CHANGES IN HYDROGEN-ION CONCENTRATION PRODUCED BY GROWING SEEDLINGS IN ACID SOLUTIONS[1]

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INTRODUCTION

The importance of the reaction (the active acidity or alkalinity) of the medium in plant life, as well as in biological processes in general, has long been recognized. Studies in this field, however, have gained an impetus with the introduction of improved and delicate methods for estimating hydrogen-ion concentration.

Taking advantage of the ease of manipulation which characterizes these methods, agricultural investigators and botanists have secured a great many data on the relation between plants and the reaction of the medium in which they grow. Much of the recent work, undertaken for the purpose of establishing fundamental principles, has been conducted with nutrient solutions of known composition and with seedlings under conditions involving the least interference from unknown disturbing factors.

Most of the investigations thus far reported have dealt primarily with the effect of the reaction of the medium on plant growth, their ultimate goal being the determination of the specific optimum reaction of the medium for every cultivated plant. Only a few investigators have attacked the problem from the opposite side, studying the effect of the plant on the reaction of the growth medium. This side of the problem, however, is of the highest importance, as it may throw light on the causes of soil acidity under natural conditions, a knowledge of which will greatly facilitate the study of the means of controlling the reaction of the soil under cultivated plants. The work here reported was designed primarily to study the effect of plant growth on the medium.

PREVIOUS WORK

Only a few investigators whose work has a direct bearing on the subject matter of this article will be quoted here.

In 1904 Veitch (*11*) [2] reported the effect of several kinds of plants on the reaction of the soil. In six years oats followed by buckwheat decreased the "total apparent acidity," as determined by the Veitch method (*10*), of nearly all the soils, some of the soils originally acid giving an alkaline reaction. On the other hand, beans followed by

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[2]Reference by italic numbers is to the literature cited on page 217.

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buckwheat during the same period increased the "total apparent acidity" of the soils used.

Breazeale and Le Clerc (*3*) found that growing wheat seedlings made a sodium nitrate solution alkaline, while solutions of potassium chlorid and potassium sulphate became acid under the same conditions.

Of the investigators using the more recent methods for determining active acidity and alkalinity, Jones and Shive (*7*) studied the effect of wheat seedlings on the hydrogen-ion concentration of a number of nutrient solutions. Wheat seedlings, after having been grown for five weeks in "Shive's Best" solution, were transferred to the nutrient solutions. The initial hydrogen-ion values of these solutions were recorded, as well as the changes resulting after the seedlings had been in contact with the nutrient for 24 and 52 hours. Invariably the changes were in the direction of decreased acidity. The initial reactions of most of the solutions ranged from P_H 4 to P_H 4.8. At the end of the experiment the reactions ranged from 5.3 to 6.1. Two of the solutions the initial reaction of which had been almost neutral remained practically unchanged under the same conditions.

Hoagland (*6*), working with barley and several varieties of beans, found that "in every instance, without an exception, nutrient solutions with an initial acid reaction reached approximately neutral reactions, varying from 6.1 to 7.2, after contact with the plant roots for varying periods of time."

Conner and Sears (*4*), while studying the effect of aluminum salts on plant growth, also found that nutrient solutions with an initial acid reaction tend to become less acid in contact with growing rye, barley, and popcorn seedlings.

Arrhenius (*1, p. 81*) reported that plant roots change the reaction of the medium, but that the direction of the change depends on the plant used. Rye brought nutrient solutions of original P_H values 3 and 9 to P_H 5.8; peas brought nutrient solutions of original P_H values 3 and 8 to 4.5; and corn brought nutrient solutions of original P_H values 3 and 7.5 to 6.5.

Later the same author (*2*) studied rice in like manner. Acid reactions in the nutrient solution used were obtained by adding hydrochloric acid and alkaline reactions by adding sodium hydroxide. In all cases the growth of the rice plant brought the reaction to P_H 6.2.

On the other hand, Olsen (*8*) reports that the kind of plant used does not affect the direction in which change of reaction takes place. He concluded that the direction depends primarily on the source of nitrogen in the nutrient solutions. When ammonium chlorid or nitrate is used, all 12 plant species tried caused the solutions to become more acid, although some plants produced the change more rapidly than others. When sodium nitrate was used, however, the solutions uniformly became more alkaline.

Results obtained in the Bureau of Chemistry (Table I) show that factors other than those given by Arrhenius and Olsen (the kind of plants and source of nitrogen) affect the direction of the change in reactions produced in nutrient solutions under the influence of growing seedlings.

TABLE I.—*Changes produced by wheat seedlings in hydrogen-ion concentration of a nutrient solution as affected by its concentration and its initial reaction* [a]

Concentration of solution.	Reaction.		
	Initial.	After 1 day.	After 3 days.
	P_H.	P_H.	P_H.
Undiluted	5.5	5.4	5.2
Do	5.1	4.8	4.6
Diluted 5 times	5.5	5.2	4.1
Do	5.1	3.9	3.6

[a] The acidity data are reported in this and the other tables in the P_H system, not because this system is believed to be the best for the purpose, but because other workers are using it and its use facilitates comparison of these results with theirs.

The nutrient solution used had the following composition:

	Gm.
Calcium nitrate	2.7
Di-potassium phosphate	1.5
Magnesium sulphate	.6
Potassium chlorid	.75
Ferrous sulphate	.01

Twenty wheat seedlings were used for each culture. They were about 4 days old when transferred from tap water to the solution. The nutrient solution was used in two concentrations—full strength and diluted five times. The initial reaction of the full-strength solution, expressed in the P_H system, was 5.5. The other initial reactions were produced by the addition of hydrochloric acid. Variations in the changes of reaction were obtained while using the same plant and solutions of the same composition. The changes were clearly affected by the initial concentration of the nutrient solution as well as by its initial reactions. The general tendency toward increasing acidity, it appears, was due to the use of very young seedlings, most of the investigators cited having worked with seedlings of more advanced age than those used here. In its present phase, however, this investigation deals primarily with the causes of which the changes under discussion are the result.

Very little work has been done to determine the causes of the changes in reaction which occur in nutrient solutions under the influence of growing seedlings. Arrhenius (*1*, *2*) assumed that these changes are due to root excretions which are regulatory and adapt the reaction of the medium to the needs of the plant. He did not, however, bring any evidence to support this assumption. His finding that the reaction of the soil in immediate contact with roots is different from its average reaction in the same vicinity does not prove that the change is due to neutralization. Selective absorption, which is the alternative, would explain the observations just as well.

Breazeale and Le Clerc (*3*), and Hoagland (*6*) also, concluded on the basis of chemical analyses that the changes of reaction produced by growing seedlings in the medium of growth are due to selective absorption. There is, however, some question as to the reliability of direct chemical analysis in dealing with the minute quantities involved, for instance, in a change from P_H 5.6 to P_H 6.8, as was the case in Hoagland's experiment.

EXPERIMENTAL WORK

PROCEDURE

An indirect method was used in this investigation. Only two explanations of the changes which take place in media under the influence of growing seedlings seem possible—neutralization by root excreta and selective absorption.

In the case of neutralization, the effect produced by the growing seedlings should be independent of the kind of acid used, as long as the initial hydrogen-ion concentration and the dissociation constants are the same. In the case of selective absorption, however, the effect of the seedlings in decreasing acidity should depend upon the chemical composition of the acid used. For instance, it would seem that, other factors being equal, the rate and absolute quantity of diminution in acidity will be greater in solutions of nitric acid than in solutions of hydrochloric acid, since nitrogen is a more essential element of plant food than chlorin. Accordingly, seedlings were grown in solutions of several acids of definite initial hydrogen-ion concentrations, and the changes in active acidity of these solutions were compared at intervals. It is assumed that the principles which govern hydrogen-ion concentration phenomena are essentially the same in solutions of pure acids and alkalies as in more complex nutrient solutions with an acid or alkaline reaction.

Only distilled water solutions were employed, as the use of nutrient solutions with the acids would have led to complications likely to interfere with a clear interpretation of the results. For instance, Conner and Sears (*4*) added hydrochloric, nitric, sulphuric, and phosphoric acids, respectively, to a Tottingham solution. As this solution contains phosphates, the addition of a strong acid would naturally cause liberation of phosphoric acid to an extent corresponding to equilibrium relations. Consequently these authors investigated largely phosphoric acid.

Another source of complication resulting from the use of a nutrient solution in this connection would be the change in its composition caused by the feeding activities of the seedlings, with the resulting establishment of new equilibria between the elements. Using the present method, practically only two factors need to be reckoned with—the seedlings and the kind of acids.

PREPARATION OF WATER CULTURES

Wheat seeds were germinated on large perforated aluminum disks floating in tap water, and the seedlings were grown there until they were about 2 inches high. Glasses of approximately 225 cc. capacity containing tap water were covered with paraffined paper perforated with holes smaller than the size of average wheat seeds. The rootlets of the seedlings were then introduced through these holes into the glasses, so that the seeds and plumules rested on the paraffined paper without coming in contact with the liquid media. The seedlings were grown in tap water for about two days to allow good root development and then for a day in distilled water before they were finally transferred to the experimental solutions.

When plants grow in the soil, the seeds are in contact with the same medium as the seedlings, and they may participate in the changes in reaction produced in the medium. In fact, Rudolfs (*9*) found that ungerminated seeds changed the initial reaction of single salt solutions. As it was the intention to limit this study to the changes produced by the metabolic processes of growing seedlings, however, this procedure, by which the prevention of contact between seeds and the experimental solutions was assured, seemed best. This procedure also made it possible to grow more seedlings in a single culture than the cork method generally used in studies of this nature.

CHANGES OF REACTION IN SOLUTIONS OF VARIOUS ACIDS

The salts of the inorganic acids selected for this experiment are commonly found in soils and are used as fertilizers. The elements which enter into their composition have various functions in plant life and are present in different quantities in plant substance. Their quantitative order is: Nitrogen, phosphorus, sulphur, and chlorin. Functionally, chlorin is considered the least important. A certain number of organic acids were used for the sake of comparison. The experiment was run in duplicate. Samples for analysis were pipetted out through a hole made in the paraffined paper cover. The P_H values were determined colorimetrically. The checks usually were very good. The figures in the tables represent in the majority of cases averages of two determinations. Five seedlings per culture were used in this experiment. The initial reactions of the acid solutions were P_H 4 and P_H 3.

Of the inorganic acids with an initial P_H value of 4, nitric acid decreased most in acidity (Table II). The differences involved were small but consistent, and reappeared when the solutions were renewed. The value of P_H 5, obtained twice in the nitric acid solution, indicates that practically all the acidity attained by the addition of the acid was eliminated, as the untreated distilled water used had an acidity of about P_H 5.3, owing to the presence of carbon dioxide. The results with the inorganic acids of the initial P_H 3 series are inconclusive, owing to the small size of the changes produced, which makes the observations more subject to experimental error.

TABLE II.—*Changes of reaction produced by growing wheat seedlings in solutions of acids*

Acid.	Reaction of solution having an initial P_H of 4.				Reaction of solution having an initial P_H of 3 after 9 days.
	After 1 day.	After 2 days.	After 3 days.	After 10 days.	
	P_H.	P_H.	P_H.	P_H.	P_H.
Hydrochloric	4.50	4.70	[a] 4.65	[b] 4.50	3.0
Nitric	4.70	5.00	[a] 4.90	[b] 5.00	3.1
Sulphuric	4.65	4.70	[a] 4.70	[b] 4.75	3.1
Phosphoric	4.60	4.80	[a] 4.80	[b] 4.70	3.1
Formic	4.65	[a] 6.10	[a,c] 6.10	6.40	6.4
Acetic	4.20	4.50	5.55	6.50	3.1
Oxalic	4.80	[a] 6.10	[a,c] 6.10	[b] 6.40	6.4
Succinic	4.00	4.40	4.90	6.40	3.0
Benzoic	4.00	4.20	4.95	6.45	3.0
Phthalic	4.00	4.00	4.60	4.50	3.0

[a] Solution renewed after this reading was obtained. [b] Seven-day contact. [c] One-day contact.

The changes which occurred in the organic-acid solutions may have been due partly or wholly to microbiological activity, as it was impracticable to keep the solutions sterile. However, oxalic and formic acids, which have the highest dissociation constants, were acted upon to a greater extent than the other organic acids, especially those in the P_H 3 series.

EFFECT OF NUMBER OF SEEDLINGS ON CHANGE OF REACTION

In order to bring out more clearly the differences in the behavior of the individual acids, the foregoing experiment was repeated, using a larger number of seedlings. It was run in duplicate and in two series, one with 10 and the other with 20 seedlings per culture, and was confined to the inorganic acids.

The relative behavior of these acids (Table III) was the same as in the previous experiment. In a general way the rate of response was proportional to the number of seedlings with both of the initial reactions.

In the 20-seedling series, with an initial value of P_H 4, the difference in behavior between nitric acid and the other acids appeared only after the solutions had been renewed twice. At this period, however, the difference between the decreased acidity of the nitric-acid solution and that of the other acids was much more pronounced than in the previous experiment.

In the solutions having an initial P_H 3 value, nitric acid was again more affected by the action of the seedlings than the other acids. Numerically the changes in total values and the differences are small, but quantitatively they are larger than those which took place in the solutions with the initial P_H 4 value. Taking the hydrogen-ion concentration of pure water as a unit, as suggested by Wherry and Adams (*12*, *13*), the decrease in acidity, for example, from P_H 3 to 3.1 would constitute a loss of 2,000 units per liter, while the entire decrease in acidity from 4 to 7 would be only 1,000 units. The fact that losses in acidity designated by the same P_H numerals vary in actual magnitude, depending upon the P_H range in which they occurred, is not always realized. Thus, Conner and Sears (*4*) believed that greater decreases in acidity were produced by growing seedlings in solutions of phosphoric acid with an initial hydrogen-ion concentration of P_H 3.9 and 4.2, which were reduced to 6.3 and 6.4, than in solutions of the same acid with an initial hydrogen-ion concentration of P_H 3.2 and 3.6, which came down to 3.5 and 4.1. Actually, however, the case is just the reverse. Figured on the same basis, the first two transformations involve losses of 1,245 and 625 units, while the last transformations involve losses of 3,150 and 1,700 units.

Nevertheless, it is significant that, while in the solutions of the lower hydrogen-ion concentrations in these experiments, as well as in those of Conner and Sears (*4*), the acidity originally present was practically exhausted, in the case of the higher concentrations the action of the seedlings seemed to have stopped while appreciable amounts of acid were still left in the solutions. But the seedlings also lost their power to reduce acidity in the solutions of the lower initial hydrogen-ion concentrations of these experiments when they were renewed several times. Evidently there are certain limits to the absolute quantities of acid upon which seedlings can act. Within these limits, however, nitric acid was more subject than the other acids to that action of the seedlings which is responsible for decreasing acidity.

TABLE III.—*Effect of number of wheat seedlings on change of reaction produced in inorganic acid solutions*

Acid.	Initial P_H.	Reaction with 20 seedlings. After 1 day.	After 2 days.	After 4 days (2-day contact).[a]	After 5 days (1-day contact).	After 6 days (2-day contact).	After 10 days (1-day contact).	Reaction with 10 seedlings. After 1 day.	After 2 days.	After 4 days.	After 5 days (1-day contact).	After 6 days (2-day contact).	After 10 days (6-day contact).
Hydrochloric	4.0	4.9	[b]5.05	[b]4.7	4.0	[b]4.0	4.4	4.7	4.8	[b]4.9	4.0	4.0	4.3
Nitric	4.0	4.9	[b]5.15	[b]5.15	4.9	[b]5.0	4.4	4.7	4.9	[b]5.2	4.4	4.4	4.25
Sulphuric	4.0	4.9	[b]5.0	[b]4.7	4.2	[b]4.3	4.4	4.7	4.8	[b]4.9	4.2	4.2	4.3
Phosphoric	4.0	5.0	[b]5.1	[b]4.85	4.0	[b]4.3	4.0	4.7	5.0	[b]5.0	4.0	4.1	4.0
Hydrochloric	3.0	3.0	3.0	3.0	3.1	3.1	3.1	....	....	....	....	....	3.0
Nitric	3.0	3.0	3.0	3.1	3.2	3.2	3.3	....	....	....	....	....	3.2
Sulphuric	3.0	3.0	3.0	3.1	3.2	3.2	3.2	....	....	....	....	....	3.0
Phosphoric	3.0	3.1	3.1	3.1	3.2	3.2	3.2	....	....	....	....	....	3.0

[a] Specified days of contact refer to P_H 4 series only.

[b] Solution renewed after this reading was obtained.

EFFECT OF PREVIOUS TREATMENT OF SEEDLINGS ON CHANGES IN REACTION OF ACID SOLUTION

The behavior of seedlings which had been grown previously in a complete nutrient solution, as compared with that of seedlings which had previously been grown in incomplete nutrient solutions, defective in chlorin, nitrogen, sulphur, and phosphorus, was studied. For instance, the seedlings which were to be grown in a solution of hydrochloric acid were first grown in a nutrient solution which was lacking in chlorin.

The nutrient solution used was diluted five times. The defective solutions were made up so that they differed as little as possible from the complete solution, except for the missing element. The seedlings were divided into two series: One series was grown for five days in the complete nutrient solution, and the other in the defective solutions. All seedlings were then grown for a day in distilled water and finally transferred to the acid solutions with an initial reaction of P_H 4. After the changes for two successive days had been recorded the acid solutions were renewed and the changes in P_H values were again recorded after a one-day and after a three-day contact. All seedlings were then transferred to the complete nutrient solutions diluted 10 times. Here they grew for two days, after which they were transferred to the complete and defective nutrient solutions, diluted 10 times. Two days later they were transferred to the acid solution with the initial reaction of P_H 3.6, in which they were kept for three days, when the changes in reaction were again recorded.

TABLE IV.—*Effect of complete and incomplete nutrient solutions in which seedlings had been previously grown on the changes produced in inorganic acid solutions* [a]

Acid.	Previous condition of solution.	Reaction.				
		After 1 day.	After 2 days. [b]	After 3 days [c] (1-day contact).	After 5 days (3-day contact).	After 12 days (3-day contact).
		P_H.	P_H.	P_H.	P_H.	P_H.
Hydrochloric	Complete	4.65	4.90	4.45	4.85	4.25
	Complete−Cl	4.60	4.70	4.50	4.65	3.95
Nitric	Complete	4.60	5.10	4.50	4.85	3.95
	Complete−N	4.55	4.70	4.60	4.70	3.85
Sulphuric	Complete	4.65	5.40	4.45	4.85	4.00
	Complete−S	4.65	4.95	4.50	4.65	3.90
Phosphoric	Complete	4.70	5.50	4.60	5.15	5.20
	Complete−P	4.60	4.80	4.65	4.70	4.00

[a] Initial P_H 4.0; number of seedlings, 15.
[b] Solutions renewed after these readings were obtained.
[c] All seedlings were held in complete (1:10) solution for 2 days, then for 2 days in complete and defective (1:10), and were then transferred back to acid solutions with an initial reaction of P_H 3.6.

The results (Table IV) show that the previous growth of the seedlings in a complete nutrient solution did not affect their activity, so far as their ability to lower the initial hydrogen-ion concentration was concerned. The previous growth of the seedlings in defective solutions, for the purpose of creating an avidity for the elements of the acids with which they were subsequently to be brought in contact, resulted, contrary to expectation, in a depressed activity with reference to changes in reaction of the acid solutions. This is shown by the three final readings (before solutions were renewed or discarded) which give consistently higher acidities for the seedlings grown previously in defective nutrient solutions. The defectiveness of the previous nutrient solution evidently created in the seedlings some functional disturbance either general or with reference to their behavior toward the elements lacking.

The most significant result obtained in this experiment, however, is that in the case of the older seedlings nitric acid had ceased to be affected by the action of the seedlings to a greater extent than the other acids. Its place was taken by phosphoric acid, as was shown by the three final readings in the series which had been grown in the complete nutrient solution.

The initial acidity of phosphoric acid solution was reduced from P_H 3.6 to P_H 5.2 in the final reading, a reduction which is strikingly greater than any obtained in the case of the other acid solutions. The differences in the behavior of the various acids were thus brought out more distinctly. The preference of the seedling for the different acids was also shown to vary with the conditions and with the stage of growth.

EFFECT OF AGE OF SEEDLINGS ON CHANGES IN REACTION IN ACID SOLUTIONS

The effect of the age of seedlings on their behavior toward nitric and phosphoric acids, which was unexpectedly brought out by the previous results, was studied further.

The usual procedure was followed. After the seedlings had been transferred to glasses and grown in tap water for three days, the roots were kept in contact with distilled water for two hours. The seedlings were then divided into two series. The seedlings of the first series were transferred to the acid solutions immediately. The seedlings of the second series were transferred to the acid solutions when 15 days old, after having been grown for 10 days in the nutrient solution diluted five times. The initial reaction of the acid solutions used was P_H 3.6, which was more suitable than the initial reaction of P_H 4, as the initial acidity was thereby increased 250 per cent and the changes produced were more pronounced.

TABLE V.—*Effect of age of seedlings on changes produced in inorganic acid solutions*[a]

Acid.	Initial age of seedlings.	Reaction.							
		After 1 day.	After 2 days.[b]	After 4 days (2-day contact).	After 6 days (4-day contact).	After 11 days (1-day contact).[b]	After 13 days (2-day contact).[c]	After 17 days (2-day contact).	After 20 days (5-day contact).
	Days.	P_H.	P_H.	P_H.	P_H.	P_H.	P_H.	P_H.	P_H.
Hydrochloric	5	4.05	4.00	3.6	3.70	.....	.....	.....	.....
Nitric[d]	5	4.40	5.10	4.3	4.70	.....	.....	.....	.....
Sulphuric	5	3.90	4.10	3.6	3.65	.....	.....	.....	.....
Phosphoric	5	4.15	4.45	3.9	3.95	.....	.....	.....	.....
Hydrochloric	15	.....	.....	.....	.....	4.80	3.90	4.00	4.35
Nitric	15	.....	.....	.....	.....	4.75	4.00	4.20	4.60
Sulphuric	15	.....	.....	.....	.....	4.90	3.90	4.30	4.50
Phosphoric	15	.....	.....	.....	.....	5.20	4.20	4.45	6.15

[a] Initial P_H, 3.6; number of seedlings, 20.
[b] Solution renewed after these readings were obtained.
[c] Transferred to complete nutrient solution (1:5) for 2 days and then back to acid solutions.
[d] Initial P_H, 3.5.

The results (Table V) show again and more clearly that the preference of the seedlings at an early stage of growth is for nitric acid and at a later stage for phosphoric acid. The age factor in this experiment also includes the factor of previous mineral nutrition. As a rule, however, the two are inseparable, as age in the sense of advanced stage of growth can not be measured merely by the number of days which elapse from the time of germination.

DISCUSSION OF EXPERIMENTAL RESULTS

The fact that the activity of seedlings in decreasing the initial acidity of the medium is preferential, resulting in the greatest decrease in acidity in one acid at one set of conditions and in another acid at another set of conditions, indicates that the cause of these changes is preferential absorption by the plants.

The term "preferential absorption" seems more appropriate here than the commonly used term "selective absorption." "Selective absorption" might imply that some substances are excluded, while "preferential absorption" indicates merely a higher rate of absorption of one substance as compared with that of another.

If the changes in the initial reaction of the acid solutions were a result of neutralization by secreta from the roots, they would be expected to be controlled by the active acidity factor only, and different acids with the same initial hydrogen-ion concentration and the same dissociation constants would behave alike. If the preferential action of the plants were in favor of nitric acid throughout, reduction by microorganisms might have suggested itself. It has been shown elsewhere (*4*), however, that the possibility of nitrate reduction is eliminated under the conditions of these experiments. But the fact that the preference of the older seedlings is for phosphoric acid lends additional strength to the absorption theory, which is further supported by the fact that in plant life nitrogen and phosphorus are, at least quantitatively, the most essential of the acid-forming elements dealt with in this investigation.

SUMMARY

Wheat seedlings were grown in solutions of hydrochloric, nitric, sulphuric, phosphoric, formic, acetic, oxalic, succinic, benzoic, and phthalic acids. The changes in reaction produced by their growth, recorded at certain intervals, show that:

Of the inorganic acids, the greatest changes were produced in nitric acid at early stages of growth of the seedlings and in phosphoric acid at later stages. Phosphorus and nitrogen being the most essential elements of plant growth contained in the acids used, it may be concluded that the changes in initial reaction produced by plants in the medium in which they grow are due to absorption rather than to neutralization.

The previous growth of the experimental seedlings in nutrient solutions deficient in acid-forming elements diminished their ability to decrease the acidity of the acid solutions. Apparently the deficiency of the previous nutrient solutions produced functional disturbances in the seedlings.

The greatest changes from the initial reactions were produced in the solutions of the organic acids. This, however, may have been due partly or wholly to microbiological activity and needs to be studied further.

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