INFLUENCE OF HYDROGEN ION CONCENTRATION ON THE GROWTH OF HIGHER PLANTS UNDER CONTROLLED CONDITIONS[1,2]

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(WITH FOUR FIGURES)

The effects of hydrogen ion concentration on plant growth occupy a prominent position in discussions of the adaptability of plants to their nutrient environment. In the last two decades, with the improvements of methods of measuring pH and particularly with the widespread adoption of the glass electrode, increasing attention has been given to the hydrogen ion concentration in soils as it may influence their suitability for different crop plants.

An understanding of the responses of plants to soil reaction is dependent: first, on the determination of the true pH of the soil; and secondly, on a knowledge of the effects of hydrogen ion concentration on plant growth. There is considerable doubt at present about the precise meaning of a soil pH measurement obtained by standard procedures including the glass electrode.[3] But even if some particular pH value were to be assigned to a soil as truly representative of the hydrogen ion concentration that happens to characterize the boundary between the soil and the plant root, there still would remain the difficulty of interpreting a soil pH value in terms of an isolated and independent variable. Is the failure of plants to thrive in an acid soil due to a high hydrogen ion concentration or to such other unfavorable factors of which a low pH is generally symptomatic; for example, a depletion of calcium and the presence of toxic amounts of aluminum or manganese in the soil solution? On the other extreme, there is the question whether poor plant growth in a soil characterized by a relatively high pH is to be attributed to a high hydroxyl ion concentration or to the unavailability of such plant nutrients as phosphate, iron, and manganese.

In addition to these indirect effects associated with pH which make it difficult to interpret the responses of plants grown in a soil, there is a dearth of information about the effects of hydrogen ion concentration on plant growth, with other factors of the nutrient environment held constant. The purpose

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[3] Stout, P. R. and Davis, L. E. Evaluation of the over-all resistance of pH meters and of glass electrodes on the apparent E.M.F. produced by clay suspensions. Paper presented before the Western Society of Soil Science at the A.A.A.S. Western Division Meetings at Pasadena, California, June 1941.

of this investigation was to secure evidence which would permit the evaluation of such direct effects of hydrogen ion concentration on the growth of higher plants. Emphasis was placed on the development of an experimental technique which would make it possible to isolate hydrogen ion concentration as a single variable, over a range of pH from 3 to 9, in gradations of 1 pH unit. For the reasons just cited the use of soil was considered unsuited to the main objective. A water culture technique suitably manipulated afforded an opportunity to control satisfactorily the ionic concentrations in the nutrient medium, including that of hydrogen ion.

Methods

The pH range from 3 to 9 was selected for study. The inclusion of alkaline reactions within the pH range raised at once the question of precipitation of nutrient ions on the alkaline side of neutrality and the subsequent alteration in the composition of the nutrient solutions with respect to ions other than hydrogen. An illustration of such indirect effects of pH on growth through an alteration of the composition of a nutrient solution is afforded by the work of REED and HAAS with calcium at alkaline reactions (**9**). In order to prevent changes in the nutrient solution because of precipitation the procedure developed in an earlier investigation (**1**), of adopting for the entire range of pH the concentration of the various ions that can be maintained at *the highest pH* investigated, was used throughout.

A standard nutrient solution was prepared and its pH adjusted to 9 by the addition of NaOH. The resulting precipitate was removed by filtering and the filtrate was analyzed for Ca, Mg, K, NO_3 and PO_4. Analysis of the filtrate served as a guide for the composition of the basic nutrient solution used in this study as given in table I. This basic nutrient solution, subse-

TABLE I

COMPOSITION OF NUTRIENT SOLUTIONS

	BASIC	LOW CALCIUM	HIGH CALCIUM
	M.	*M.*	*M.*
KH_2PO_4	0.00006	0.00006	0.00006
K_2SO_4	0.0015	....	0.0065
KNO_3	0.010	0.013	....
$Ca(NO_3)_2$	0.002	0.0005	0.007
$MgSO_4$	0.001	0.001	0.001

quently adjusted with either NaOH or H_2SO_4 to the various pH values, was used in all experiments unless otherwise indicated.

In order to avoid precipitation at pH 9, it was necessary to reduce drastically the concentration of phosphate ion. As the plants grew, the solutions were regularly tested for phosphate and additions up to the original concentration were made as needed.

In several experiments varying amounts of calcium were supplied to plants grown at pH 3, 4, 5 and 6. The three solutions, low calcium, medium, and high calcium furnished 20, 80 and 280 p.p.m. of calcium, respectively.

Sulphate was the only ion, other than hydrogen and hydroxyl, whose concentration varied in the pH as well as in the calcium series. Since the variations in the concentration of the sulphate ion in the respective nutrient solutions were regarded as of comparatively small physiological significance, this ion was selected for maintaining the balance of the electro-ionic charges.

The adjustment of the alkaline reaction entailed the addition of NaOH. In order to compensate for this introduction of sodium, Na_2SO_4 was added to nutrient solutions in amounts computed to furnish as much sodium as was added in the form of NaOH to the solution maintained at pH 9; that is, the nutrient solution which required the largest amount of base.

A special problem demanding attention was that of supplying the heavy metals iron and manganese. As the inorganic salts of these are insoluble in alkaline solutions it was decided to furnish these metals in the form of humates which remain soluble over the pH range 3 to 9 and are not precipitated by phosphate (**7**). A synthetic potassium humate solution was prepared from sucrose according to the procedure of HORNER, BURK, and HOOVER (**7**). Stock solutions of humate iron and manganese were made by adding to the potassium humate solution a solution of each metal as a sulphate to constitute 10 per cent. by weight of the humate. The pH of the resulting humate metal solution was adjusted to around 7.

Two mg. each of manganese and iron as the respective humate metals were added to a liter of nutrient solution. No further additions of either iron or manganese were made during the growth of the plants except when the entire nutrient solution was changed.

No deliberate addition of zinc, copper, or molybdenum was made to the nutrient medium. The absence of deficiency symptoms of these micronutrients justified the reliance which was placed on the impurities contained in the ordinary distilled water and salts used (**10**). As these metal impurities were free to combine with the humate accompanying the iron and manganese, no other provision was made to insure their availability throughout the pH range. 0.5 p.p.m. of boron was furnished to all cultures as H_3BO_3.

In order to provide a wide basis in arriving at conclusions on effects of hydrogen ion concentration on the growth of higher plants three different species were included in this study: tomato (*Lycopersicum esculentum*), lettuce (*Lactuca sativa*), and Bermuda grass (*Cynodon dactylon*). The Marglobe variety of tomato and the Imperial 847 variety of lettuce were used. Several experiments were carried out with each species but the responses of the tomato plant were investigated most intensively.

The seed was germinated on moist cheesecloth which was suspended on a Pyrex glass tray filled with redistilled water. When the seedlings attained a height of several inches they were transferred to previously described (**1**) iron tanks of 115 liters capacity. From six to ten (generally ten) plants, each supported in a cork, were placed in a tank and grown for a period of 5 weeks in the experimental nutrient solutions.

The fresh weights were usually expressed as averages of the ten plants grown in each tank. For fresh weight determinations the shoots were weighed directly and the roots were centrifuged before being weighed (**5**).

As pointed out in a previous paper (**1**), it is well to consider, in studying the effects of hydrogen ion concentration, the reaction of the culture medium in the zone directly adjacent to the absorbing root surfaces. These are in a dynamic equilibrium with the immediately adjacent zone of the culture medium and continuously alter its composition and reaction. That the reaction in this zone may be different from that a short distance away from the roots was shown by NIGHTINGALE (**8**).

The use of a suitable stirring device to bring about a continuous circulation of the nutrient solution within the tank is a material aid in the removal of such gradients. In the experiments under consideration the aeration technique served not only as a means of maintaining a high oxygen tension around the root but also as an effective stirring device, continuously mixing the nutrient solution and thus contributing to the maintenance of a uniform reaction and composition.

Porous carbon tubes, $\frac{3}{4}$ inch in diameter, extending through the entire length of the tanks, were used as aerators. They were connected by means of rubber tubing to an air line of 10 pounds pressure. A glass rod was placed inside each aerator to prevent the latter from floating. Two aerators provided each tank with a rapid stream of fine air bubbles without causing undue agitation of the nutrient solution.

The hydraulic jack and screw press method of expressing sap from frozen plant tissues (**5**) was followed. A pressure of 2000 lb. per square inch was used.

All pH measurements whether of the nutrient solution or of the expressed plant sap were made with the glass electrode.

The experimental technique provided for the following general devices in the prevention of large shifts from the original reaction of the culture medium: (a) Large volume of nutrient solutions in relation to the number of plants—between 10 to 20 liters to a plant. (b) Weekly changes of the nutrient solution as the plants grew older. (c) Continuous circulation of the solution within the tank brought about by the rapid bubbling of air. Changes in reaction and composition of the culture medium brought about by the metabolic activities of the plants were thus distributed over a large volume of solution and rendered quantitatively less pronounced.

The maintenance of the original pH was also aided by a continuous-drop device which consisted of a 500-ml. volumetric flask inverted in a 150-ml. beaker, both being supported on a ring stand above the tank. The flask and the beaker were filled with either NaOH or H_2SO_4 of suitable concentration (N/10 or N/100), and a measured amount was delivered into the respective tanks by means of a bent capillary tube, one end of which was supported by a cork in the beaker and the other delivering the acid or base to the tank, through a funnel inserted in a cork in the cover of the tank. The rate of delivery was adjusted by raising or lowering the level of the liquid in the beaker with reference to the tip of the delivery end of the capillary tube. To insure rapid mixing the cork supporting the funnel through which the acid or base was being introduced into the tank, was placed in the cover of the tank directly over an aerator.

An attempt was made to maintain the initial pH of the nutrient solution with fluctuations not exceeding $\pm$ 0.2 pH. The combination of the control devices used was more than equal to maintaining the initial pH of the acid nutrient solutions within these limits. At the less acid reactions, however, and particularly at pH 8 and 9, the plants, especially as they grew larger toward the end of the five-week period, shifted the initial reaction beyond the limits indicated. The pH in each tank was determined twice daily by means of the glass electrode and when necessary adjusted with NaOH or H_2SO_4.

Results

The general plan of the investigation afforded an opportunity to test the validity of the observed responses not only by using different species of plants but also by repeating a given experiment with one plant at various seasons of the year. The principal conclusions of this study as illustrated by the data presented, are based on magnitudes far exceeding those assignable to errors of variability in the plants used.

Effect of external pH on growth

With all plants at all times a complete failure of growth occurred at pH 3. The roots of the seedlings were unable to grow in the nutrient solution maintained at this hydrogen ion concentration, and collapsed soon after their immersion. In some cases as illustrated by that of the Bermuda grass (fig. 3), if the level of the nutrient solution was allowed to drop somewhat in the tank, a tuft of roots developed *above* the solution. In no case, however, was root growth observed in the nutrient solution kept at pH 3. Such limited growth of shoots at pH 3 as is shown in figure 3 was probably occasioned by a restricted absorption by the roots above the level of the nutrient solution which in turn was made possible by the fine spray produced by the aerators or perhaps by the wick-like absorption of the injured roots in the solution or by both.

On the other extreme, injury and a marked reduction in growth were observed in plants grown at pH 9 (table II and figs. 1, 2, 3). In no case, however, was it as pronounced as at pH 3. Of the plants used, the relatively best growth was made by Bermuda grass. But even this plant which is commonly noted for its resistance to alkali injury was incapable of normal growth in a nutrient solution maintained at pH 9.

TABLE II

EFFECT OF THE PH OF THE NUTRIENT SOLUTION ON GROWTH

EXTERNAL PH	AVERAGE FRESH WEIGHT IN GRAMS					
	TOMATO		LETTUCE		BERMUDA GRASS	
	SHOOTS	ROOTS	SHOOTS	ROOTS	SHOOTS	ROOTS
	gm.	*gm.*	*gm.*	*gm.*	*gm.*	*gm.*
3	....	....	....	....	8.6	2.9
4	22.3	13.0	85.1	26.0	83.0	24.3
5	83.2	23.5	285.4	50.8	88.5	20.3
6	92.7	19.1	292.6	44.7	104.9	14.8
7	80.9	19.4	162.8	28.1	102.2	15.7
8	49.1	15.4	165.1	36.5	72.1	10.3
9	4.3	2.7	8.2	5.3	20.7	4.9

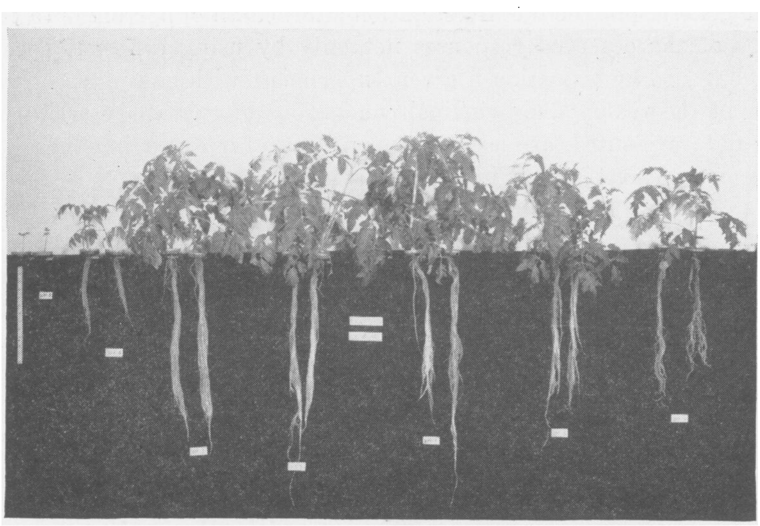

FIG. 1. Effect of external pH on the growth of tomato. From left to right: pH 3, 4, 5, 6, 7, 8, and 9.

Unlike the plants grown at pH 3, some root growth, particularly in the case of Bermuda grass, was observed in the nutrient solution proper at pH 9. Above the level of the nutrient solution healthy appearing roots were in evidence. As for the shoots, a general reduction in growth was common to all plants grown at pH 9. In the case of the tomato plants a purpling on the under side of leaves, characteristic of phosphate deficiency was observed at that pH. This observation is interesting in the light of the data on absorption of phosphate at pH 9 (**3**).

Definite growth of shoots and roots was obtained with all plants at pH 4,

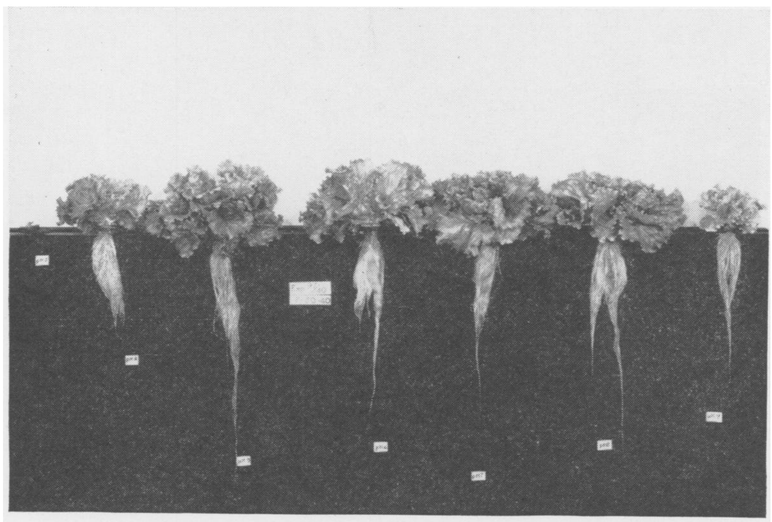

FIG. 2. Effect of external pH on the growth of lettuce. From left to right: pH 3, 4, 5, 6, 7, 8, and 9.

but with the exception of Bermuda grass, it was distinctly restricted (table II, figs. 1 and 2). Bermuda grass at pH 4 grew very well, fully on a par with plants at higher pH values (table II, fig. 3). This was confirmed in several experiments carried out at different seasons of the year.

Good growth with all plants was obtained in the range of pH above 4 and below 8. Some curtailment of growth was noticeable at pH 8; there is little doubt, however, that within this range of pH, variations in hydrogen ion concentration *per se* are associated with no drastic consequences to the growth of the plant. The general suitability of this relatively wide range of pH between 4 and 8 for the growth of higher plants warrants more emphasis than the fluctuations in growth reflected in table II. Although the data presented here as well as other experiments not included in this report suggested a possible "optimum pH" at around 6, it is indeed questionable whether this was not merely a reflection of a particular ionic proportion in the nutrient solution. Changing the relationships between ions is, as will be shown presently in the case of calcium, a factor in determining the response of plants in certain ranges of hydrogen ion concentration.

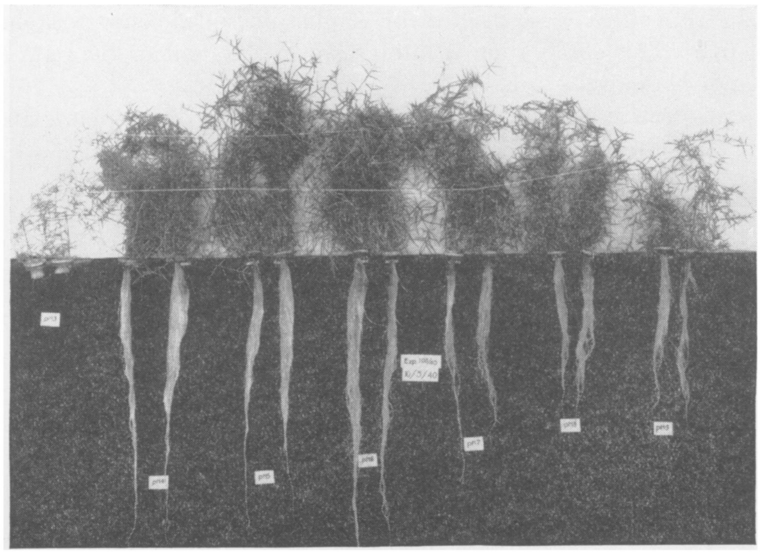

FIG. 3. Effect of external pH on the growth of Bermuda grass. From left to right: pH 3, 4, 5, 6, 7, 8, and 9.

EFFECT OF CALCIUM ON THE GROWTH OF PLANTS IN AN ACID MEDIUM

Results from a parallel investigation (**3**) have suggested that at least one of the causes of toxicity of an acid reaction is to be sought in the interference of a high hydrogen ion concentration with the absorption of calcium from a low level of supply. Experiments were set up, therefore, to compare the growth of plants in nutrient solutions ranging from pH 3 to 6 with three levels of calcium: 20, 80 and 280 p.p.m. The basic nutrient solution as given in table I furnished 80 p.p.m. of calcium and the "low-" and "high-calcium" solutions supplied 20 and 280 p.p.m., respectively. Since the large volumes of the regularly changed nutrient solution in relation to the number of plants insured against the depletion of calcium at the lower concentrations, it is justifiable to interpret the responses noted below, in terms of true concentration differences. The results for lettuce and tomato are presented in figure 4.

No effect of the higher calcium concentration was noted at pH 3. The influence of hydrogen ion concentration at that pH dominated at all three calcium concentrations and complete failure of growth resulted. A distinctly favorable effect of increased calcium supply was noted, however, at pH 4. With lettuce, progressively improved growth was obtained as the calcium concentration increased to 280 p.p.m., whereas with the tomato the marked increase in growth occurred upon increasing the calcium concentration from 20 to 80 p.p.m. A further increase to 280 p.p.m. was not associated with a large increase in growth. The noteworthy fact, however, for both kinds of plants at pH 4, was the pronounced favorable response to an increase in the concentration of calcium in the nutrient medium. The best

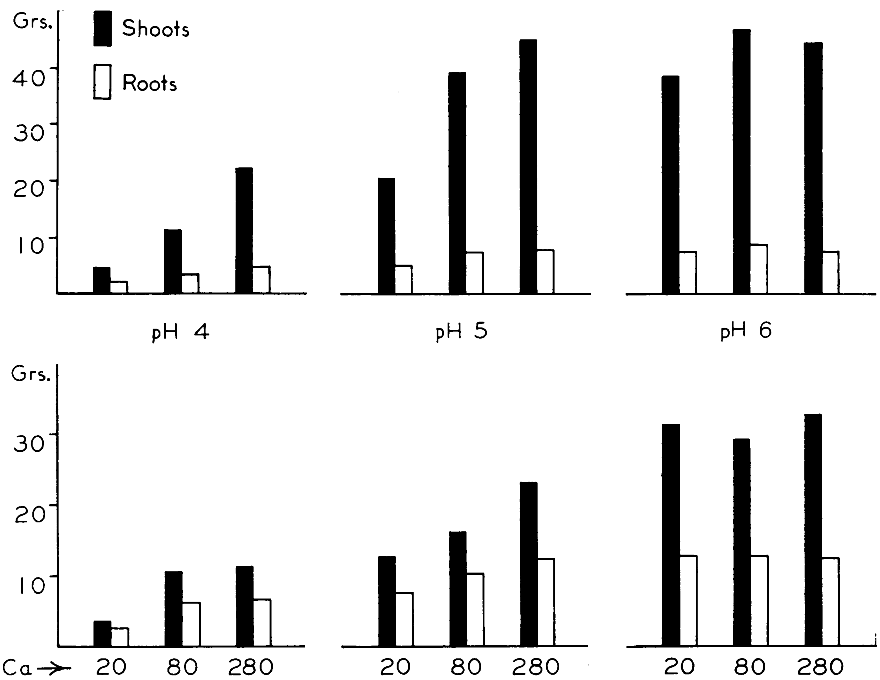

FIG. 4. Effect of calcium concentration on the growth of acid reactions of letture (above) and tomato (below). Fresh weight given in grams.

plants at pH 4 (plants grown with the highest supply of calcium) made as much growth as the poorest plants at pH 5—plants grown with the lowest supply of calcium.

The favorable effect of a higher calcium concentration on growth was also observed at pH 5 for both lettuce and tomato. At pH 6, however, no such response from increasing the calcium supply was found with either species; it will be noted, however, that at this pH, about equally good growth was obtained with all three levels of calcium supply. The best plants at pH 5, *i.e.*, those supplied with 280 p.p.m. of calcium, made approximately as much growth as the plants grown at pH 6.

Effect of external hydrogen ion concentration on the pH of expressed sap

A point frequently raised in discussions of hydrogen ion effects on plants is one relating to changes in the pH of cellular fluids as a result of variations in the external reaction. The pH values of the expressed sap of plants grown throughout the range of hydrogen ion concentration considered in this investigation are given in table III.

It is recognized that these data fail to throw light on possible variations in the reaction of individual tissues, caused by external pH, of which the epidermis and the cortex of the root would be of special interest. In expressing the sap of a root or a shoot a composite sample of several tissues is obtained and a possible fluctuation in the reaction of one tissue may be masked by the pH of other tissues. Despite this difficulty of interpretation inherent in the method, however, the pH determinations of expressed sap were made to determine whether some correlation existed between large differences in the external pH and that of the expressed sap.

The results given in table III show that the wide fluctuations in the hydrogen ion concentration of the nutrient solution have not been reflected in the pH of the expressed sap. The relative constancy of the reaction of the sap of the aerial portions of the plant was particularly consistent but this was also true of the roots, with the exception of Bermuda grass. With this grass there was found at both extremes of the external pH a corresponding shift in the pH of the root sap. These fluctuations, however, were small relative to the respective changes in the external hydrogen ion concentration and are regarded as not materially detracting from the principal conclusion: namely, that the reaction of the sap is relatively unaffected by shifts in the pH of the nutrient medium.

TABLE III

Effect of external hydrogen ion concentration on the pH of expressed sap

pH of nutrient solution	pH of expressed sap						
	Tomato			Lettuce		Bermuda grass	
	Leaves	Stems	Roots	Shoots	Roots	Shoots	Roots
3	......	......	......	......	......	5.8	......
4	6.1	6.1	6.6	6.1	6.1	6.0	5.6
5	6.2	6.1	6.4	6.1	6.2	6.1	6.0
6	6.1	6.1	6.3	6.1	6.0	6.1	6.0
7	6.0	6.1	6.2	6.0	6.0	6.1	6.2
8	6.1	5.8	6.0	6.0	6.2	6.0	6.3
9	6.1	5.8	6.4	6.1	6.3	6.0	6.7

At pH 3 no root growth occurred and obviously no pH measurement on the sap was possible. In one case, howover, enough sap for a pH determination was expressed from the previously mentioned tufts of root which grew above the level of the solution maintained at pH 3 and its pH was found only 0.1 lower than that of sap of roots grown at pH 4.

Effect of Ca on the pH of plant sap

It was deemed desirable to determine whether the favorable effect of calcium on growth at acid reactions (fig. 4) was associated with any changes in the pH of the expressed sap. As shown by the results of the pH determinations assembled in table IV, the increase of calcium concentration in the

TABLE IV

Effect of calcium on the pH of expressed sap of plants grown in acid solutions

pH of nutrient solution	Calcium in the nutrient solution	pH of expressed sap				
		Lettuce		Tomato		
		Shoots	Roots	Leaves	Stems	Roots
	p.p.m.					
pH 4	20	6.1	6.1	6.0	6.0	6.4
	80	6.1	6.1	6.1	6.1	6.6
	280	6.1	6.2	6.2	6.1	6.5
pH 5	20	6.1	6.1	6.1	6.1	6.6
	80	6.1	6.2	6.2	6.1	6.4
	280	6.1	6.1	6.1	6.0	6.3
pH 6	20	6.2	6.2	6.1	6.0	6.4
	80	6.1	6.0	6.1	6.1	6.3
	280	5.9	6.0	6.0	6.0	6.2

nutrient solution had no effect, within the limits of experimental error, on the pH of the sap.

Discussion

As pointed out previously, the main efforts in this work were directed toward securing data, which by distinguishing between the direct and indirect effects of hydrogen-ion concentration, would surmount the obvious difficulty in evaluating the true effects of the external reaction on plant growth. The data under discussion were obtained by means of an experimental technique that allowed for the variation of hydrogen ion concentration between pH 3 and 9, while the concentration of all nutrients (except sulphate) remained constant. Two principal conclusions can be drawn: First, that fatal or profoundly adverse effects of external reaction are encountered only at extremes of acidity and alkalinity (pH 3 and 9); and second, that, with certain reservations, fluctuations in hydrogen ion concentration *per se,* within the relatively wide range of pH between 4 and 8, are not inimical to the welfare of the plants so far studied.

These effects of hydrogen ion concentration on growth are explicable by the results of the experiments on the relation of hydrogen ion concentration to nutrient absorption (**3**). It is not implied that the relation of external reaction to nutrient absorption is to be regarded as the sole or even the principal cause of the reported effects of pH on growth. Nor is it at all certain on the basis of the present evidence that the influence of pH on absorption is not in itself a reflection of a primary injury to the absorbing root cells. What is noteworthy, however, is the fact that the evidence of the absorption experiments can in itself account for the observed growth responses.

It was shown (**3**) that at pH 3 the plants were unable to absorb calcium and phosphate and at pH 9 phosphate absorption was drastically curtailed. At pH 4 and 5, but not at the less acid reactions, tomato and lettuce showed a diminished calcium absorption (**3**).

These findings can account for the failure of growth at pH 3 and 9 and for the favorable effect on growth of an increased calcium supply at acid reactions (fig. 4). They also suggest that at the extremes of the relatively wide, physiologically suitable range of external pH between 4 and 8, good growth is possible only if special safeguards assuring a favorable supply of nutrient ions are observed. On the acid side a high concentration of calcium in the nutrient medium is a prerequisite to good growth. Above pH 7 special attention must be given to the supply of the heavy metals (iron, manganese) which, unless made available from such sources as humate compounds, may become deficient.

Likewise, the decreased absorption of phosphate at alkaline reactions raises the question whether, similar to the case of calcium at acid reactions, a higher phosphate concentration at reactions between pH 7 and 9 would in turn lead to improved growth. We have no evidence on this point at present but it is to be noted that, unlike calcium at acid reactions, the limited solubility of phosphates at alkaline reactions precludes any material increases in concentration of soluble phosphate in the nutrient solution. Similar questions might be raised with regard to the supply of heavy metals at alkaline reactions, particularly at pH 8, at which the reduction in the absorption of phosphate is perhaps not great enough to account for the decline in growth. The absorption of Ca, Mg, K and NO_3 at pH 8 was comparable to that at more acid reactions.

The evidence under consideration lends support to the view that the effects of external reaction on growth are largely dependent on the other components of the nutrient medium [compare (**4**)]; by proper attention to them, an initially adverse response to a certain hydrogen ion concentration can be favorably modified. There is, however, some justification for regarding the pH range above 5 and below 7 as particularly suitable for the growth of higher plants. This does not imply that good growth outside this range is impossible or even difficult to obtain. In fact, ample evidence to the contrary is available. Within this range, however, good growth is possible with least attention to questions of availability and suitable concentration of nutrients in the culture medium. Only in this restricted sense can we regard an external reaction around pH 6 as being optimal. These observations are in harmony with the results of an earlier investigation (**1**), which failed to disclose a definite optimal pH with either ammonium or nitrate nitrogen. It is recognized that, in the absence of special measures, the initial pH of the nutrient medium is subject to change as a result of the metabolic activities of the plant including nutrient absorption. This is of course relevant to all discussions of effects of the external reaction on plant growth.

Experimental verification was found for the point of view that the pH of a soil—ignoring for the moment the difficulty of measuring or deciding what the pH of a soil really is—can only have meaning when interpreted not as an independent variable but as a measurement reflecting the interaction of several factors peculiar to a given soil. It was shown that within relatively wide limits an acid or alkaline reaction in itself does not necessarily result in a serious impairment of growth. The pH of a soil is a helpful measurement in predicting and interpreting plant responses in so far as it serves as an indicator of the probable interrelations between plant nutrients. The significance of an acid pH in a soil will be determined by the extent to which it reflects a deficiency of calcium, and not infrequently magnesium, or the presence in the soil solution of toxic amounts of aluminum or manganese. On the other hand, the interpretation of an alkaline soil reaction cannot easily be differentiated from the question of availability of such plant nutrients as phosphate, iron or manganese.

If these premises are accepted, it follows that generalizations about plant responses to a given soil reaction are valid only for soils in which these indirect effects of reaction are similar. Little can be gained from comparing the reactions of soils which differ in parent material, climatic conditions prevalent during weathering, buffering capacity, organic matter content, etc. To cite only one example, good growth is encountered in certain acid peat or muck soils known for their high calcium-supplying power whereas a similar acid reaction is generally associated with crop failure in all leached, mineral soils. Indeed, the question may be legitimately raised whether the observed adaptations of the so-called acid-loving and alkali-tolerant plants to particular soil reactions should not be more appropriately related either to a high or a low requirement of some nutrients such as calcium, iron, and manganese or to the relative tolerance of some toxic constituent such as aluminum. In this connection it will be of interest to institute further inquiries on the relation of organic matter to the availability of metals in the form of humates under alkaline soil conditions. The assigning of definite minimum, optimum, and maximum pH values to specific crops, based on experience with some particular soils, is open to question.

Special mention should be made of calcium nutrition. It was found that at acid reactions lettuce and tomato required for best growth a higher concentration of calcium than at reactions approaching neutrality. This observation is of particular interest since a high acidity in soils generally coincides with a low calcium supply. The plant thus suffers from a double disadvantage. Its increased physiological demand for calcium is met by decreased supply. It seems reasonable to associate in part at least, the good growth sometimes encountered in acid mucks or other acid soils rich in organic matter to the high calcium-supplying power of these soils. These considerations of some of the aspects of soil reaction may be appropriately concluded with a restatement of the difficulty in determining the true hydrogen ion concentration of the soil—root interphase.

The observed stability of the pH of expressed sap of plants grown in a wide range of external reactions is in accord with other experiments reported from this laboratory (**2**, **6**).

Summary

A water culture method is described for the study of the effects of external hydrogen ion concentration within the range of pH 3 to 9. Its essential features provided, among others, for the maintenance of the same concentration of calcium, magnesium, potassium, nitrate, and phosphate ions as well as for the availability of iron and manganese throughout the entire pH range.

The results show that profoundly adverse effects of hydrogen, or hydroxyl, ion concentration, isolated from other variables, are found only at extremes of acidity or alkalinity. With tomato, lettuce, and Bermuda grass, complete failure of growth occurred at pH 3 and a marked decline was observed at pH 9.

Within a relatively wide range of pH between 4 and 8, fluctuations in the hydrogen ion concentration are tolerated by plants provided an adequate supply of all nutrient elements is maintained.

Growth of tomato and lettuce in acid nutrient solutions at pH 4 and 5 was favorably affected by increasing the concentration of calcium in the nutrient solution. At pH 6, however, the growth obtained at low and high concentrations of calcium was equally favorable.

The external reaction of the nutrient solution had no significant effect on

the pH of the expressed sap of either shoots or roots, with the possible exception of extremes unfavorable for growth.

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LITERATURE CITED

1. ARNON, D. I. Ammonium and nitrate nitrogen nutrition of barley at different seasons in relation to hydrogen-ion concentration, manganese, copper and oxygen supply. Soil Sci. **44**: 91–121. 1937.
2. ———. Effect of ammonium and nitrate nitrogen on the mineral composition and sap characteristics of barley. Soil Sci. **48**: 295–307. 1939.
3. ———, FRATZKE, W. E., and JOHNSON, C. M. Hydrogen ion concentration in relation to absorption of inorganic nutrients by higher plants. Plant Physiol. **17**: 515–524. 1942.
4. ÅSLANDER, ALFRED. Acidity resistance and feeding power of plants. Svensk Bot. Tidskr. **29**: 27–44. 1935.
5. BROYER, T. C., and HOAGLAND, D. R. Methods of sap expression from plant tissues with special reference to studies on salt accumulation by excised barley roots. Amer. Jour. Bot. **27**: 501–511. 1940.
6. HOAGLAND, D. R., and BROYER, T. C. Hydrogen-ion effects and the accumulation of salt by barley roots as influenced by metabolism. Amer. Jour. Bot. **27**: 173–185. 1940.
7. HORNER, C. K., BURK, D., and HOOVER, S. R. Preparation of humate iron and other humate metals. Plant Physiol. **9**: 663–669. 1934.
8. NIGHTINGALE, G. T. Ammonium and nitrate nutrition of dormant delicious apple trees at 48° F. Bot. Gaz. **95**: 437–452. 1934.
9. REED, H. S., and HAAS, A. R. C. The effect of hydroxyl-ion concentration on the growth of walnut roots. Amer. Jour. Bot. **11**: 78–85. 1924.
10. STOUT, P. R., and ARNON, D. I. Experimental methods for the study of the role of copper, manganese, and zinc in the nutrition of higher plants. Amer. Jour. Bot. **26**: 144–149. 1939.