

## ABSORPTION OF NUTRIENTS AND PLANT GROWTH IN RELATION TO HYDROGEN ION CONCENTRATION.

By OLOF ARRHENIUS.

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

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During the last few years studies on the effect of hydrogen ion concentration upon growth have given a clue to many hitherto unsolved problems. It would appear that this factor also plays an important rôle in the absorption of nutrient substances. Hoagland (6) in a brilliant investigation has shown that the intake of nutrients depends to a great extent on the pH value of the solution, and Hixon (4) found that the reaction of the nutrient solution affected the salt content and chemical composition of the plant.

This problem is of fundamental importance, especially in relation to the solubility of nutrient salts at different pH values. The author has therefore made some preliminary studies, the results of which are here described.

The experiments were carried out in the Laboratory of Plant Physiology of Harvard University and in the Wolcott Gibbs Memorial Laboratory. I take this opportunity to thank all who have given me assistance in the work. My warmest thanks also go to Professor W. J. V. Osterhout and Professor T. W. W. Richards for their friendly help and great kindness.

Unfortunately it was so late in the year (the experiments ran from the end of September to the end of November) that the best season of growth was passed and therefore only the results of the last month could be used. Large and rapid variations of temperature out of doors caused considerable variations in the greenhouse; some days the temperature range was 30°C., but on the average only 10°.

The experimental technique was as follows: Glass jars holding 1 gallon each were covered with black paper; in order to avoid excessive absorption of heat they were enclosed in white boards. Disks of

galvanized iron netting ( $\frac{1}{4}$  inch mesh) were cut to fit inside the jars. These disks were covered with a layer of paraffin (commercial parawax). Two wires, also paraffined, were fastened on opposite sides of each disk. With a hot wire 100 holes were bored in each disk equally distant ( $\frac{1}{8}$  inch) from each other. In these holes the seeds were placed. 3 liters of the nutrient solution were poured into the jar and the disk was suspended by the wire so that the solution was level with the lower surface of the disk. Then the seeds were covered with filter paper and placed in the dark for germination. After 3 days the filter paper was removed and the cultures left for 1 day in the laboratory and then transferred to the greenhouse. In order to avoid accumulation of carbon dioxide and lack of oxygen the solutions were aerated every day by pressing 2 to 3 liters of air (free from carbon dioxide) through each jar. The reaction of the solution changed considerably and it was therefore adjusted every day by adding acid or alkali to it. The solutions were changed every fortnight and the loss by transpiration measured.

During the first period of growth the germinated seeds were counted every day. After 2 weeks the cultures were thinned so that every fourth or fifth plant was left. The thinning was carried out in accordance with a definite plan, so that it was entirely a matter of chance whether a good or a bad plant was left. In this way any subjective selection was avoided. When plants are grown in any solution, those best adapted to it thrive best. Therefore it is not permissible in such an experiment as this to allow the seeds to germinate in one solution and afterward transfer them to another solution of different composition. Furthermore one should not take a given number of the best in every culture, for this would involve a selection of those best adapted and would give an erroneous result. The thinning must be done quite objectively, without taking into consideration whether the plant appears to be healthy.

When changing the solution every fortnight the length of tops and roots was measured. At the same time 1 liter of the solution was taken out for analysis. After 1 month the number of plants was reduced to 10, and after a fortnight more to 5. When the experiment was finished the plants were dried and roots and tops weighed separately.

As culture solution a Hoagland (6) solution (0.78 atmosphere) was used. This is supposed to imitate a rich soil solution. The hydrogen ion concentration was changed by adding NaOH or HCl. These were chosen because of the relatively unimportant rôle their ions play as plant nutrients.

After use as nutrient media for a fortnight the solutions were analyzed for K, Ca, Mg, PO, NO<sub>3</sub> and SO<sub>4</sub>, using a new method of analysis by employing the centrifuge (1). As test plants, wheat and radish were used. In Table I certain results of the experiment are shown. The percentage of seeds germinated is found under germina-

TABLE I.

	pH 3	4	5	6	7	8	9	10
<b>Wheat.</b>								
Germination, <i>per cent.</i> . . . . .	68	67	96	78	92	60	53	85
Duration of life, <i>per cent.</i> . . . . .	0	40	90	78	90	42	42	72
Rate of germination. . . . .	0.27	0.32	0.33	0.35	0.43	0.20	0.22	0.24
Dry weight of roots, <i>mg.</i> . . . . .	0	23	58	22	30	54	56	28
“ “ “ tops, <i>mg.</i> . . . . .	0	120	233	88	96	108	112	104
<b>Radish.</b>								
Germination, <i>per cent.</i> . . . . .	15	22	24	29	29	31	33	35
Duration of life, <i>per cent.</i> . . . . .	0	0	12	15	22	15	26	21
Rate of germination. . . . .	0.02	0.03	0.05	0.04	0.05	0.07	0.05	0.05
Dry weight of roots, <i>mg.</i> . . . . .			7	10	31	18	21	7
“ “ “ tops, <i>mg.</i> . . . . .			38	68	87	73	113	63

tion per cent. Under duration of life is given the per cent of seeds living after 2 months. The rate of germination is calculated as follows: Suppose that twenty-five seeds are in the culture; after 2 days eight have germinated; after 3 days, five more; after 4 days, ten more; and between the 5th and 9th days none germinate. One divides the number of seeds germinating each day by the current number of that day and adds the results. In order to get the average this sum is divided by the total number of seeds. For the example mentioned above, one thus gets:

$$\frac{\frac{8}{2} + \frac{5}{3} + \frac{10}{4}}{25} = 0.32$$

If all seeds had germinated on the 1st day the result would be 1; if on the 2nd, 0.5; if on the 3rd, 0.33, etc. In this way the rate of germination is expressed in a more uniform and logical manner than hitherto. The table shows that the seeds germinate quite well within very wide limits; the rate of germination is more influenced by higher concentrations. This is in full agreement with the statement of Olsen (7) that the quality of germination is more dependent on the pH of the substrate than the quantity is. The determinations of dry weight give, when plotted against pH, a curve with two maxima. This seems to be a general rule for plant growth (2), as first observed by Hixon (4) and verified by later experiments. The investigations of Olsen (7) and Hoagland (5) do not speak for or against this type of curve since they have both been working on the acid side and have never gone over to the alkaline. This is because Fe, Ca, Mg and  $\text{PO}_4$  are precipitated by increasing alkalinity. Figures on the solubility of such salts are very scarce and inaccurate, but it may be mentioned that the most insoluble calcium phosphate (the tribasic one) is soluble in about 100 to 150 parts per million (9), and as the concentration of Hoagland's solution is about 200 there will be a precipitate formed, but enough to satisfy the needs of the plant for several days will remain in solution, and as soon as part of it is used up by the plant the precipitate will be partly dissolved. It therefore seems that in this experiment the solubility effect plays a very unimportant rôle.

From Table II and Figs. 1 to 6 it is easily seen that the intake of salt is very strongly influenced by the hydrogen ion concentration. But there is no correspondence between maximal salt absorption and maximal growth of the plants as measured by weight. The curves show that, except in the case of K with radish and  $\text{PO}_4$  and Mg with wheat, the minimum of growth corresponds approximately to the maximum absorption of salt and that in all cases, except in that of Mg with wheat and perhaps  $\text{NO}_3$  with radish, the maxima of growth are correlated with minima, or nearly so, of the absorption curves. This, which at first glance is rather surprising, harmonizes with the fact, which has been observed by a number of investigators, that salts are absorbed in greater amounts in solutions unfavorable to growth than in favorable solutions (*cf.* Waynick (11)). The most

recent investigations on this subject are those of Osterhout (8) and Brooks (3). Brooks, investigating the permeability of *Nitella* by making spectroscopic tests of the cell sap, found that the intake of salt (in her experiments Li, Sr, and Cs were used) was greater in

TABLE II.

	Millionths of a gram-equivalent absorbed daily per plant.						
	pH 4	5	6	7	8	9	10
<b>Ion.</b>							
K.....	4.3	2.9	4.3	0	—	1.8	0
Ca.....	0	1	37	—	25	25	3
Mg.....	26	30	13	0	0	4	13
PO <sub>4</sub> .....	19	4	8	21	10	8	5
NO <sub>3</sub> .....	66	10	32	29	0	4	4
SO <sub>4</sub> .....	23	16	20	15	0	2	15
<b>Wheat.</b>							
Water, absorbed daily per plant, cc.....	3.1	7.3	2.5	2.7	4.8	3.1	3.1
Dry weight of roots, mg.	23	58	22	30	54	56	28
“ “ “ tops, mg.	120	233	88	96	108	112	104
K.....		22	0	11	29	21	7
Ca.....		29	1	11	23	0	0
Mg.....		44	26	27	16	18	18
PO <sub>4</sub> .....		22	16	7	35	15	17
NO <sub>3</sub> .....		8	13	22	22	23	0
SO <sub>4</sub> .....		4	25	17	34	29	20
<b>Radish.</b>							
Water absorbed daily per plant, cc.....		1.9	3.2	3.1	4.0	3.6	2.4
Dry weight of roots, mg.		7	10	31	18	21	7
“ “ “ tops, mg.		38	68	87	73	113	63

The figures represent the average for 1 month (the last two columns for 2 weeks).

unbalanced than in balanced solutions. Similarly, we may suppose that in the solutions whose pH is most favorable for growth, the normal permeability of the plant is preserved (just as in a balanced solution) and that in consequence less salt is taken up than in less favorable solutions where the permeability has been abnormally increased. On the other hand some investigators (True and Bartlett (10)) state that the greatest absorption of salts occurs in the most

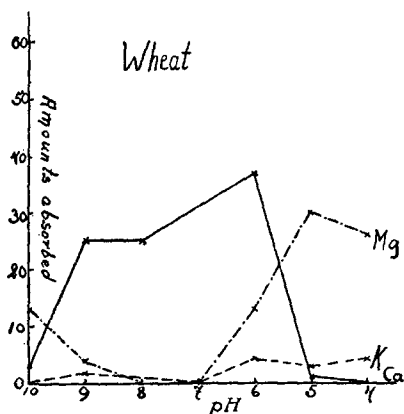


FIG. 1.

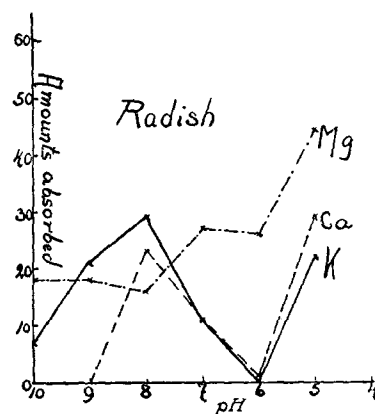


FIG. 2.

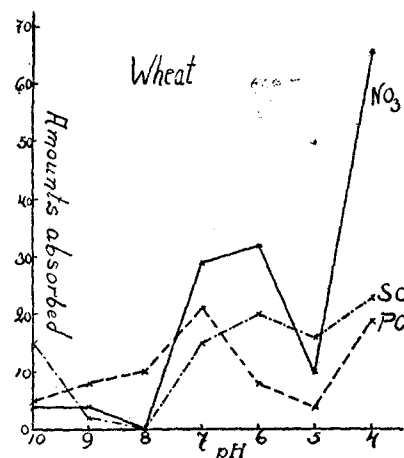


FIG. 3.

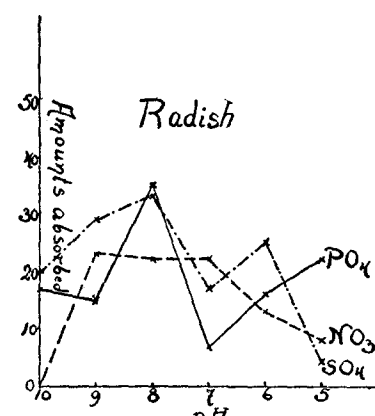


FIG. 4.

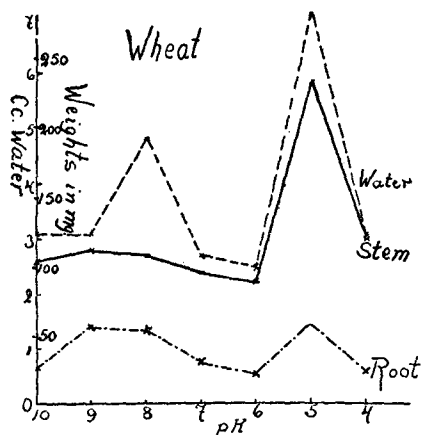


FIG. 5.

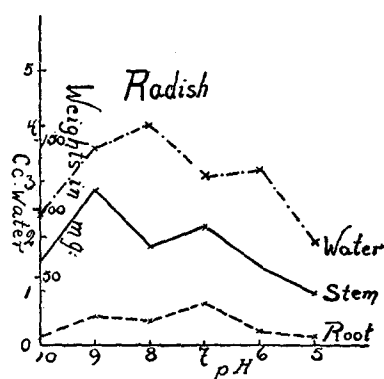


FIG. 6.

The abscissæ denote pH. The ordinates in Figs. 1 to 4 denote amounts absorbed (in millionths of a gm. equivalent); in Figs. 5 and 6 the figures at the left of the vertical line denote average daily absorption of water per plant, while those at the right denote the dry weights of stem and root.

favorable solutions. The discrepancy may be due in part to the fact that in the experiments of Waynick and the author, the concentration of nutrient substances was kept practically constant and that the pH was varied, while in the experiments of True and Bartlett this was not the case. In addition the technique and methods of measurement were entirely different.

The water is taken up quite independently of the salts, but there is a good agreement between growth and the intake of water. This is probably due in part to the increased transpiration when the leaf surface increases.

The great increase in absorption of anions by wheat in solutions of pH 4 may be explained as the result of injurious action on the roots which favors penetration, and to chemical combination, possibly due in part to the formation of protein salts, since the reaction of the solution lies on the acid side of the isoelectric point of most proteins.

Except in this case there is no selective absorption by which to explain the changes in reaction, as the result of which the solution tends to approach a point near pH 6.

#### SUMMARY.

The absorption of nutrients depends to a large extent on the reaction of the substrate. At maximal growth the intake of salt is at minimum. Different ions are very differently affected. The intake of water is independent of the absorption of salts.

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