this salt under the conditions to which the plants were subjected was satisfied by a concentration of $48M \times 10^{-6}$.

The growth rate in general increases with the concentration in the more dilute members of the series and reaches a general level which with considerable variation is maintained. This general level is attained at the point of maximum absorption.

CALCIUM SULPHATE. EXPERIMENT 3

Fourteen solutions of calcium sulphate were studied, in concentration ranging from 12 to $168M \times 10^{-6}$, the regular interval between adjacent members of the series being $12M \times 10^{-6}$. The experiment ran seventeen days, during which time great temperature variations were noted.

The curves presented in figure 3 show a very active absorption by the roots in all the solutions, excepting only the distilled water check. As usual, the distilled water extracted electrolytes from the roots until a fairly constant concentration was reached at which excretion was perhaps balanced by the reabsorption of the same ions. The phase of balance between the two processes was followed by the usual increasing leakage of electrolytes from the roots as they approached exhaustion.

In all CaSO_4 solutions from 12 to $72M \times 10^{-6}$ absorption was active, beginning in the upper part of this range on the first day of the experiment. Under the influence of this absorption the ion concentration of the six weaker solutions fell rapidly to a point approaching on about the tenth day that of the distilled water at that time and becoming much weaker in ions toward the close of the experiment than even the distilled water itself. It is probable that in these more dilute solutions the roots absorbed practically all the salts they could and reduced the concentration to the unavailable minimum. This unavailable minimum was represented by a concentration of CaSO_4 from 12 to $18M \times 10^{-6}$. A culture containing 500 c.c. of a $72M$

$\times 10^{-6}$ solution of CaSO_4 was reduced in concentration through absorption to a little over $12M \times 10^{-6}$, and provided four lupine

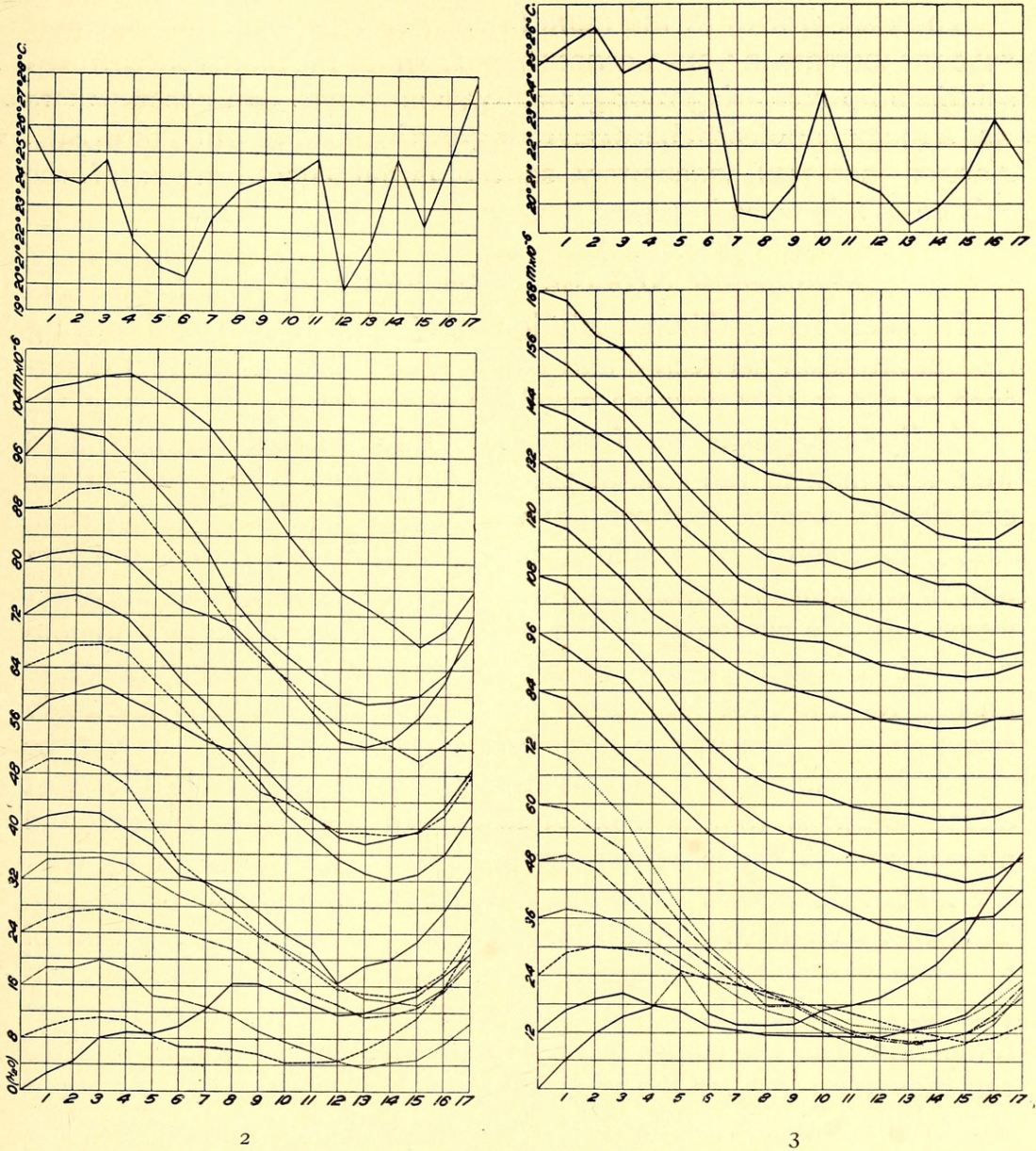


FIG. 2. Curves showing the changes in concentration of the $\text{Ca}(\text{NO}_3)_2$ solutions used in experiment 2.

FIG. 3. Curves showing the changes in concentration of the CaSO_4 solutions used in experiment 3.

seedlings with all the CaSO_4 which they were able to absorb during their short life in the dark. In the cultures which offered an increased

salt concentration the maximum net absorption did not rise, seeming to indicate a surplus of calcium sulphate over the quantity which could be absorbed.

The root growth in the more dilute solutions seemed to increase with the increase in CaSO_4 concentration but in the more concentrated solutions no increasing root growth was apparent. In general there was a rough parallelism between root growth and absorption of CaSO_4 . Neither increased indefinitely as the initial concentration of the culture solution was increased.

MAGNESIUM NITRATE. EXPERIMENTS 4 AND 5

In experiment 4 thirteen solutions of $\text{Mg}(\text{NO}_3)_2$ were used ranging in concentration between 8 and $104M \times 10^{-6}$ with a constant difference of $8M \times 10^{-6}$ between members of the series. In view of the markedly toxic properties of magnesium salts the concentrations used were less than in the case of the calcium salts. The course of the experiment covered fourteen days. Here, as in the $\text{Ca}(\text{NO}_3)_2$ solutions, the roots were unable to absorb electrolytes during the first day in a quantity sufficient to make up for the real and apparent losses. In the weaker solutions (8 to $24M \times 10^{-6}$) the loss preponderated over such possible absorption as may have taken place so greatly for the first four days as to leave the solutions markedly richer in ions than at the beginning of the experiment. It will be noted that the net loss of ions from roots was greater in the most dilute solutions (8 and $16M \times 10^{-6}$). In the more concentrated members of the series, absorption predominated more promptly over loss and at a generally increasing ratio as the concentration increased. This was seen both in the shortening of the preliminary period of apparent loss and in the greater rapidity of absorption during comparable intervals. In general, absorption began to assume its most rapid rate after the elapse of about four days and continued to show this maximum rate for the succeeding seven or eight days. At about the twelfth day, or, in the more dilute members of the series a day earlier, the roots began to lose ions more rapidly than they absorbed them, a reversal of action due probably to approaching exhaustion. This loss rapidly increased and the more dilute solutions at the close of the experimental period were richer in electrolytes than at the beginning.

An instructive accident happened in the culture containing a con-

centration of $80M \times 10^{-6}$. After showing the usual record of absorption for eight days, the solution on the ninth day showed a marked increase in ions. This increase was continued at a rapid and rather uniform rate till the close of the experiment. An examination at that time showed that one plant was injured at a point near the surface of the solution and by the leaching of electrolytes from the dead tissues had furnished a source of contamination.

A study of the growth of the primary roots in the different solutions of $Mg(NO_3)_2$ showed that while in the lower and higher concentrations the rate was about equal to that seen in distilled water, a better growth prevailed in the medium concentrations (32 to $72M \times 10^{-6}$) with a fairly well marked maximum in solutions 48 to $64M \times 10^{-6}$. This region of better growth coincided fairly well with that in which the maximum absorption took place. There were many evidences of toxic action in the stronger concentrations. The great reduction of the laterals, the development on the primary roots of occasional discolored tissue and the frequent appearance of reddish blotches at the bases of the hypocotyls may be mentioned here. These characteristics of Mg action will be again referred to in connection with another experiment involving higher concentrations in which these features come out more clearly.

In experiment 5, a second series of thirteen solutions of $Mg(NO_3)_2$ was used in concentrations lying between 12 and $156M \times 10^{-6}$, with

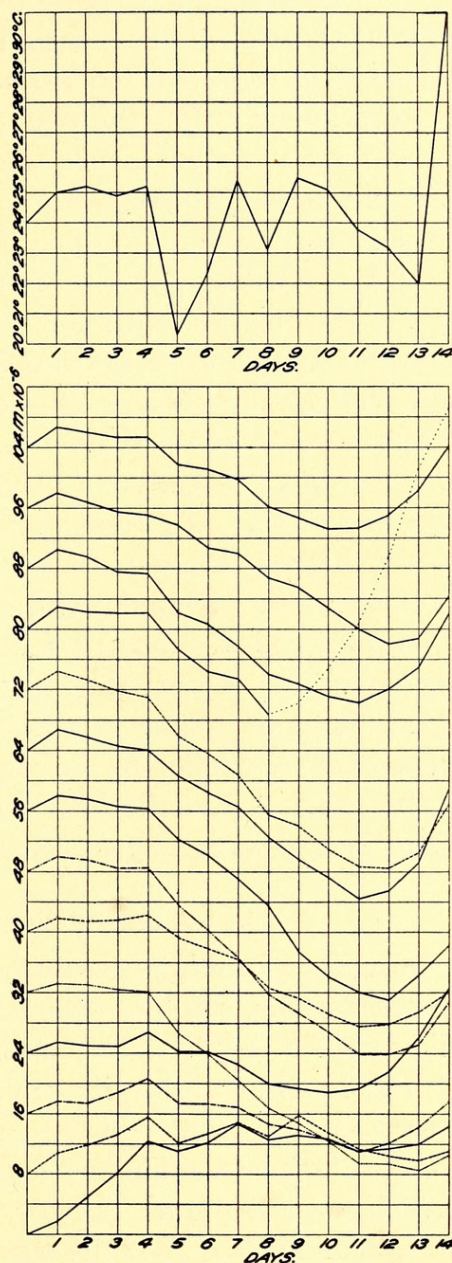


FIG. 4. Curves showing the changes in concentration of $Mg(NO_3)_2$ solutions used in experiment 4.

a constant interval of $12M \times 10^{-6}$ between members of the series. The experiment lasted 16 days. The results are plotted in figure 5.

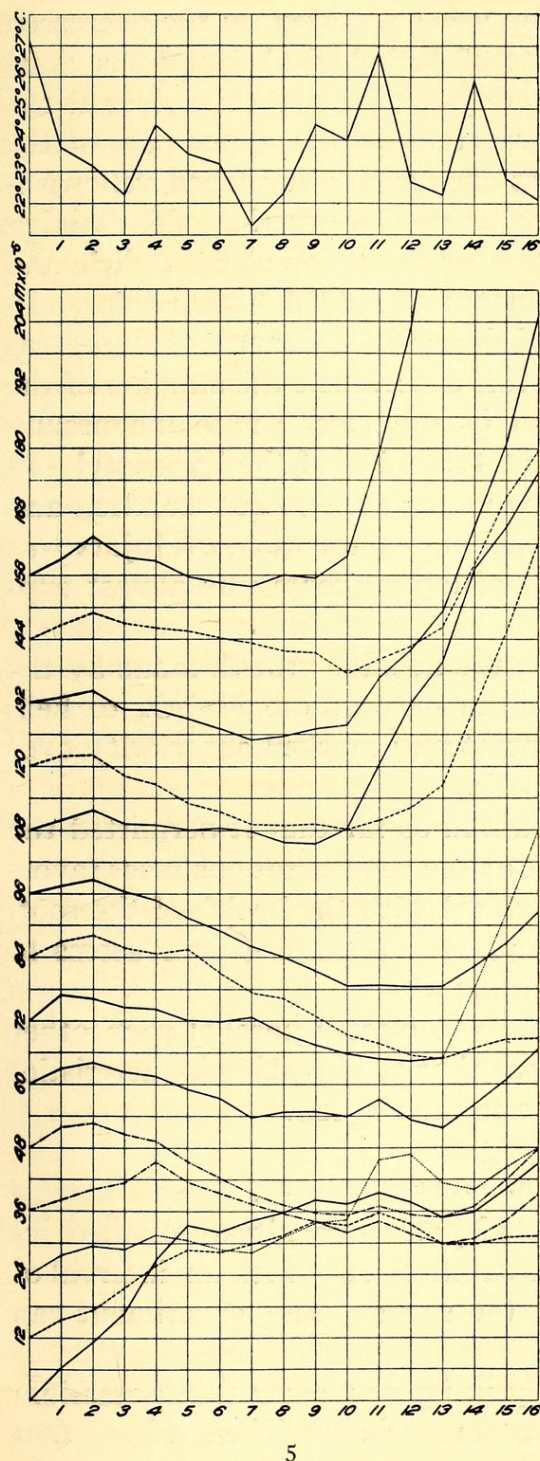
The same general characteristics noted in experiment 4 are again seen in this experiment and need not receive special mention. It will be noted in those concentrations exceeding the maximum salt content of experiment 4 that the toxic action of the salt became more marked, as was seen in the earlier onset of the antemortem leaching phase. The practical disappearance of an absorption phase in solutions about $96M \times 10^{-6}$ probably indicates the same thing.

An interesting point to be noted in both experiments is the reduction of the weaker solutions to a common salt content. In experiment 4 on the tenth and eleventh days the weakest four $Mg(NO_3)_2$ solutions and the distilled water check agreed in having an ion content of about $12M \times 10^{-6}$ calculated as $Mg(NO_3)_2$. Since the $32M \times 10^{-6}$ solution was reduced to $12M \times 10^{-6}$ the net reduction in concentration due to salt absorbed was approximately $20M \times 10^{-6}$. In some of the higher concentrations the reduction was somewhat greater. In experiment 5 a similar situation was seen. On the ninth and tenth days the weakest four salt solutions and distilled water had a like ion concentration, representing in the strongest of these four salt solutions a reduction of about $12M \times 10^{-6}$. This is somewhat greater than the average reduction in the solutions containing a considerable surplus of the salt. Again the best growth and the greatest absorption were found in a general way to coincide.

MAGNESIUM SULPHATE. EXPERIMENT 6

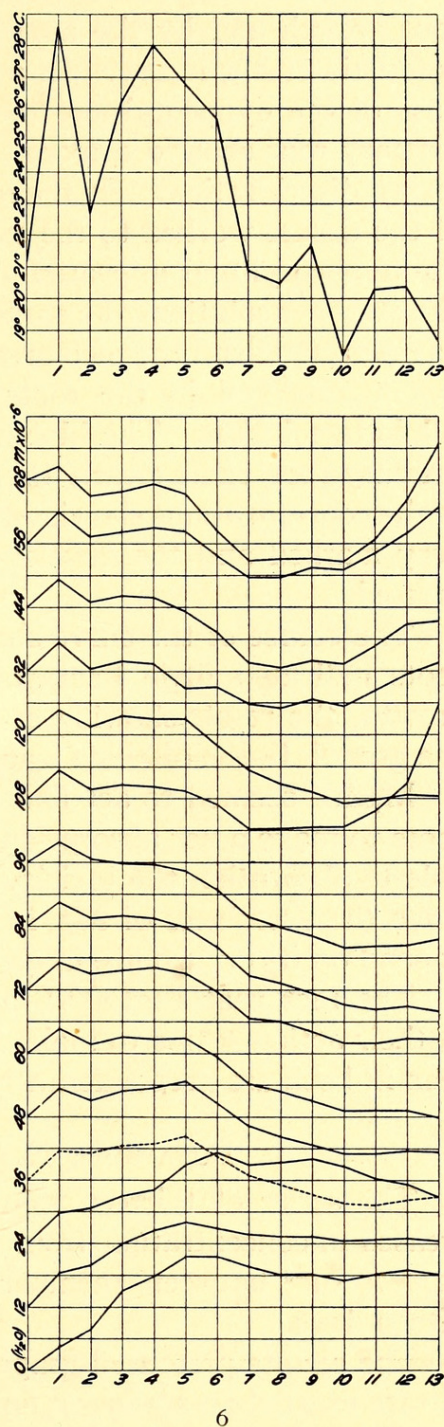
Magnesium sulphate solutions were made up in fourteen different concentrations, running from 12 to $168M \times 10^{-6}$, the regular interval being $12M \times 10^{-6}$. The experiment ran thirteen days.

The results graphically presented in figure 6 show that the action of magnesium sulphate is essentially the same as that of the nitrate. Those solutions having the least salt caused the excretion of electrolytes from the roots. As the concentration increased to somewhat more than $24M \times 10^{-6}$ the roots were able to absorb, this absorption rising somewhat with the increase in concentration until a salt content equal to about $120M \times 10^{-6}$ was reached. Beyond this point, a further increase of salt was not accompanied by any increase of absorption. There was a tendency in the higher concentrations here used toward a reduction of absorption, due probably to the toxic



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FIG. 5. Curves showing the changes in concentration of the $\text{Mg}(\text{NO}_3)_2$ solutions used in experiment 5.



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FIG. 6. Curves showing the changes in concentration of the MgSO_4 solutions used in experiment 6.

action of the salt. This supposition was supported by the decreased root growth and by the appearance of pathological symptoms characteristic of Mg injury. In a mild degree of injury the xylem at the base of the hypocotyl and more especially in the upper part of the primary root showed a more or less extensively developed yellowish-brown discoloration. As the injury became more serious this staining of the tissues worked to the surface near the union of the radicle and the hypocotyl and appeared as a blotch of reddish-brown color. In the stronger solutions the surface of the radicles showed sunken areas having a reddish-brown color. In this experiment the staining of the xylem appeared in the roots even in the most dilute magnesium sulphate solution. The blotching at the union of the hypocotyl and primary root came clearly into view in the $48M \times 10^{-6}$ solution and in the concentrations showing the maximum absorption, the injury was very marked and the development of lateral roots was almost suppressed.

The course of the curve showing the average growth made by the roots indicated little tendency on the part of the $MgSO_4$ to help growth, the result showing at no point any marked superiority over the growth in the distilled water check.

$MgSO_4$ seemed to act like calcium in so far that it permitted the roots to make a net absorption, but at the concentrations most favorable to absorption the toxicity interfered with the health of the root. Thus the usefulness of Mg, in the absence of other $+$ ions, seems to depend on its occurrence in great dilution.

The fact that $Mg(NO_3)_2$ and $MgSO_4$ closely parallel each other in their action seems to make it clear that the specific characteristics seen in both are preponderantly due to the Mg ion.

POTASSIUM NITRATE. EXPERIMENT 7

The series of thirteen solutions of potassium nitrate studied increased in concentration from 32 to $416M \times 10^{-6}$ with an interval of $32M \times 10^{-6}$ between members of the series. The experiment ran fifteen days.

The results presented graphically in figure 7 show that potassium nitrate exerted an action on lupine roots markedly different from that seen in the cases of calcium and magnesium salts. In the weaker solutions (32 to $160M \times 10^{-6}$) the plants behaved very much as they do in distilled water. During the first four or five days the roots

showed a marked loss of electrolytes, this loss decreasing somewhat in magnitude as the concentration of the solution increased. After this preliminary period of steady loss, the roots seemed to gain the ability to resist the action of the solutions and during the remaining ten days maintained themselves without affecting in a decided way the electrolytic concentration of the media. The loss of ions which took place during the first four or five days remained as the net result of the ionic exchange between the solutions and the roots.

In the solutions of higher concentration, a similar period of preliminary loss was seen, diminished, however, in comparison with that seen in the more dilute members of the series. The following recovery was, however, more complete and the roots were often able to absorb sufficiently to bring the solution back to approximately the original concentration. In some cases the absorption phase developed sufficiently to show a net absorption by the roots prior to the setting in of the final leakage. Such a result was seen in the cultures growing in solutions of the original concentrations 224, 228, 320, and 352 $M \times 10^{-6}$. Such a net gain, however, never quantitatively equalled that seen in $\text{Ca}(\text{NO}_3)_2$. The roots of *Lupinus* with difficulty maintained a net absorption in KNO_3 solutions.

This result was reflected, to a great degree, in the growth of the roots placed in these solutions. Poor growth was the rule in the

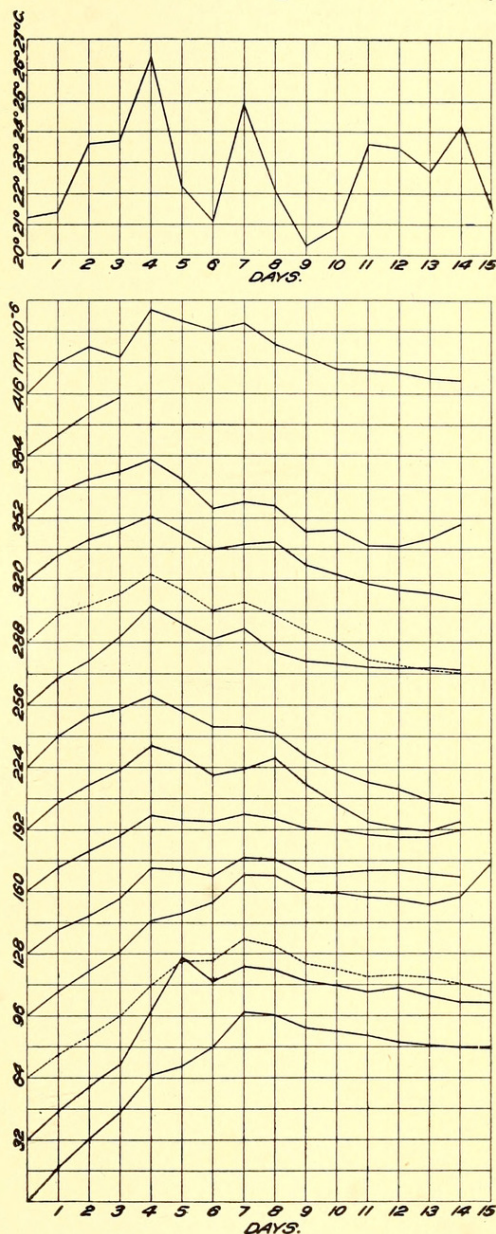


FIG. 7. Curves showing the changes in concentration of the KNO_3 solutions used in experiment 7.

solutions which show a strong extraction of ions from the plant, a slight improvement being seen in those solutions in which a more

active absorption took place. The solutions of KNO_3 seemed furthermore to induce or accompany a general debility in the seedlings. This was shown by the large number of plants that for reasons not obvious deteriorated in the cultures. Individuals developing increased leakage due, perhaps, in part to injury not marked enough to lead to detection and removal were probably largely responsible for the irregularity of the results. The $256M \times 10^{-6}$ solution compared with the neighboring solutions showed an aberrantly high loss of ions from the roots and probably represented the partial failure of one or more individuals in the culture.

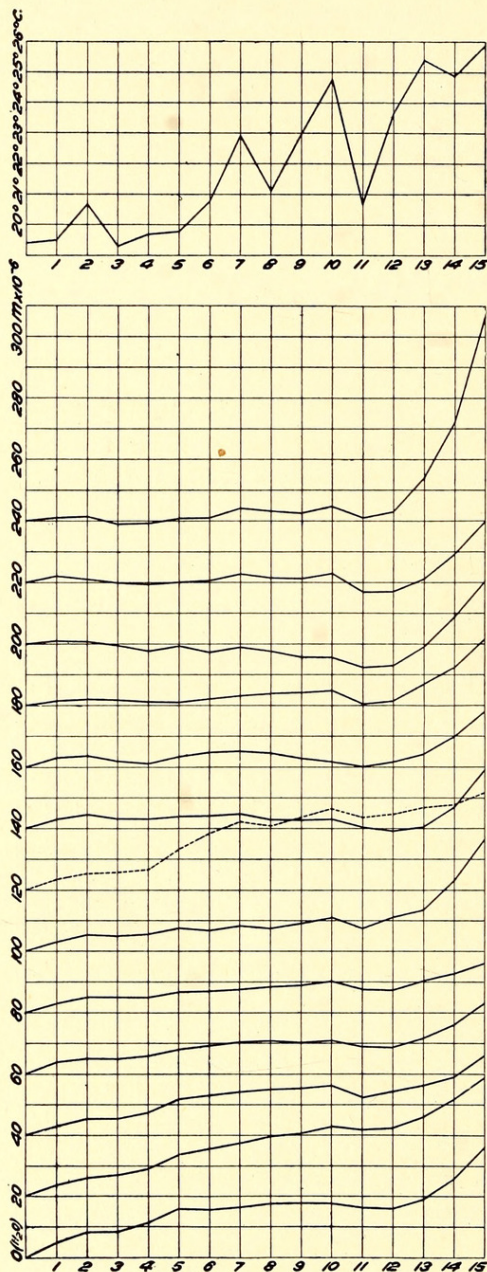


FIG. 8. Curves showing the changes in concentration of the K_2SO_4 solutions used in experiment 8.

POTASSIUM SULPHATE. EXPERIMENT 8

Twelve solutions of K_2SO_4 were made varying in concentration from 20 to $240M \times 10^{-6}$, the concentration interval being $20M \times 10^{-6}$. The experiment ran fifteen days. The results are plotted in figure 8.

Potassium sulphate shows a physiological action very similar to that of potassium nitrate. In the more dilute solutions, 20 to $120M \times 10^{-6}$, the plants lost ions to the medium in a measure approximately like that seen in the corresponding nitrate series. In both

salts an absorption phase appeared in the more concentrated solutions.

In K_2SO_4 a small net absorption was seen in concentrations ranging from 140 to $204M \times 10^{-6}$. The similarity of the records of the more dilute solutions of K_2SO_4 to that of the distilled water check is seen at a glance. In the higher concentrations an equilibrium seemed to be immediately established between the roots and the solution, the result being seen in the slight change in ion concentration which took place until the leakage due to approaching collapse set in.

The growth made by the roots of seedlings grown in these solutions was equal to or less than that seen in distilled water.

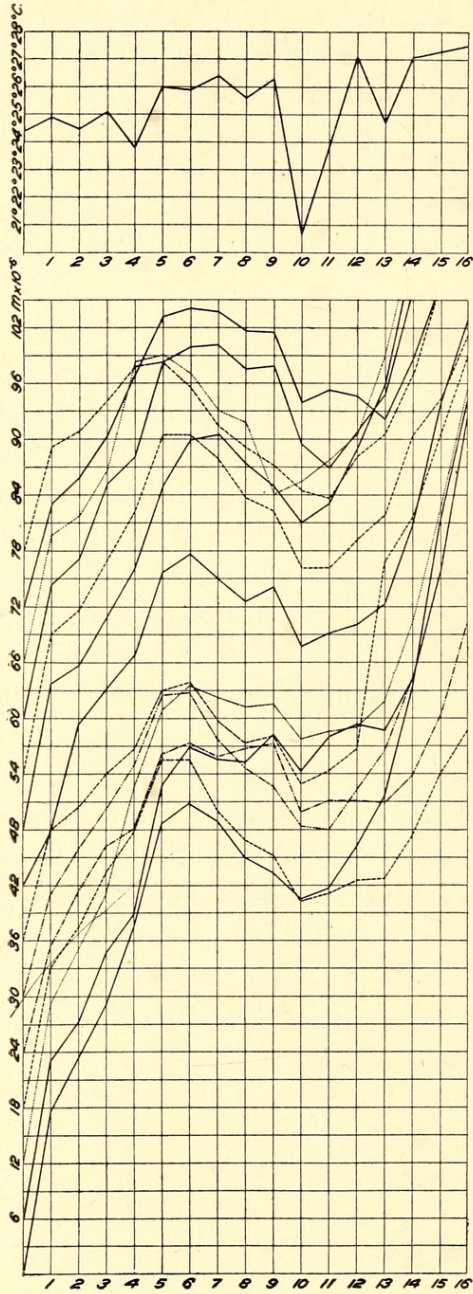
POTASSIUM DIHYDROGEN PHOSPHATE. EXPERIMENTS 9 AND 10

The range of concentration of solutions of potassium phosphate studied lay between 6 and $208M \times 10^{-6}$, the fixed interval between members of the series being $6M \times 10^{-6}$ in experiment 9 and $16M \times 10^{-6}$ in experiment 10. The experiment was continued fifteen days in the stronger solutions, sixteen or seventeen days in the weaker ones. The results are graphically shown in figures 9 and 10.

The striking fact shown by these curves is an almost unrelieved loss of salts by the seedlings in all concentrations tested. During the first four or five days a period of rapid gain in concentration by the medium was seen, followed by a period of slackened loss by the plants. Even in this second period, which corresponds in the salts previously studied to the time of most rapid absorption, the usual result seen is an interval in which a more or less well marked equilibrium was maintained. In 64, 96, 176, and $192M \times 10^{-6}$ solutions, absorption predominated by a narrow margin for several days, but in the other members of the series the loss of ions by the roots was the rule. The final period of loss by the plants due to approaching breakdown was a very marked feature, at times an exaggerated one.

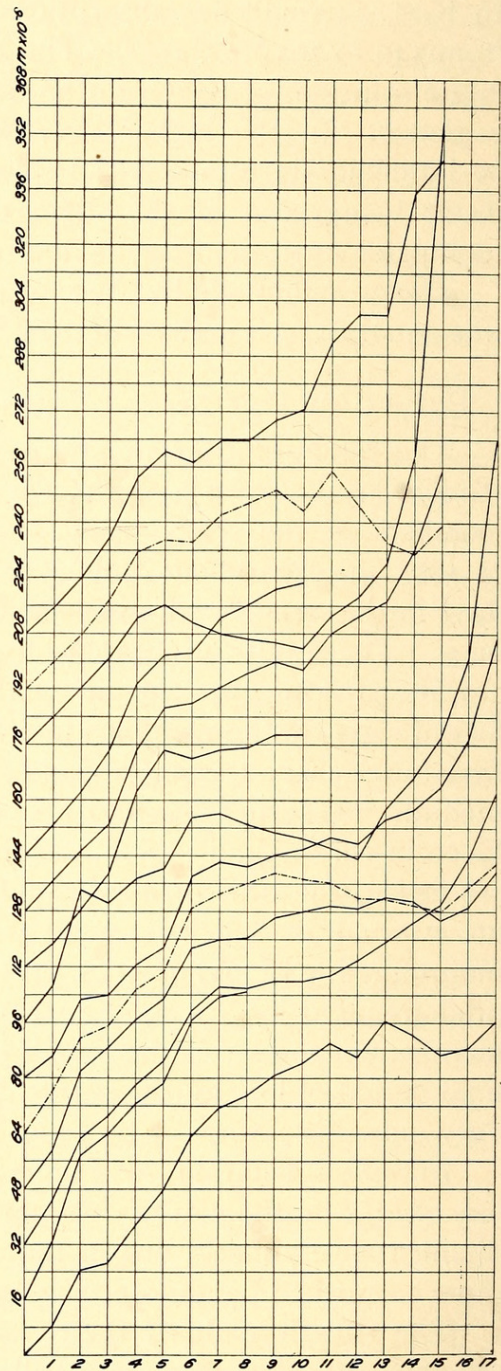
In every solution of the series the result was a marked net loss of ions by the plants. In none was this net loss so great as in the distilled water check, but in the weaker solutions the leaching of the roots seemed to be almost as severe.

The growth made by the roots in no case showed any considerable advance over that made in distilled water. Indeed, the whole picture presented by this salt in the concentrations here studied strikingly resembled that presented by distilled water. Further evidence, showing the harmful action of KH_2PO_4 , was seen in the loss of about 15 per cent. of the plants used in the cultures. In several cases entire cultures had to be abandoned.



9

FIG. 9. Curves showing the changes in concentration of the KH_2PO_4 solutions used in experiment 9.



10

FIG. 10. Curves showing the changes in concentration of the KH_2PO_4 solutions used in experiment 10.

POTASSIUM CHLORIDE. EXPERIMENT 11

The series of solutions of this salt, thirteen in number, covered concentrations ranging from 32 to $416M \times 10^{-6}$ with a regular difference of $32M \times 10^{-6}$ between concentrations. The experiment ran fourteen days. The results are shown in figure 11.

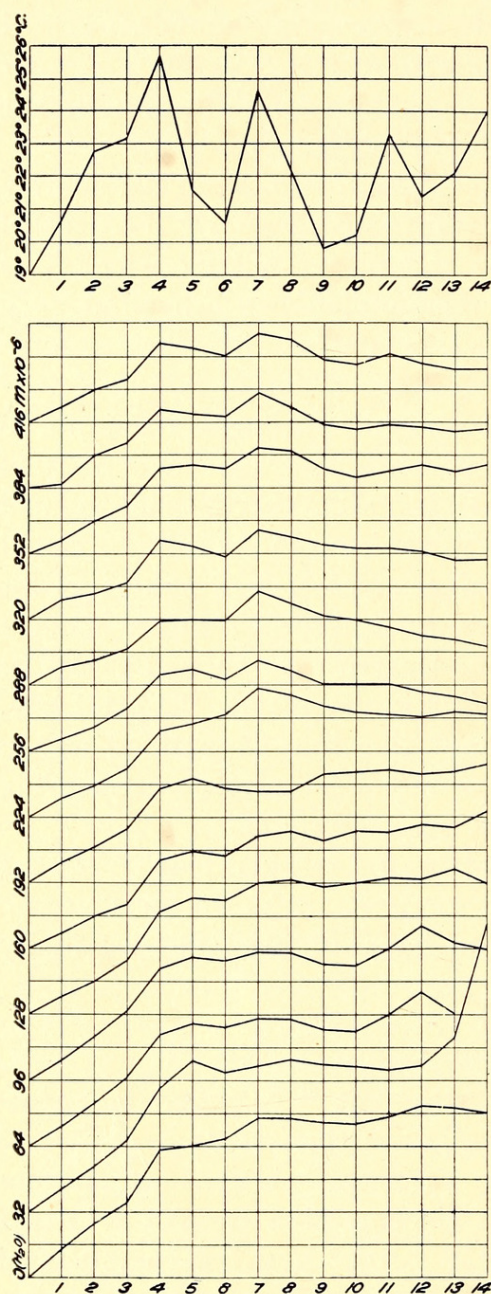
The record of these solutions showed a quite remarkable similarity of behavior regardless of the concentration as is shown by the parallel course of the curves. The result is the more striking when it is noted that the solution curves not only parallel each other but very greatly resemble that of the distilled water control. No clear absorption took place in any solution until a concentration of $224M \times 10^{-6}$ was reached. In this concentration and the stronger ones, up to $320M \times 10^{-6}$, there was slight absorption during the latter part of the period. In general the roots in KCl solutions may be said to have lost heavily for four days after which the net loss of ions still proceeded at a slower rate, at times with the maintenance of an equilibrium for several days. In a few cases slight gains of absorption over leakage were seen but generally the loss preponderated over the gain. In no culture did the total absorption approach in magnitude the total loss. The action of KCl solutions is strikingly like that of distilled water, differing, however, in that the higher members of the series bring about a less marked initial loss of ions from the roots.

The growth of the primary roots showed a marked gain over that in distilled water in but one culture, $128M \times 10^{-6}$. In its effect on the growth of roots, KCl in the concentrations studied acted essentially like distilled water.

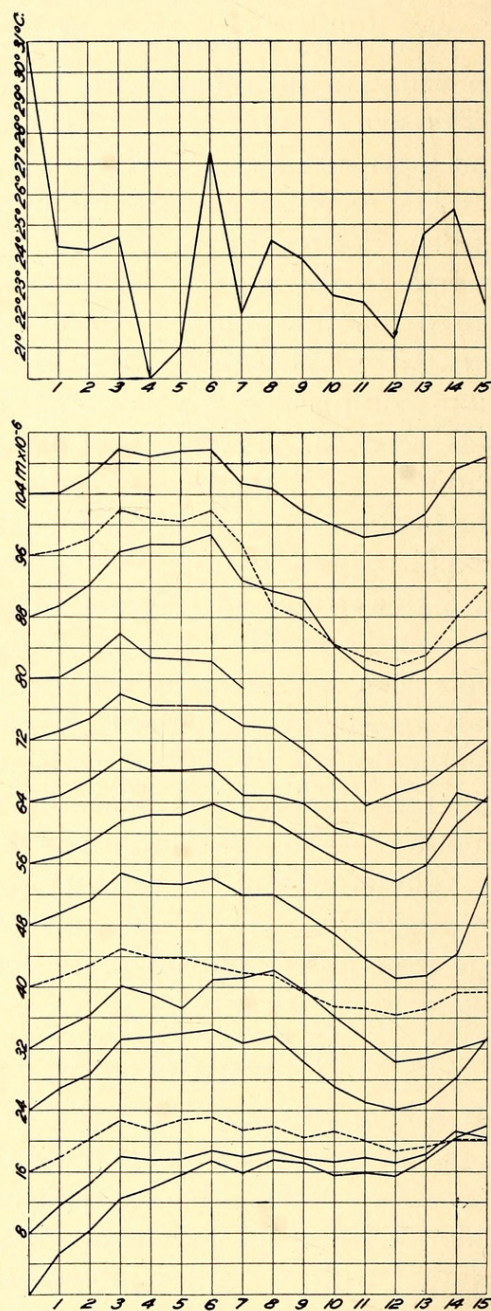
SODIUM CHLORIDE. EXPERIMENTS 12 AND 13

A comparison of the action of Na with that of K under the conditions of these experiments being desired, two experiments were carried out with NaCl. In experiment 12 thirteen solutions of sodium chloride were prepared ranging in concentration from 8 to $104M \times 10^{-6}$ with a regular interval of $8M \times 10^{-6}$ between members of the series. The experiment ran fifteen days. The curves are shown in figure 12.

An inspection of the record of these cultures shows that NaCl is very similar in its action to several potassium salts. After an initial period of three days during which the roots in all solutions gave up ions an absorption phase set in which reached its maximum on the



II



I2

FIG. 11. Curves showing the changes in concentration of the KCl solutions used in experiment II.

FIG. 12. Curves showing the changes in concentration of the NaCl solutions used in experiment I2.

eighth to twelfth day. This absorption phase in all except the more dilute solutions resulted in a very slight net absorption before the final escape of salts due to exhaustion set in. In the more dilute members of the series, 8 to $16M \times 10^{-6}$, the solutions through absorp-

tion came to a level then prevailing in the distilled water control culture, viz., about $20M \times 10^{-6}$. This record recalls most forcibly the situation found in solutions of KNO_3 and K_2SO_4 .

A somewhat similar experiment dealing with this same salt was carried out in a series showing a somewhat wider range of concentrations. Experiment 13 covered 12 dilutions of NaCl ranging from 32 to $384M \times 10^{-6}$, with a regular interval of $32M \times 10^{-6}$ between members of the series. The experiment ran eighteen days. The results are plotted in figure 13.

In this series during an initial period of about three days the solutions increased more rapidly in ions than was the rule during the following ten to twelve days. This second period was marked in the weaker solutions by a poorly developed absorption phase from about the thirteenth to the sixteenth day. The withdrawal of ions, however, was never sufficient to

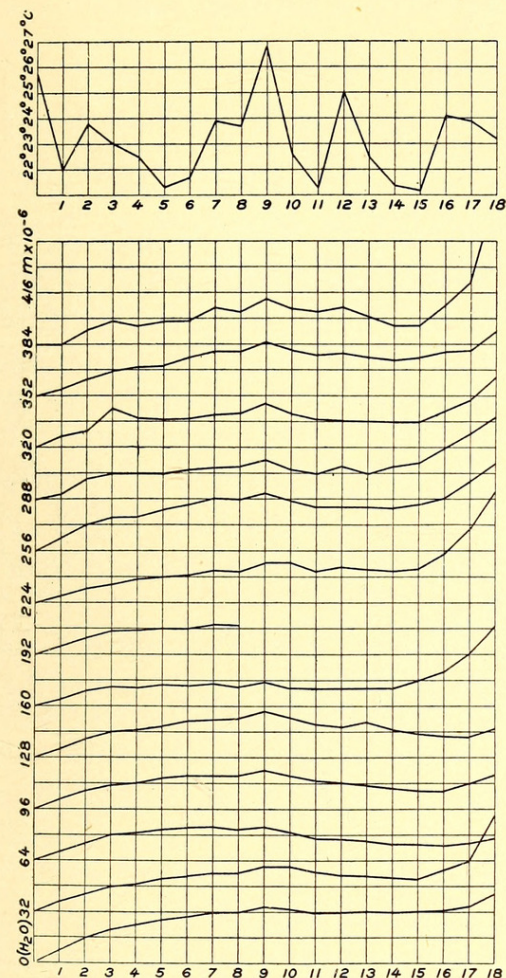


FIG. 13. Curves showing the changes in concentration of the NaCl solutions used in experiment 13.

overcome the previous accessions and in no solution was a net absorption seen, although in no case was the net deficit very great. On the fourteenth to sixteenth day, varying with the individual culture, marked gain in the ion content was seen in nearly all solutions, the losses marking the exhaustion of the vigor of the plant.

The general behavior of this series again suggests that of certain of the potassium salts. The results of these experiments with NaCl

seem to group this substance with those in which root absorption is greatly reduced and to suggest a close parallel between the NaCl solutions and distilled water.

The growth of the roots in the NaCl solutions here tested was depressed to or below the point characteristic of distilled water.

CONCLUSIONS

1. Roots of *Lupinus albus* grown in darkness in distilled water give up their salts to the water at a varying rate until the death of the plants occur through exhaustion of the reserves.

2. KH_2PO_4 and KCl solutions act essentially like distilled water in the concentrations studied by us. Solutions of K_2SO_4 and KNO_3 show a slight absorption phase resulting in a minimal net gain in salts to the plant but otherwise differ little from the phosphate and chloride.

3. Absorption and growth take place in NaCl essentially as in KNO_3 and K_2SO_4 .

4. Solutions of $\text{Mg}(\text{NO}_3)_2$ and MgSO_4 support a slight but clearly developed absorption phase resulting in a net gain in salts to the plant. A net leakage of salts is seen in the more dilute solutions, and toxic action in those of greater concentration.

5. Calcium nitrate and calcium sulphate in all concentrations studied are actively absorbed by the roots and apparently enable the plants to retain possession of the salts already present.

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