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HYDROGEN ION CONCENTRATION AND THE COMPOSITION OF NUTRIENT SOLUTIONS IN RELATION TO THE GROWTH OF SEED PLANTS

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Introductory

By the use of the terms mineral nutrition or salt requirements of plants there is connoted a group of physiological processes and environmental conditions in which the mineral salts play an important rôle. Without entering into an elaborate discussion of these terms it may at least be pointed out that perhaps neither one is satisfactorily comprehensive. The last-mentioned is vague, and the other inadequate, due to the fact that when plants are grown in a so-called nutrient solution, as is well known, it is not merely the nutrient rôle the effects of which are followed. The concentration of the solute molecules and component ions of the culture solution directly affect the turgor, or osmotic surplus; the proportions of the ions—particularly of the cations—influence the permeability relations, which, operative through the protoplasts, seem to be the fundamental consideration in certain "antagonism" phenomena; the composition of the salts employed determines the acid-alkali equilibrium, that is, the hydrogen ion concentration, the influence of which is apparently most complex; and these and other possibilities affect ultimately growth, which, in part, of course, involves the incorporation into the living framework of the ions of the component salts.

For several years[1] the writer has given attention, as occasion permitted, to the reaction of the medium as affecting growth in soil solutions, also its effect upon toxic action; but it is only within the past two years that opportunity has been taken from time to time to examine this factor critically and so far as practicable in respect to physiologically balanced nutrient solutions.

The illuminating contributions of Clark and Lubs ('17) on the colorimetric determination of the hydrogen ion concentration of culture media for microörganisms, and of other biological fluids, effected so great an improvement in the simpler technique involving active acidity and alkalinity that there is now available a convenient, rapid, and sufficiently accurate method of investigating the hydrogen ion relations in connection with the salt requirements of higher plants. On the other hand, the extensive contributions of Schreiner and Skinner ('10, '10a, '11, '12), Tottingham ('14), Shive ('15), McCall ('16), and many others, on salt requirements and the constitution of the mineral nutrient solution have made it possible to select, within certain limits, well-balanced solutions as points of departure. In the work here reported, therefore, the writer has not concerned himself to any great extent with an investigation of the effects of variations in the proportions of the different salts involved in the nutrient solution. In this last-mentioned direction the recent literature represents a rapid advance both in technique and in result, and while, as will be pointed out later, the problem may not be finally solved, it has certainly been placed on a rational basis.

The triangle-diagram scheme was first rendered of biological significance by Schreiner and Skinner, referred to above, and it was effectively employed by them in studies of the relations of plants to certain toxic agents which might exist in the soil and in studies of the ameliorating action of the nutrient ions, K, NO_3, and PO_4, upon such deleterious compounds. They likewise investigated by this means the growth of wheat as affected by different ratios of phosphate, nitrate, and potassium. The same general diagram scheme has been perfected and advan-

[1] During the progress of these investigations the writer has had much assistance in the details of the culture work from various members of the graduate laboratory, to all of whom he is indebted, especially to Mrs. Emily Schroeder, Research Assistant, 1918–19, and Mr. R. W. Webb, Research Assistant, 1919–20.

tageously applied by Tottingham in his elaborate account of nutrient solutions, and by Shive, McCall, and others in intensive analyses of physiological balance. The effect of variation in H-ion concentration may be approached finally in the same way. In this rather general survey of certain aspects of the subject, however, it has seemed that the factors are for the most part too complicated for most economical treatment by this method alone.

Technique and Materials

In the earlier work I selected for comparative studies on the influence of variation in H-ion concentration two solutions only: namely, a slight modification of Shive's R_5C_2, considered his best solution of optimal concentration, and a much modified Crone solution developed in this laboratory. Later there was added the R_6C_1 solution of Livingston and Tottingham, and ultimately some other combinations which seemed worthy of consideration.

The partial volume-molecular proportions of the particular Shive solution employed are as follows: KH_2PO_4, 0.0180; Ca $(NO_3)_2$, 0.0052; and $MgSO_4$, 0.0150. Ferric phosphate in small amount is added, the partial concentration being 0.0044 gm. per liter of solution. This insoluble salt is used at such a low concentration that its presence as a precipitate is scarcely perceptible. I have employed the same salts in the same proportions, except that "soluble ferric phosphate" has been substituted for the insoluble iron salt in all cases not otherwise indicated. This substance is described as consisting of scales of ferric phosphate with sodium citrate, possibly as a single salt. The exact molecular composition of this iron-furnishing substance is unknown. From the description in the National Standard Dispensatory (1905) it will be seen that it is commonly made by the addition of 50 gms. ferric citrate and 55 gms. sodium phosphate, uneffloresced, to 100 cc. distilled water. It is barely possible that four salts are present, namely, sodium and ferric phosphate and sodium and ferric citrate. This salt combination possesses the advantage of solubility to a high degree, yielding what appears at first to be a true solution but seems in reality a colloidal solution of high dispersity. Used in such extreme dilution as indicated in the Shive solution, there is no noticeable precipitation, even on standing. There is every reason to believe that this substance is an excellent source of iron. The Shive solution prepared in this way is designated solution A, and it is best to think of it as solution A, because, as developed later, Shive does not report the P_H for his solutions, and this three-salt solution may possess very different values in plant growth, depending upon the grade or reaction of the monobasic phosphate employed.

The original Crone solution is made up as follows: water, 1000 cc.; KNO_3, 1 gm.; $CaSO_4$, .5 gm.; $MgSO_4$, .5 gm.; $Ca_3(PO_4)_2$, .25 gm.; and $Fe_3(PO_4)_2$ .25 gm. In our solution we have halved the concentration of the first two salts, omitted the tricalcium phosphate, and substituted for the ferrous phosphate the "soluble iron phosphate" above mentioned. In fact, the solution as I have used it may no longer be called the Crone solution, but it was of interest in this work at the time, not because it was expected to compare favorably with solution A above, but rather because it differed widely in the combinations of the components and had afforded in my work very good, healthy growth. The partial volume-molecular proportions are as follows: KNO_3, 0.00495; $CaSO_4$, 0.000726; $MgSO_4$, 0.000526; and "soluble iron phosphate," 0.125 gm. per 1000 cc. It will be noted that this is in reality a four-salt solution differing also notably from the earlier solutions of Sachs, Knop, Pfeffer, and Meyer. Inasmuch as the iron salt supplies also the phosphate, this B solution contains a higher concentration of Fe than the usual culture solution. There is more or less precipitation of a light or slowly settling iron salt, when the combined solution is prepared. However, by adding the soluble ferric phosphate last and at the greatest dilution possible under the conditions a light precipitate only is formed, and this develops slowly in the form of suspension films. It introduces no difficulties into the preparation of the solution, though perhaps renders its composition somewhat less definite. The films are so light that it is not difficult to remove uniform samples from the stock flasks. The osmotic value of this solution has not been determined, but it is obviously much less than that of the Shive solution, the latter being about 1.75 atmospheres.

The solution of Livingston and Tottingham, here designated solution C, possesses the following partial volume-molecular concentrations: KNO_3, 0.0216; $Ca(H_2PO_4)_2$, 0.0026; and $MgSO_4$, 0.0150. Iron is supplied as in the case of solution A, the modified Shive solution. It is assumed that this solution has approximately the osmotic value of solution A above described.

The methods of experimentation employed were in large measure those which I have described elsewhere ('11). "Well-seasoned" tumblers holding somewhat more than 250 cc. were used as culture vessels in all cases, the process of seasoning new tumblers consisting of filling them with a weak acid-dichromate cleaning solution and then steaming in the autoclave for one hour at 15 pounds pressure. Subsequently the tumblers were thoroughly washed and rinsed with distilled water. The distilled water used here and in preparing the solutions was in some series from a Stokes still and in other series double distilled from glass. After transferring, with pipette or burette, the required amounts of each constituent stock solution to the tumbler, the volume was made up to 240 cc. In those cases in which Canada field peas were used the tumblers were covered with heavy paraffined paper made fast by rubber bands. Small holes were punched in the paper and the radicles of the seedlings inserted. Additional support for the growing seedlings was afforded by means of wire supports. In the case of both wheat and corn the seedlings were inserted into notches or holes in a paraffined cork, the latter just fitting the mouth of the tumbler. All cultures contained ten plants, and duplicate tumblers were arranged in every case not otherwise indicated.

In most of the experiments here reported Merck's blue label chemicals have been employed, but under the conditions existing at the time it was not possible to be entirely uniform in this regard, and other standard reagents were used where necessary. No recrystallization or other purification method was applied to any salt employed in the culture solutions. Stock solutions of convenient concentration were prepared, and so far as practicable every factor and procedure was made uniform, or comparable, throughout. It soon became evident that the content of free phosphoric acid in the dihydrogen potassium phosphate was not constant in the different makes and bottles of the reagent necessarily used, and a closer examination of this point as the work progressed indicated clearly that we were not securing the uniformity of P_H in the solution which we felt that we might reasonably expect. It was not anticipated that the standard as indicated by Sörensen ('09–'10) and others would be attained unless the reagent were guaranteed free from phosphoric or other acids. The variation in P_H is often too great to make it at all certain what is meant when this salt is designated merely as acid potassium phosphate. One manufacturer who was appealed to on account of the variability referred to, assured the writer that it was not possible to furnish the salt free of phosphoric acid under the existing conditions.

In this work the hydrogen ion concentration was invariably determined by the method of Clark and Lubs ('17), employing both their standard solutions and their indicators. The standard solutions in this connection, however, were prepared with salts recrystallized two or three times, and the greatest care was given to every detail of the method. They were not controlled by the electrode method but by close comparison with the established effective ranges of the different indicators, especially, also, indicators with overlapping ranges. When making comparisons there was arranged for each indicator a set of seasoned serological test-tubes each containing 5 cc. of any standard solution within the range of the particular indicator. The various sets were arranged on a rack with white paper background. From 3 to 5 drops of the indicator solutions were used. Inasmuch as many of the culture solutions employed were without color, sufficiently accurate determinations were readily made with the unaided eye. In the case of solution B, however, and likewise in certain cases referred to later, where a few algae appeared in the solutions, recourse was had to the method employing the colorimeter (Duggar and Dodge, '19) and later more especially to the micro-colorimeter (Duggar, '19).

The seedlings used in various phases of the work were wheat (*Triticum vulgare*), corn (*Zea Mays*), and field peas (*Pisum arvense*). In all the work reported in tables I–VI, also XI–XIX, the wheat was of the variety Fultz, and that reported in tables VII–X was with a new variety, the Pacific Coast Blue Stem, supplied from the Plant Introduction Garden of the Bureau of Plant Industry at Chico, California. The latter had been found by Dr. H. S. Reed to be particularly good for solution culture work, and my experience is entirely confirmatory. The other seed were from selected but unnamed field varieties.

The seed were immersed over night in running water, and then the peas and corn placed for germination on paraffined wire netting over pans of well-washed, moist sphagnum. They were covered with moistened paper toweling, over which was inverted other pans, though ample ventilation was provided. The wheat was treated in much the same way except that it was germinated over water frequently changed. As soon as the plumules emerged light was admitted. After properly placing the seedlings, ten to each tumbler, they were left in diffuse light, in the room in which set up, for 12 to 24 hours in order to become better adjusted to the conditions before being installed in the greenhouse.

In some of the earlier experiments a complete series was arranged under a single set of conditions, and in such cases the tumblers were placed upon a rotating table. In much of the later work, however, more than one set of conditions was involved, so that the use of rotating tables was not practicable, and under the circumstances special care was taken with properly placing and spacing the tumblers on lattice tables, likewise shifting the order of the cultures so as to be wholly comparable.

In all cases as the plants were harvested, the remains of the seed, or cotyledons, were cut away. This was found necessary inasmuch as otherwise a considerable error would be introduced in the weights of those cultures in which relatively little growth occurred; for it was in such plants that the seed were incompletely exhausted. On removal from solutions containing precipitates the roots were thoroughly washed, and in all cases quickly and uniformly dried of surface water on absorbent gauze.

The criterion of growth on which stress is laid in this paper was total green weight. Other data included green weight of tops, average length of shoot (or leaf), dry weight, and general appearance—including root characteristics. Total green weight is, for the present purpose, entirely satisfactory and has the advantage in these relatively short-interval cultures of expressing as truly as may be the growth and health of the plants. Dried leaves and withered tips count for little. Average length of leafy shoot is included in some of the tables, but this affords merely an index of stockiness or attenuation of the plants.

The purpose in this work was to get results not only in respect to growth relations with variations in the H-ion concentration, but also, especially in the later work, to secure data in respect to the extent of change in the P_H of the medium in which the plants had grown. The time interval which the plants were permitted to remain in the cultures between changes of solution was generally 6 to 7 days, but in certain cases referred to later this interval was diminished or increased for special reasons indicated in connection with the tabulated data. During any interval, however, distilled water was added as required. In general, it seemed to the writer that the practical value of a particular mineral nutrient solution should rest in part upon its capacity to furnish favorable growth conditions for a period not too limited, that is, the solution should possess among other favorable characteristics, if possible, the quality of resisting unfavorable change over a period of one week or even longer.

Had the nutrient solutions used been merely solutions A and C, in which phosphate is supplied as the acid salts, it would have been simple to change the H-ion concentration towards neutrality by the use of various proportions of a dibasic salt. However, it was at the same time desired to increase the H-ion concentration, that is, to diminish the P_H exponent in order to determine approximately the favorable P_H limits. Moreover, changes in solution B could not be readily effected in the manner indicated without material changes in composition. It was therefore determined to use, in general, 0.1 n NaOH and approximately 0.1 molar H_3PO_4 in shifting the H-ion concentration. Actually, the concentrations employed were 0.1 n NaOH and 0.092 molar H_3PO_4. The stock solutions were so arranged as to concentration that the amounts of alkali or of acid introduced might first be diluted considerably with distilled water. In this way there was less danger of precipitating out the calcium salt, as insoluble calcium phosphate, for example, in solution A, before the critical P_H was reached, also other possibilities of precipitation in the case of solution B.

The problem was then to shift the hydrogen ion concentration of the solutions used without disturbing any more than necessary the composition of the medium. From preliminary tests of solutions A and B it was inferred that the chief interest might attach to the addition of alkali to solution A and of acid to solution B. The P_H exponent of the former is low, but in the latter it more nearly approaches neutrality. It is seen that the active acidity of the Shive solution is due to dihydrogen potassium phosphate, and the relatively slight variation in the proportions of the other practically neutral salts may be assumed not to change materially the hydrogen ion concentration. In this sense, therefore, the 108 solutions tested by Shive are probably nearly identical and determine, in respect to growth, the values of the proportions of the nutrient ions present in the solutions only in relation to this one value of P_H. This value might, of course, be assumed to be most favorable under all environmental conditions, but it is equally possible that it is not. This is a factor which should be given most careful consideration in all mineral nutrient, or salt-balance, studies as well as in studies upon toxic action.

As a convenient index to the content of the various cultures a simple scheme of notation has been devised, which, with very slight call upon the memory, enables one to see at a glance the constitution of the culture medium. This involves a system of letters and numerals as explained below. The initial letter of a culture refers to the general constitution of the nutrient solution, and as stated above there are three such solutions. The modified Shive solution employed is designated A; the solution remotely based on the Crone formula is solution B; and the Livingston-Tottingham solution, C. The next letter is invariably a small letter and denotes the plant employed; thus w designates wheat; p, Canada field peas; and c, corn; while x is employed where more than a single kind of plant is designated, or where no particular plant is specified. A culture index such as ApO, BpO, or CpO, etc., refers to the use of peas with the solutions mentioned without the addition of acid, alkali, or other constituent. When acid or alkali is added an inclined line represents, in this case, neutrality, and when figures are given above the line mentioned they represent cc. of 0.092 molar phosphoric acid; and when given below they represent cc. of 0.1 n sodium hydroxide. Thus Ap/10 indicates the addition of 10 cc. of 0.1 n NaOH to the A solution with peas. For the purpose of this paper we have considered molar phosphoric acid to be the sum of the values derived by titration against normal alkali, using as indicators both phenolphthalein and methyl orange.

I have attempted to control or counterbalance, in a measure, the addition of phosphorus when added as phosphoric acid by the introduction in one or two cultures of an amount of phosphorus in the form of the secondary salt equivalent to the acid added. At the same time, however, the addition of this salt necessarily shifts slightly the hydrogen ion concentration toward neutrality. The addition of sodium in the form of the alkali was in a measure controlled by adding as sodium sulphate an amount of this cation which is equal to that supplied in 10 cc. of alkali. As the work has progressed some other variations have been employed, notably the addition of solid calcium carbonate (1 gm. per culture, 240 cc.) to solution B, likewise of solid aluminium hydroxide, and of kaolin, the addition of phosphate in part as the primary salt and in part as the secondary salt, also variations in the form and amount of phosphate employed, and significant changes in the proportions of solution B. Modifications of the culture indices denoting such changes will be explained as these are introduced.

Experimental Data

There are given in tables I, II, and III the results of the first tests conducted with wheat, corn, and peas respectively, using solutions A and B. In consulting these tables it is to be remembered that the "culture indices" are intended to afford briefly all necessary facts concerning the constitution of the solution, and an explanation of these has been made on p. 9, so far as the unmodified solutions and those containing additions of acid and alkali are concerned. In the tables referred to above, K/10 and K/20 represent respectively additions of K_2HPO_4 to balance the amounts of phosphoric acid added in cultures with similar numerals; and Na indicates the addition of sodium sulphate to equal the quantity of gram atoms of Na in 10 cc. of n/10 NaOH.

The wheat cultures were grown 17 days, the corn 21, and the peas 18. The solutions were renewed and water loss was supplied as previously noted. The determination of the hydrogen ion concentration "after" growth in the case of corn furnishes an index of the change in the solution after the plants had grown in it for 10 to 12 days, representing the final interval. In this particular case the intervals between changes of solution were made rather long, with the idea of emphasizing conditions. The experiments were begun early in November under favorable growing conditions. The daily evaporation rate from a standardized spherical evaporimeter averaged 11 cc. per day.

TABLE I
(Series 1, Wheat)
SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH; SOLUTIONS A AND B

No.	Culture indices	Total gr. wt. (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	Initial P_H of sol.
1	AwO	4.92	0.4077	24.32	4.0
2	Aw /5	4.62	0.3916	23.89	5.6
3	Aw /10	5.20	0.4135	23.69	5.9
4	Aw /15	3.94	0.3550	21.24	6.1
5	AwNa	4.72	0.3792	25.93	4.0
6	BwO	4.52	0.3545	24.19	7.0
7	Bw /5	4.94	0.3498	23.36	8.4
8	Bw /10	5.83	0.4090	22.27	9.0(+)
9	Bw 5/	2.53	0.2522	16.48	4.6
10	Bw 10/	0.69	0.1176	8.26	3.2
11	Bw 20/	0.67	0.1134	6.56	3.0(−)
12	$BwK_2/10$	6.38	0.4390	26.34	6.2
13	$BwK_2/20$	5.80	0.3996	25.94	6.2

From series I, table I, also fig. 1, it is seen that with wheat there is indication that the addition of a certain amount of alkali, shifting slightly the H-ion concentration, is beneficial, though Aw/5 is irregular. Wholly unexpected is the extent of the growth in certain of the B cultures. Introduced empirically, this solution has not only yielded well, but in their vigorous, green appearance these cultures rank highest. The addition of alkali to solution B is beneficial, possibly from the addition of the sodium ion or from the slight increase in the concentration

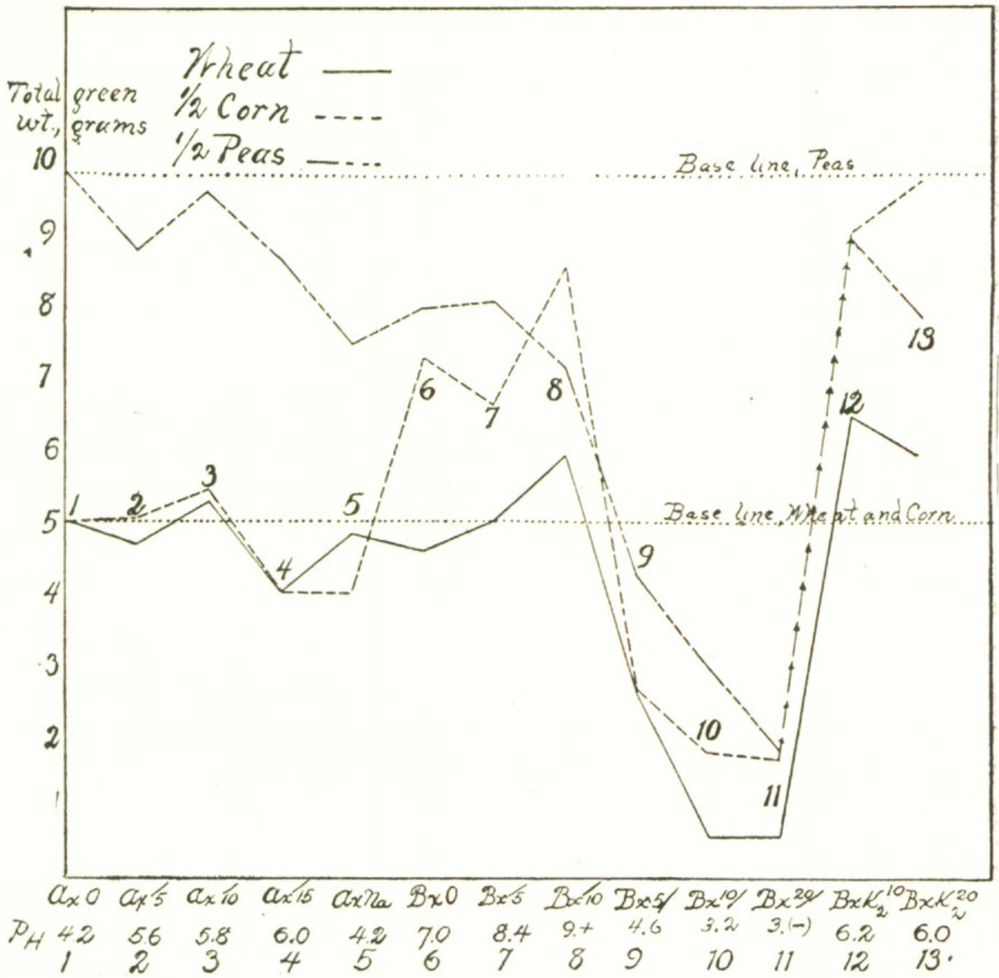

Fig. 1. Total green weight of wheat, corn (½), and Canada field peas (½), in solutions A and B, with variations—chiefly in H-ion concentration.

of the solution; and even more favorable is the addition of small amounts of secondary phosphate. With corn, table II, the shift towards alkalinity in the A solution affords slightly increased growth, but it is an important fact that there is a rapid falling off in the neighborhood of P_H 6. This is approximately the H-ion concentration at which precipitation begins. With this crop, the B solution alone, solution B plus small amounts of alkali, and solution B with the addition of dibasic phosphate yield strikingly heavier than solution A. On the other hand, peas, under the conditions of these experiments, made maximum growth in the relatively acid solution A.

TABLE II
(Series 1, Corn)

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH; SOLUTIONS A AND B

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H	
						Initial	After gr.
1	AcO	9.84	2.91	0.5452	22.02	4.0	5.4
2	Ac /5	9.94	2.74	0.6139	22.64	5.6	5.6
3	Ac /10	10.71	2.43	0.7642	22.97	5.9	5.9
4	Ac /15	7.90	2.25		20.36	6.1	6.0
5	AcNa	7.92	2.56	0.4652	14.49	4.0	5.2
6	BcO	14.35	4.22	1.0198	25.79	7.0	5.0
7	Bc /5	13.12	2.70	0.8102	26.28	8.4	8.0
8	Bc /10	16.90	3.95	1.0271	29.24	9.0(+)	8.4
9	Bc 5/	5.23	1.17	0.4606	14.67	4.6	4.0
10	Bc 10/	3.43	0.70	0.5387	10.54	3.2	4.0
11	Bc 20/	3.32	0.41	0.5617	8.42	3.0(−)	4.0
12	$BcK_2/10$	17.75	3.94	1.0170	31.84	6.2	7.2
13	$BcK_2/20$	19.22	4.51	1.1881	30.09	6.2	6.6

TABLE III
(Series 1, Peas)

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH; SOLUTIONS A AND B

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	Initial P_H of sol.
1	ApO	19.47	6.44	1.1014	27.84	4.0
2	Ap /5	17.37	5.31	0.9368	27.92	5.6
3	Ap /10	17.71	5.51	1.0155	29.42	5.9
4	Ap /15	17.10	5.42	1.0140	26.76	6.1
5	ApNa	14.77	5.57	0.8786	25.60	4.0
6	BpO	15.72	5.76	0.9200	25.10	7.0
7	Bp /5	15.86	5.10	0.8559	27.40	8.4
8	Bp /10	14.10	4.56	0.7822	25.59	9.0(+)
9	Bp 5/	8.27	2.70	0.6558	15.83	4.6
10	Bp 10/	5.85	1.78	0.5184	12.98	3.2
11	Bp 20/	3.47	0.93	0.3770	7.59	3.0(−)
12	$BpK_2/10$	17.69	5.17	0.9770	29.19	6.2
13	$BpK_2/20$	15.39	4.79	0.8660	27.18	6.2

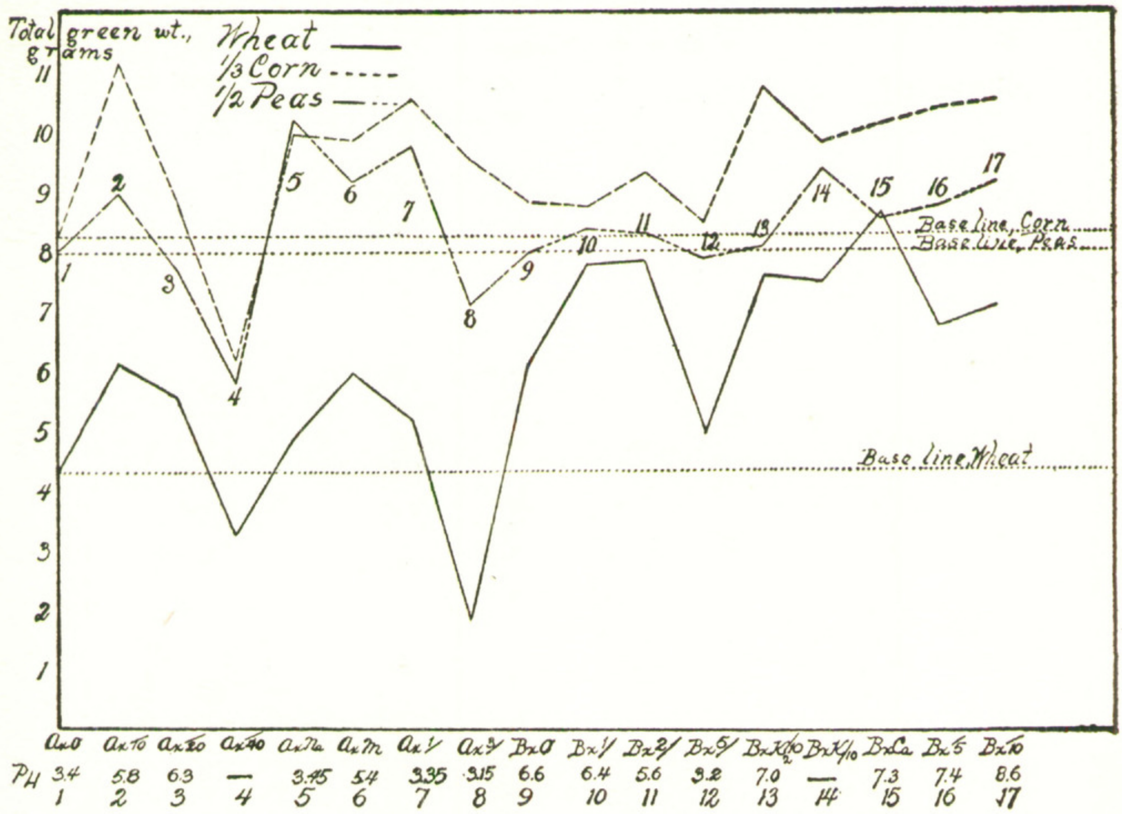

Fig. 2. Total green weight of wheat, corn (⅓), and Canada field peas (½), in solutions A and B, with variations—chiefly in H-ion concentration. The base lines are drawn through cultures strongly acid, P_H 3.4.

A point of considerable interest, emphasized particularly by the results with peas, is that the range of most favorable growth with respect to hydrogen ion concentration differs materially with the constitution of the nutrient solution; thus the addition of acid to the B solution, although shifting the H-ion concentration towards that of the A solution, exhibits a corresponding rapid diminution of the growth quantities. From these data alone it is not possible to formulate an explanation of the fact last mentioned, but it is probably related in part to ionic conditions, in part to the composition and state of aggregation of the iron and calcium particles, or to other, indetermined factors.

It should be pointed out, that in examining the curve, fig. 1, and all subsequent curves, a horizontal, or base line, is drawn through the growth quantity representing generally the unmodified solution A, so that all cultures may be compared with this,

TABLE IV
(Series 2, Wheat)
SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	Initial P_H of sol.
1	AwO	4.39	.545	24.37	3.4
2	Aw /10	5.30	.611	24.75	5.8
3	Aw /20	4.56	.533	22.74	6.3
4	Aw /40	3.21	.431	19.80	*
5	AwNa	4.86	.556	25.01	3.45
6	AwM	5.93	.542	23.04	5.4
7	Aw 1/	5.21	.569	24.63	3.35
8	Aw 3/	1.79	.306	16.38	3.15
9	BwO	6.07	.503	21.86	6.6
10	Bw 1/	7.76	.625	23.96	6.4
11	Bw 2/	7.82	.657	24.40	5.6
12	Bw 5/	4.96	.500	21.81	3.2
13	BwK_2/10	7.60	.623	26.18	7.0
14	BwK /10	7.51	.602	25.45	
15	BwCa	8.67	.810	25.32	7.3
16	Bw /5	6.75	.570	23.24	7.4
17	Bw /10	7.08	.606	24.49	8.6

* Heavy precipitate.

and the number of points in the curves above or below the base lines indicates for each crop, under the conditions reported, the relative increase or decrease in green weight.

The change in the P_H of the solutions occurring as a result of contact with the roots was followed only in the case of corn. As a rule, in the more acid solutions the reaction is shifted somewhat towards neutrality, but irregularities occur in solution B, some of which may be related to changes not due to the interchange of ions between roots and solution.

The second series of experiments, the results of which are included in tables IV, V, and VI, also plotted in fig. 2, was carried through during late November and early December. The conditions were much the same in general as those prevailing during the earlier work. There was this difference, however, that while the first series was placed on latticed tables in greenhouses with proper spacing to provide for favorable and uniform condi-

TABLE V
(Series 2, Corn)
SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	Initial P_H of sol.
1	AcO	25.44	7.63	2.325	32.33	3.4
2	Ac /10	33.52	7.96	2.567	32.91	5.8
3	Ac /20	26.14	6.36	2.170	30.71	6.3
4	Ac /40	18.28	5.10	1.642	22.26	*
5	AcNa	29.94	7.89	2.001	32.49	3.45
6	AcM	29.48	8.10	2.139	27.57	5.4
7	Ac 1/	31.56	8.18	2.337	32.56	3.35
8	Ac 3/	28.60	6.06	1.888	32.06	3.15
9	BcO	26.46	8.60	2.515	33.71	6.6
10	Bc 1/	26.19	9.34	2.232	33.31	6.4
11	Bc 2/	27.86	10.29	2.151	33.03	5.6
12	Bc 5/	25.35	7.75	2.108	30.50	3.2
13	$BcK_2/10$	32.25	11.48	2.476	33.51	7.0
14	BcK /10	29.48	9.96	2.453	29.46	
15	BcCa	30.42	11.80	2.852	34.55	7.3
16	Bc /5	31.20	10.68	2.530	34.65	7.4
17	Bc /10	31.55	9.90	2.767	33.98	8.6

* Heavy precipitate.

tions, the second series was placed upon the rotating table and rotated throughout the period of culture. The rotating table employed was that previously described (Duggar and Bonns, '18) except that there was substituted for the special pot platforms a continuous platform constructed above the radiating arms and the secondary motion was, of course, eliminated. The wheat was grown 21 days, while the corn and peas were grown 24 days. One change of solution was made after about 12 days of growth. It is, therefore, a rather severe test of growth quantities when infrequent renewals of solutions are made. The water loss from transpiration was supplied about every second day.

In determining the hydrogen ion concentration of the solutions employed at the beginning of the experiment it was found that the active acidity of solution A was 3.4, consequently much greater than the theoretical. This was found to be due to the

TABLE VI
(Series 2, Peas)
SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H	
						Initial	After gr.
1	ApO	16.01	5.29	1.351	24.02	3.4	4.6
2	Ap /10	17.89	6.21	1.473	22.72	5.8	5.8
3	Ap /20	15.34	5.30	1.332	19.93	6.3	6.0
4	Ap /40	11.55	4.68	1.124	12.49	*	6.8
5	ApNa	20.30	7.20	1.603	26.03	3.45	4.4
6	ApM	18.28	6.15	1.418	24.19	5.4	6.4
7	Ap 1/	19.39	6.60	1.505	24.50	3.35	4.6
8	Ap 3/	14.17	5.22	1.262	21.13	3.15	4.2
9	BpO	15.91	5.70	1.326	19.59	6.6	6.2
10	Bp 1/	16.69	6.13	1.410	22.16	6.4	6.0
11	Bp 2/	16.58	5.82	1.391	22.48	5.6	6.0
12	Bp 5/	15.78	5.33	1.316	20.24	3.2	4.6
13	$BpK_2/10$	16.12	5.91	1.413	19.01	7.0	6.6
14	BpK /10	18.75	6.87	1.501	21.33		5.2
15	BpCa	17.15	6.18	1.393	23.44	7.3	8.0
16	Bp /5	17.49	6.32	1.389	19.21	7.4	7.4
17	Bp /10	18.38	6.29	1.413	21.65	8.6	8.0

* Heavy precipitate.

use of a new supply of monobasic potassium phosphate. This was a high-grade reagent, but was not guaranteed free of phosphoric acid, and no such guaranteed salt was then obtainable. The determinations indicate very clearly that attention must be paid to the determinations of the P_H value whenever such experiments on nutrition are conducted. This series of experiments must be examined and interpreted in the light of the P_H value referred to. Nevertheless, it should be pointed out here, though emphasized later, that the P_H exponent of the more acid solutions is rapidly increased with the growth of the crop. The increased acidity is doubtless due to an excess of acid in the preparation of the salt. This relatively high acidity affected, of course, to a degree the P_H of other solutions to which alkali was added.

In general, this series is an extension and continuation of the previous work, modified particularly by the addition of certain cultures not included in the previous series. Attention may be drawn to the inclusion of cultures in which the hydrogen ion concentration of the A series was increased by slight additions of phosphoric acid, as in Ax 1/, Ax 3/, likewise in solution A the substitution for one-half the quantity of the monobasic salt by an equivalent of the dibasic potassium phosphate, this being designated AxM. In the B solution there were also introduced cultures to which relatively small amounts of phosphoric acid were added, Bx 1/, Bx 2/, and Bx 5/, also one culture in which was included 1 gm. of solid calcium carbonate, BxCa. A fresh quantity of the salt in the case last mentioned was introduced with each change of solution. A general examination of the total green weight quantities in the case of wheat indicates that under the conditions of this experiment the maximum growth quantities were obtained with the B solution. Small amounts of phosphoric acid or of either phosphate ($BxK_2/10$ and BxK/10) gave an increase in growth over the unmodified solution, and within the range of hydrogen ion concentration which prevailed in this culture solution relatively little influence was exerted by changes in P_H except in the case of one culture, Bw 5/, where the hydrogen ion concentration was increased to P_H 3.2. On the other hand, with the A solution it is clear that the addition of alkali to the unmodified solution is generally beneficial, at least at concentrations up to and including Aw /10, in which culture the P_H exponent is raised to 5.8. Further addition of alkali gives a falling off in the growth quantities. In the culture Aw /20 where the hydrogen ion concentration is P_H 6.3, precipitation occurred and a marked decline in growth is apparent, although the reaction of the medium is the same as that which in the B series promoted an amount of growth approaching the maximum. This is one of the many indications pointing clearly to the probability that the most favorable hydrogen ion concentration, or range of concentration, for a particular nutrient solution does not necessarily correspond to that which is most favorable with the solution of entirely different constitution. The growth quantity recorded for Aw 1/ is not strictly in line with the discussion above. The duplicates differed considerably. We have here, of course, two factors involved: (1) increase in acidity, and (2) slightly increased PO_4 concentration.

With respect to corn it will be seen that the maximum yield occurs in culture Ac /10, although maximum root growth occurs in several B cultures. As between the different cultures in the A series the results are much the same as in the case of wheat except that the AcM culture with a combination of mono- and dibasic phosphate does not exhibit the benefit reported in the previous case. On the other hand, when one examines the data for dry weight quantities it will be found that maximum growth, as before, occurs in the B solution and in the culture to which solid calcium carbonate was added. Moreover, the next best growth is found in the addition of a slight amount of alkali to the B solution.

Throughout this work it will be noticed that the variation in total growth amounts between the various cultures of peas, differing mainly in P_H, is not so marked as that shown by the other two plants used in these experiments. Again, there were considerable differences between different plants in the same culture (more marked, however, in the case of wheat), and this indicates beyond any doubt that the variability of the seed is a factor which may affect to a slight extent the regularity of the results. In any event, the maximum growth with peas in this series occurred when a small amount of sodium sulphate was added. The amount of growth in the unmodified A solution is considerable in spite of the high acidity, yet there appears to be a slight advantage in the addition of a small quantity of alkali, although the latter is rendered doubtful by a comparison of cultures ApO, Ap 1/, and Ap 3/. In solution A Canada field peas are apparently only slightly affected by changes in hydrogen ion concentration up to the point of precipitation of the phosphate as the insoluble calcium salt. The curve, fig. 2, exhibits all the necessary data for growth comparison. Since these experiments were made it has been found that a frequent laboratory grade of acid potassium phosphate will give a P_H anywhere from 3.5 to 4.5, but more frequently less than 4.0.

Change in P_H after plants had grown in the solution was followed in the case of peas, with a result much like that of the first series. The more acid solutions are shifted towards neutrality, but solutions with exponents greater than 5.8 or 6.0 may vary scarcely at all, while the more alkaline solutions are generally shifted toward neutrality.

TABLE VII

(Series 3, Wheat)

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH; SOLUTIONS A, B, AND C; RENEWAL EVERY FOUR DAYS

No.	Culture indices	Total gr. wt. (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H		
					Initial	End 2nd per.	End 4th per.
1	AwO	1.92	0.325	12.02	4.8	4.8	4.8
2	Aw 9/10 K	7.92	1.054	18.04	5.3	5.6	6.0
3	Aw 4/5 K	6.27	0.776	17.08	5.5	5.5	5.5
4	Aw 3/5 K	6.36	0.814	14.82	6.0	5.8	5.8
5	Aw 1/2 K	10.18	1.211	20.52	6.1	5.7	6.1
6	Aw 3/10 K	6.55	0.789	17.12	6.4	6.1	6.1
7	Aw h/Al	5.21	0.862	17.26	3.6	3.6	5.3
8	AwAl	6.39	0.893	17.60	5.3	5.4	5.8
9	BwO	8.24	1.124	19.96	5.9	7.1	7.1
10	2(BwO)	7.65	1.010	19.27	5.8	7.3	8.0
11	BwK_2	3.22	0.500	15.00	7.1	7.4	7.8
12	BwCa	6.47	0.950	21.34	7.6	7.6	7.8
13	BwAl	13.85	1.954	25.33	7.1	7.4	7.7
14	CwO	5.60	0.683	14.89	4.8	5.6	6.5
15	CwNH	3.71	0.603	14.87	4.3	4.6	4.8
16	CwGC	5.29	0.796	16.21	6.7	7.0	7.8
17	CwGP	4.37	0.640	14.10	7.1	7.0	7.4
18	Cw /1	8.44	1.045	18.54	5.3	5.8	7.2
19	Cw /2	7.72	1.022	16.96	5.8	6.0	6.6
20	Cw /5	6.15	0.928	16.23	6.4	6.4	7.3
21	CwAl	8.20	1.178	20:74	5.4	5.8	7.0

Series 3 was arranged with a view to repeating some of the work previously conducted and likewise to an extension of it. Two plants, wheat and corn, were employed, and the subdivisions of the series may be appropriately designated 3w4, 3w10, 3c4, and 3c10, indicating respectively (3w4) cultures with wheat, solutions renewed every 4 days; (3w10) cultures with wheat, solutions changed every 10 days; (3c4) cultures with corn, solutions changed every 4 days; and (3c10) cultures with corn, solutions changed every 10 days. In this case, therefore, a culture of any plant in a particular solution with a change of solution every 4 days, was duplicated by a similar culture in which the solution was renewed every 10 days.

Sections 3w4 and 3c4 of this series were grown on the rotating table, while sections 3w10 and 3c10 were grown in another green-

TABLE VIII
(Series 3, Wheat)

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH; SOLUTIONS A, B, AND C; RENEWAL AFTER A TEN-DAY INTERVAL

No.	Culture indices	Total gr. wt. (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H		
					Initial	End 1st per.	End 2nd per.
1	AwO	2.55	0.482	12.40	4.8	4.6	4.8
2	Aw 9/10 K	5.04	0.765	15.29	5.3	5.6	6.3
3	Aw 4/5 K	5.50	0.812	14.07	5.5	5.2	5.9
4	Aw 3/5 K	5.52	0.748	13.76	6.0	5.6	6.1
5	Aw 1/2 K	5.53	0.849	12.23	6.1	5.5	6.4
6	Aw 3/10 K	1.06	0.262	10.64	6.4	6.0	6.1
7	Aw h/Al	2.52	0.506	13.61	3.6	3.8	4.9
8	AwAl	4.40	0.668	13.52	5.3	5.5	6.1
9	BwO	7.62	1.079	20.12	5.9	7.6	7.4
10	2(BwO)	7.90	1.094	19.11	5.8	7.6	8.0
11	BwK_2	2.82	0.470	14.42	7.1	8.2	8.5
12	BwCa	5.12	0.789	17.14	7.6	7.8	8.8
13	BwAl	10.30	1.622	26.65	7.1	7.6	8.0
14	CwO	4.95	0.707	14.10	4.8	5.9	6.7
15	CwNH	5.57	0.858	16.15	4.3	4.6	5.3
16	CwGC	5.50	0.846	16.91	6.7	7.6	8.8
17	CwGP	1.70	0.308	10.77	7.1	7.4	7.6
18	Cw /1	7.10	0.995	16.24	5.3	6.2	7.7
19	Cw /2	6.42	0.887	16.62	5.8	6.4	7.6
20	Cw /5	5.50	0.778	16.28	6.4	6.8	7.4
21	CwAl	6.45	0.971	14.67	5.4	6.4	7.4

house, and the cultures were distantly spaced on a lattice table, or bench, constructed with the idea of providing for all cultures uniform circulation, or conditions favoring uniform water loss. The light relations were perhaps somewhat more favorable for the group of cultures renewed at four-day intervals. This series was begun on May 14. During the first two weeks the weather was moderate and cloudy, while during the last week it was bright and warm, perhaps too warm for the best growth of wheat. While the evaporation from a standardized spherical atmometer was low, seldom exceeding 12 gms. per day, during the first two weeks it rose to a maximum of 27.8 and 25.4 as a record for the two houses on May 31.

The modification in the A group of cultures in this series consisted chiefly in the introduction of K_2HPO_4 as a source of part

TABLE IX
(Series 3, Corn)

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH; SOLUTIONS A, B, AND C; RENEWAL EVERY FOUR DAYS

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H		
						Initial	End 2nd per.	End 4th per.
1	Ac h/1	9.55	1.70	1.422	16.78	3.4	3.4	5.2
2	Ac h/2	32.10	7.08	3.301	27.92	3.7	4.1	5.6
3	AcO	50.61	12.94	4.716	35.74	4.8	4.8	5.6
4	Ac 9/10 K	33.08	10.24	3.015	26.58	5.3	5.6	5.8
5	Ac 4/5 K	41.12	10.13	3.898	30.50	5.5	5.3	6.2
6	Ac 3/5 K	40.90	9.76	3.820	29.60	6.0	5.6	6.3
7	Ac 1/2 K	40.80	12.98	3.434	29.98	6.1	5.6	6.9
8	Ac 3/10 K	47.20	15.24	3.915	31.75	6.4	6.0	6.9
9	Ac h/Al	16.57	3.82	2.117	19.93	3.6	4.6	5.3
10	AcAl	27.78	7.85	3.288	23.05	5.3	5.2	6.3
11	BcO	36.06	9.65	4.107	29.32	5.9	6.8	6.8
12	2BcO	49.72	13.75	5.159	34.11	5.8	7.1	7.0
13	BcK_2	43.23	12.12	4.290	30.94	7.1	7.0	7.0
14	BcCa	36.41	11.01	4.305	29.78	7.6	7.2	7.2
15	BcAl	37.90	12.45	4.597	32.46	7.1	7.1	5.7
16	CcO	29.02	8.58	2.920	23.95	4.8	5.2	7.2
17	CcNH	20.44	4.68	2.307	22.44	4.3	4.6	4.6
18	CcGC	33.33	9.86	3.210	25.82	6.7	6.8	7.7
19	CcGP	32.82	8.83	3.061	26.57	7.1	6.6	7.8
20	Cc /1	35.83	10.82	3.437	29.01	5.3	5.6	7.8
21	Cc /2	35.32	8.80	3.306	27.84	5.8	6.1	7.6
22	Cc /5	35.70	10.25	3.271	28.18	6.4	6.4	8.0
23	CcAl	41.83	12.33	4.201	29.98	5.4	5.7	7.6

of the potassium and phosphate ions. The stock solution of this salt was made to contain the same number of gram atoms of PO_4 as the stock solution of KH_2PO_4. These solutions were then combined so that the ratios of monobasic to dibasic phosphate were respectively 9: 1, 4: 1, 3: 2, 1: 1, and 3: 7, the culture indices being Ax 9/10 K, Ax 4/5 K, Ax 3/5 K, Ax 1/2 K, and Ax 3/10 K, with the P_H of the solutions affected as indicated in the tables. In culture AxO, another high grade of KH_2PO_4 was employed, and the P_H exponent is higher than the theoretical; while in the Ax h/1 cultures, used especially in the case of corn, the more acid grade is employed. Ac h/2 is intermediate in

TABLE X

(Series 3, Corn)

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH; SOLUTIONS A, B, AND C; RENEWAL AFTER A TEN-DAY INTERVAL

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H		
						Initial	End 1st per.	End 2nd per.
1	Ac h/1	13.70	3.15	2.080	22.42	3.4	5.1	6.4
2	Ac h/2	18.13	3.83	2.268	23.77	3.7	5.4	6.3
3	AcO	34.42	7.75	3.922	31.65	4.8	4.0	5.2
4	Ac 9/10 K	34.82	9.10	3.282	29.64	5.3	5.6	5.3
5	Ac 4/5 K	34.12	7.72	3.298	27.17	5.5	5.1	5.3
6	Ac 3/5 K	37.62	9.70	3.589	28.07	6.0	5.6	5.4
7	Ac 1/2 K	41.80	11.30	3.784	28.76	6.1	5.6	5.4
8	Ac 3/10 K	37.50	12.56	3.397	27.25	6.4	5.8	6.4
9	Ac h/Al	19.67	4.34	2.491	23.23	3.6	5.2	6.1
10	AcAl	32.29	9.22	3.389	25.70	5.3	5.8	5.3
11	BcO	28.26	8.78	3.366	24.36	5.9	7.2	5.5
12	2BcO	38.04	7.77	4.525	30.22	5.8	7.7	5.3
13	BcK_2	43.00	12.63	4.172	31.83	7.1	8.0	5.8
14	BcCa	29.85	9.20	3.617	26.59	7.6	8.4	7.3
15	BcAl	27.80	7.70	3.271	27.75	7.1	7.0	5.6
16	CcO	30.65	8.40	2.923	24.84	4.8	5.6	7.6
17	CcNH	14.44	3.80	1.994	23.85	4.3	4.6	5.8
18	CcGC	27.50	6.97	2.788	23.94	6.7	7.6	8.4
19	CcGP	32.37	8.90	3.145	23.83	7.1	7.3	8.2
20	Cc /1	31.85	7.20	3.060	26.95	5.3	6.2	7.5
21	Cc /2	34.50	9.35	3.005	29.65	5.8	6.4	7.4
22	Cc /5	38.90	9.25	3.487	29.43	6.4	7.0	7.1
23	CcAl	25.06	5.89	2.699	24.74	5.4	6.4	7.7

acidity between AcO and Ac h/1, with salt proportions the same. Again, to other cultures containing these two grades of phosphates there were added to each culture vessel (and with each renewal) 1 gm. of solid aluminium hydroxide of the highest purity procurable. The latter are designated AxAl and Ax h/1 Al respectively.

In the B group cultures were prepared with the addition of solid aluminium hydroxide (BxAl), as above, also with solid calcium carbonate BxCa, with the addition of a small amount of K_2HPO_4 (BxK_2), and the unmodified solution of double strength [2(BxO)].

The C group of cultures (Livingston-Tottingham medium) is here introduced for the first time. Explanations already given explain the culture indices in this group, except in the following cases: CxNH, CxGC, and CxGP. In the first mentioned one-half the atomic proportion of nitrogen is supplied as $(NH_4)_2SO_4$, and in the last two calcium glycero-phosphate is added to replace monobasic calcium phosphate. In CxGC the atomic proportion of Ca is kept the same as in CxO, while in CxGP it is the phosphorus which is equivalent.

Under the conditions of these experiments the Aw cultures, particularly, were less satisfactory than usual, possibly in large part due to the high temperature prevailing towards the end of the period. The series was discontinued earlier than planned owing to the drying of the leaf tips of wheat and even of some entire plants. On the whole the wheat cultures show many inconsistencies, but despite this also some strikingly interesting results.

Increasing the P_H exponent by means of the dibasic phosphate may under these extreme conditions more than treble or quadruple the growth quantities. It is probably a matter of shifting the sum of conditions from the side of toxicity to that of growth maintenance. Even in the case of the C solution, increasing the P_H exponent is here a factor in promoting growth increase. Under other conditions I have not found this to be true, as will be indicated later.

The addition of aluminium hydroxide is under these conditions distinctly favorable, as seen by comparing the following pairs, AwO and AwAl (also AwO and Aw h/Al), BwO and BwAl, CwO and CwAl. The value of this reagent is doubtless in part due to its action as a buffer.

The temperature was most favorable for the corn cultures, and they exhibited, on the whole, an unusually vigorous growth. The green weight determinations are an accurate indication of growth extent but not of appearance. The B group was dark green in color, with heavy purplish stems; while both the A and C groups were strongly chlorotic. Chlorosis was much intensified during the last week of growth, and it seemed probable that if these cultures were longer maintained, a considerable reduction in the growth rate would occur. It is assumed, how-

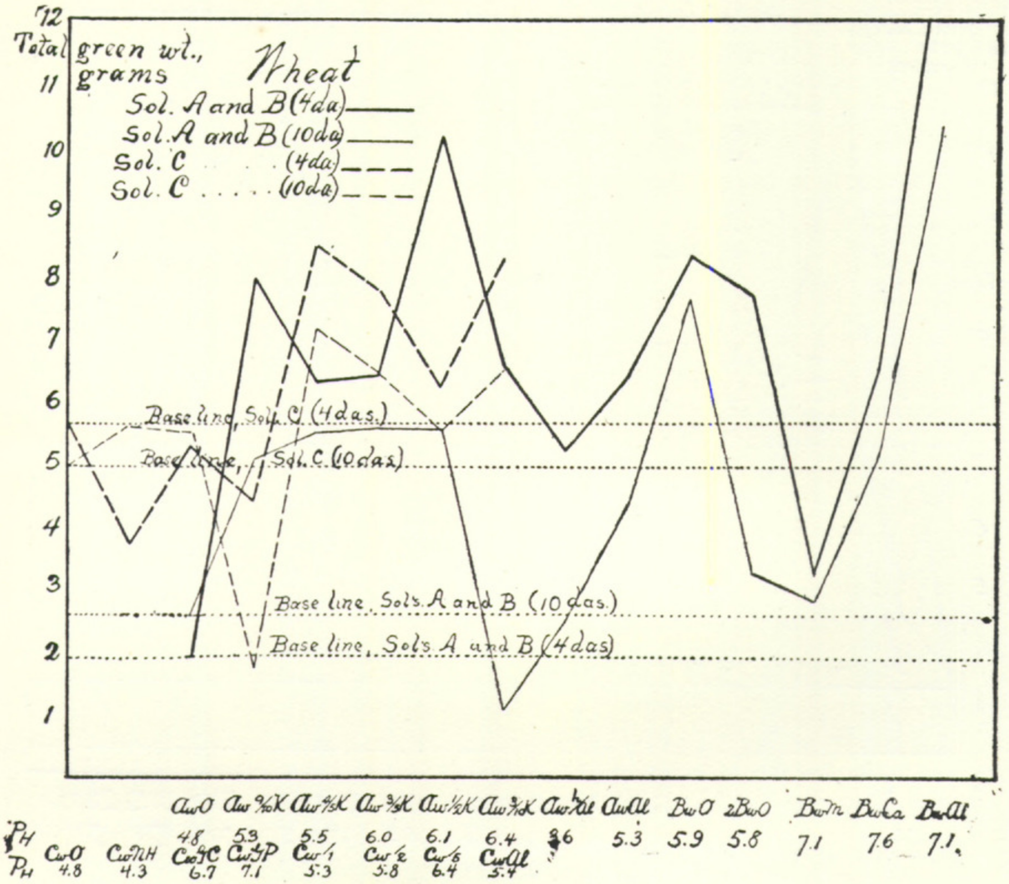

Fig. 3. Total green weight of wheat in solutions A, B, and C, with modifications effected largely by combinations of phosphates or by the introduction of "insoluble" buffers. Intervals between the renewal of solutions were 4 and 10 days.

ever, that in these cases the chlorosis may be related to inadequate iron supply, and not to faulty proportions of the main salt constituents.

The Ac h/1, Ac h/2 and Ac h/Al cultures all show the injurious effect of high acidity; but with the initial value of P_H 4.8 the best growth in the one lot is in the A solution, though practically approached in the double strength of the B solution [2(BcO)]. Aside from the considerable variation in cultures differing only slightly in composition or in P_H, the chief point of interest is the depressing action of the ammonium salt in both lots (BcNH).

The curves, figs. 3 (wheat) and 4 (corn), exhibit diagrammatically the data above discussed, and require no explanation, further than to point out that the results with solution C appear

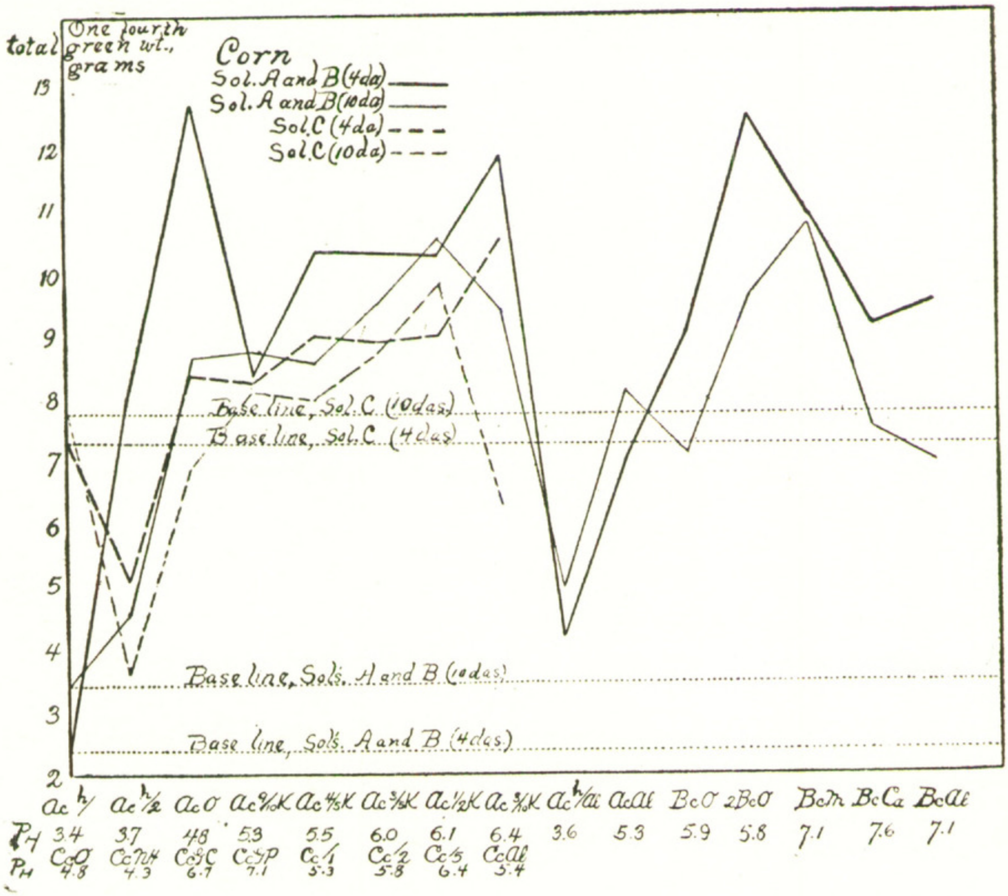

Fig. 4. One-fourth total green weight of corn in solutions A, B, and C. See further explanation under fig. 3.

in the same region of fig. 3 as solution A merely because it was necessary to do this in order to present all the data in a single figure.

In order to include solution C again in the tests, and at the same time to change somewhat the range of hydrogen ion concentrations in the A and B solutions, as well as to repeat the former work, a more extensive series of experiments was arranged with wheat, corn, and peas as indicated by the results in tables XI–XIX. Meanwhile, it had been determined from preliminary experiments that nutrient solutions of diverse constitution seem to be considerably influenced by the conditions under which the cultures were grown. There was, therefore, introduced into this series three sets of conditions. On account of the fact that other experiments were under way in the green-

TABLE XI

(Series 4, I—Wheat [moist, high temperature])

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H	
					Initial	After gr.
1	AwO	4.19	.491	30.71	3.4	4.0
2	Aw /5	4.10	.400	26.77	4.6	5.3
3	Aw /10	3.78	.399	27.00	5.8	4.4
4	Aw 1/	2.60	.338	24.63	3.35	4.4
5	Aw 3/	2.22	.328	22.08	3.15	3.6
6	AwNa	3.83	.468	30.10	3.45	3.8
7	AwM	4.65	.485	29.23	5.4	4.0
8	BwO	5.22	.469	32.96	6.6	7.2
9	Bw /5	4.90	.466	32.84	7.4	7.6
10	Bw /10	4.65	.424	32.04	8.6	8.2
11	Bw 1/	5.38	.491	32.06	6.4	7.2
12	Bw 5/	5.35	.472	31.33	3.2	6.8
13	Bw 10/	.95	.177	12.26	2.8	3.8
14	BwK_2 /10	5.13	.466	35.55	7.0	7.2
15	BwCa	5.70	.539	34.23	7.3	6.6
16	CwO	4.82	.465	29.12	4.2	6.4
17	Cw /5	4.17	.401	24.78	6.4	7.0
18	Cw /20	2.25	.301	18.85	7.6	7.2
19	Cw 1/	4.05	.403	26.50	3.6	6.4
20	Cw 5/	2.47	.296	20.85	3.2	5.2
21	CwNa	4.50	.441	28.72	4.2	6.6

houses at the same time no particular effort was made to control accurately the conditions of growth. The following general conditions were decided upon: (I) Moist high temperature, (II) moist low temperature, and (III) dry high temperature. These conditions are relative, of course, and all supported good growth. "Moist" in the sense here used simply means that by frequent sprinkling of walls and floors the humidity was raised above that of the usual greenhouse compartment. However, in the case of those cultures placed under conditions of high moisture and high temperature there was also necessary a slight degree of shade. This caused the plants to grow up rather quickly. As a result of this rapid growth in this section of the series it was determined to take down all cultures after about 15 days except those placed under the conditions referred to as moist, low

TABLE XII
(Series 4, II—Wheat [moist, low temperature])
SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H	
					Initial	After gr.
1	AwO	3.72	.681	16.81	3.4	4.0
2	Aw /5	10.87	1.373	22.90	4.6	6.0
3	Aw /10	8.85	1.087	21.40	5.8	6.4
4	Aw 1/	4.42	.736	16.75	3.35	4.0
5	Aw 3/	3.27	.579	16.23	3.15	3.4–3.5
6	AwNa	6.80	.862	19.28	3.45	5.8
7	AwM	11.24	1.323	24.20	5.4	6.6
8	BwO	10.92	1.035	20.75	6.6	7.0
9	Bw /5	8.40	.912	19.27	7.4	7.6
10	Bw /10	9.02	.924	22.12	8.6	8.1
11	Bw 1/	7.37	.908	20.69	6.4	7.1
12	Bw 5/	9.17	.910	20.06	3.2	7.2
13	Bw 10/	.90	.209	8.80	2.8	3.6
14	BwK_2 /10	8.82	.984	19.46	7.0	7.5
15	BwCa	11.64	1.354	20.51	7.3	7.4
16	CwO	6.75	.870	18.54	4.2	7.7
17	Cw /5	6.77	.826	16.93	6.4	7.8
18	Cw /10	5.60	.681	12.85	7.6	8.6
19	Cw 1/	7.22	.915	18.90	3.6	7.7
20	Cw 5/	7.55	.916	18.17	3.2	7.5
21	CwNa	7.75	.853	18.78	4.2	7.8

temperature. On account of conditions prevailing at the time, sections I and III were actually maintained from 16 to 18 days. The plants in section II were permitted to run from 25 to 27 days. This was an extreme test of the tolerance of these solutions, and no change of the nutrient medium was made in any culture throughout the entire period of growth. The water lost by transpiration was, however, replaced from day to day.

A general survey of the blocks of cultures represented by solutions A, B, and C gives evidence that under conditions of rather moist air and high temperature (table XI) wheat grown without change of solution for 18 days exhibits less striking differences in the maximum growth quantities than may be seen in the earlier series of cultures. Nevertheless, the highest value, whether of total green weight or of dry weight, is found in culture

TABLE XIII
(Series 4, III—Wheat [dry, high temperature])
SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H	
					Initial	After gr.
1	AwO	2.77	.395	19.70	3.4	4.8
2	Aw /5	5.50	.582	26.23	4.6	5.8
3	Aw /10	5.61	.601	24.90	5.8	6.1
4	Aw 1/	1.78	.287	17.14	3.35	3.4
5	Aw 3/	1.55	.248	16.33	3.15	3.4
6	AwNa	3.66	.441	23.70	3.45	3.6
7	AwM	3.35	.390	21.89	5.4	5.0
8	BwO	7.43	.658	26.54	6.6	7.2
9	Bw /5	7.25	.733	30.97	7.4	7.6
10	Bw /10	5.64	.493	22.37	8.6	8.6
11	Bw 1/	4.72	.554	24.38	6.4	8.6
12	Bw 5/	5.42	.566	25.19	3.2	7.3
13	Bw 10/	.17	.092	6.67	2.8	2.9
14	$BwK_2/10$	6.40	.615	26.58	7.0	7.9
15	BwCa	7.39	.765	28.62	7.3	8.2
16	CwO	4.49	.510	21.60	4.2	7.2
17	Cw /5	4.97	.576	23.43	6.4	7.6
18	Cw /20	3.32	.450	20.20	7.6	8.2
19	Cw 1/	4.80	.491	23.66	3.6	7.0
20	Cw 5/	2.00	.298	19.02	3.2	5.0
21	CwNa	4.50	.522	24.00	4.2	7.4

BwCa. Several other cultures in the B block, notably Bw 1/ and Bw 3/, exceed slightly all those of the C block by either of the 2 important criteria, that is, green weight or dry weight. Under these conditions the tolerance of high hydrogen ion concentration is generally marked, as shown in cultures AwO, AwNa, Bw 5/, and Cw 1/. Likewise the range of tolerance and of strong growth is considerable.

In section II of this series with wheat (table XII) it is the inference from the data that when grown for a longer period (25 days) under cooler conditions wheat is less resistant to high hydrogen ion concentration. This is shown in part by the fact that the 4 cultures yielding highest in green weight are BwCa, AwM, BwO, and Aw /5. There is, however, no striking falling off, on the whole, as hydrogen ion concentration increases to

TABLE XIV

(Series 4, I—Corn [moist, high temperature])

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H	
						Initial	After gr.
1	AcO	19.05	4.42	.593	34.72	3.4	4.2
2	Ac /5	27.32	6.80	1.786	40.20	4.6	4.6
3	Ac /10	18.85	3.87	.305	38.58	5.8	6.0
4	Ac 1/	14.83	4.01	1.136	30.48	3.35	6.3
5	Ac 3/	9.45	3.28	1.129	29.23	3.15	6.4
6	AcNa	6.44	3.09	.973	22.77	3.45	6.6
7	AcM	24.02	4.80	1.615	38.24	5.4	6.5
8	BcO	22.31	4.93	1.781	38.63	6.6	5.2
9	Bc /5	19.77	2.44	1.452	39.65	7.4	6.4
10	Bc /10	21.12	4.97	1.538	39.64	8.6	6.1
11	Bc 1/	20.93	3.81	1.726	40.85	6.4	5.6
12	Bc 5/	21.55	4.33	1.724	41.25	3.2	4.4
13	Bc 10/	9.02	2.38	.936	22.71	2.8	7.1
14	BcK_2 /10	25.56	4.44	1.770	43.46	7.0	5.2
15	BcCa	19.02	2.70	1.572	43.40	7.3	7.2
16	CcO	20.02	4.70	1.396	27.26	4.2	7.7
17	Cc /5	16.11	3.28	1.105	26.72	6.4	7.4
18	Cc /20	15.81	4.81	1.207	22.18	7.6	7.9
19	Cc 1/	19.81	4.88	1.341	33.56	3.6	7.6
20	Cc 5/	26.72	6.67	1.780	31.02	3.2	7.6
21	CcNa	18.81	3.94	1.165	30.62	4.2	7.7

about P_H 3.2, although there is not the consistency which might be expected between cultures AwO, Cw 1/, Cw 5/, and Bw 5/.

Where the conditions involved a relatively dry atmosphere and a high greenhouse temperature the response of the organism to the different culture solutions is of special interest. The three cultures with highest green weight yields are all in the B block, namely, BwO, BwCa, and Bw /5. These are so far ahead of the cultures in the A and C blocks, irrespective of hydrogen ion concentration within the usual range, as to leave no doubt whatever that for continued cultivation in the same solution for a period of 18 days the B solution is decidedly the most favorable culture medium. In this case too we have as definite an indication as has been afforded as to the limitation imposed by hydrogen ion concentrations. With an exponent

TABLE XV

(Series 4, II—Corn [moist, low temperature])

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H	
						Initial	After gr.
1	AcO	8.77	3.25	1.007	15.83	3.4	5.6
2	Ac /5	22.81	8.44	1.703	22.98	4.6	6.0
3	Ac /10	23.10	8.94	1.521	22.78	5.8	6.2
4	Ac 1/	21.97	6.94	1.933	21.75	3.35	5.8
5	Ac 3/	11.28	2.82	1.303	15.65	3.15	6.0
6	AcNa	19.30	7.91	1.744	20.56	3.45	6.0
7	AcM	27.56	10.69	2.078	22.72	5.4	6.0
8	BcO	18.90	7.50	1.828	20.64	6.6	6.4
9	Bc /5	31.99	14.50	2.508	23.51	7.4	5.9
10	Bc /10	28.63	14.54	2.213	21.84	8.6	7.0
11	Bc 1/	23.61	7.74	2.423	24.14	6.4	4.8
12	Bc 5/	27.80	10.60	2.464	23.44	3.2	6.0
13	Bc 10/	15.50	6.20	1.366	16.19	2.8	5.6
14	BcK_2 /10	36.30	6.44	2.950	23.50	7.0	5.7
15	BcCa	26.03	10.11	2.699	23.57	7.3	7.4
16	CcO	34.60	11.02	2.763	24.66	4.2	7.6
17	Cc /5	28.47	9.72	2.350	23.59	6.4	7.6
18	Cc /20	20.90	6.75	1.868	20.10	7.6	8.6
19	Cc 1/	23.52	7.55	1.966	23.40	3.6	7.6
20	Cc 5/	21.22	6.70	1.687	22.15	3.2	7.6
21	CcNa	24.60	9.07	2.090	19.74	4.2	7.6

below P_H 4 there is definite diminution of growth in every instance, except Bw 5/. AwM seems to be distinctly out of harmony in this group. The suggestion from culture Bw /10 is that under these climatic conditions a relatively low degree of alkalinity, probably about P_H 8, would represent the limit for most favorable growth in a solution thus constituted.

The results with corn grown in a moist atmosphere at a high temperature are perhaps more erratic than in any other section of the work. At least with the data at hand it is extremely difficult to interpret these results. It would appear that the best growth is in culture Ac /5, and it is closely followed by Cc 5/, the last solution being close to the usual limit of growth in respect to hydrogen ion concentration. In both these cases the increase in the growth over that in BcK_2/10, AcM, and BcO is

TABLE XVI

(Series 4, III—Corn [dry, high temperature])

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H	
						Initial	After gr.
1	AcO	24.43	8.59	1.812	24.35	3.4	5.9
2	Ac /5	25.90	7.94	1.751	22.81	4.6	6.0
3	Ac /10	17.22	5.28	1.360	27.64	5.8	6.2
4	Ac 1/	21.80	5.60	1.667	31.24	3.35	4.0
5	Ac 3/	17.49	4.61	1.405	23.65	3.15	4.6
6	AcNa	16.00	4.70	1.231	27.17	3.45	5.6
7	AcM	30.41	9.61	2.014	32.26	5.4	6.2
8	BcO	19.89	6.30	1.604	27.07	6.6	4.0
9	Bc /5	20.89	7.11	1.756	29.80	7.4	6.8
10	Bc /10	20.90	5.85	1.810	30.41	8.6	6.8
11	Bc 1/	23.00	9.25	1.637	27.75	6.4	5.0
12	Bc 5/	20.02	7.70	1.442	29.59	3.2	4.2
13	Bc 10/	1.64	.43	.285	5.11	2.8	3.4
14	BcK_2 /10	24.52	9.89	1.665	31.33	7.0	5.2
15	BcCa	23.44	8.81	1.867	32.53	7.3	7.8
16	CcO	16.62	4.97	1.125	25.67	4.2	7.8
17	Cc /5	18.52	5.20	1.180	32.71	6.4	8.0
18	Cc /20	11.28	4.06	.835	14.88	7.6	8.0
19	Cc 1/	20.56	5.65	1.407	29.97	3.6	7.9
20	Cc 5/	8.63	1.61	.856	20.75	3.2	7.6
21	CcNa	15.54	5.57	1.122	25.31	4.2	7.8

largely an increase in the growth of roots. It is perhaps possible that the partial shade of this series referred to above has been a factor in the irregularities which prevail throughout. There is no basis on which to explain the growth in AcNa. Turning, however, to table xv, indicating the results with corn grown at low temperature and higher humidity the data are notably different from the preceding. In this case the most favorable medium is culture $BcK_2/10$, rather closely followed by CcO and less closely by Bc5/. In this section it is also notable that the maximum root growth occurs over a range of hydrogen ion concentration from 4.2 to 8.6. Exclusive of culture CcO the higher growth quantities are obtained for the different solutions at relatively low hydrogen ion concentration, that is, with media approaching neutrality more or less. This is particularly ob-

TABLE XVII
(Series 4, I—Peas [moist, high temperature])

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H	
						Initial	After gr.
1	ApO	12.53	4.15	1.010	28.46	3.4	3.5
2	Ap /5	13.82	4.15	1.059	31.05	4.6	4.2
3	Ap /10	13.92	3.87	1.062	13.25	5.8	5.8
4	Ap 1/	11.55	3.42	.937	28.00	3.35	4.7
5	Ap 3/	11.93	3.17	.990	29.68	3.15	5.8
6	ApNa	12.56	3.93	1.024	31.42	3.45	4.6
7	ApM	12.81	3.93	.966	30.00	5.4	4.6
8	BpO	10.60	3.02	.839	25.87	6.6	6.4
9	Bp /5	13.17	3.64	.957	31.97	7.4	7.5
10	Bp /10	9.80	3.11	.746	32.47	8.6	7.6
11	Bp 1/	11.17	3.47	.809	23.37	6.4	7.0
12	Bp 5/	11.12	2.89	.842	26.22	3.2	5.8
13	Bp 10/	7.59	2.21	.623	23.29	2.8	4.8
14	BpK_2 /10	12.30	3.61	.936	26.62	7.0	7.3
15	BpCa	12.55	3.50	.937	29.57	7.3	7.6
16	CpO	12.44	3.39	.974	25.34	4.2	5.2
17	Cp /5	8.19	2.16	.657	21.66	6.4	6.2
18	Cp /20	10.52	2.93	.928	22.37	7.6	7.5
19	Cp 1/	12.50	3.50	.982	26.02	3.6	5.0
20	Cp 5/	6.93	2.01	.605	21.36	3.2	4.2
21	CpNa	10.72	3.06	.923	22.35	4.2	5.4

servable in cultures Ac /10, Bc /5, Bc /10, BcCa, and Cc /5. Corn grown under conditions of high temperature and low humidity exhibits a maximum in AcM followed respectively by BcK_2/10, Ac /5, BcCa, and Bc 1/. An examination of block A would seem to indicate that P_H 3.4 to 4.6 is entirely favorable in this medium, but there is a striking difference between Ac/10 and AcM, which is not readily explainable.

In table XVII it may be noted again that slight variations in the culture medium do not materially affect the growth of peas when grown under the conditions there indicated. The A solution with the addition of alkali yields, it is true, the maximum growth quantities, but these quantities are only slightly in excess of those obtained with the same solution unmodified or of several cultures in the B block, notably Bp /5, BpK_2/10, and

TABLE XVIII
(Series 4, II—Peas [moist, low temperature])

SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H	
						Initial	After gr.
1	ApO	17.72	6.55	1.772	19.07	3.4	5.5–5.6
2	Ap /5	25.71	12.17	2.290	18.06	4.6	6.0
3	Ap /10	24.26	9.72	2.299	20.00	5.8	5.9–6.0
4	Ap 1/	21.05	9.00	1.980	17.77	3.35	5.9
5	Ap 3/	22.52	9.44	2.183	19.18	3.15	5.6
6	ApNa	20.69	8.52	.889	17.61	3.45	5.7
7	ApM	25.65	11.20	2.310	19.87	5.4	
8	BpO	13.87	8.26	1.400	15.82	6.6	6.1–6.2
9	Bp /5	13.65	5.18	1.308	14.74	7.4	7.1
10	Bp /10	18.57	7.54	1.704	15.63	8.6	7.6
11	Bp 1/	16.93	6.61	1.590	17.38	6.4	6.0
12	Bp 5/	16.14	7.59	1.378	13.30	3.2	6.0
13	Bp 10/	9.55	3.88	.881	10.98	2.8	5.5
14	BpK_2 /10	18.11	8.90	1.455	16.26	7.0	6.2
15	BpCa	20.17	8.23	1.944	19.28	7.3	7.4
16	CpO	16.44	6.44	1.650	13.85	4.2	7.2
17	Cp /5	16.31	6.10	1.762	13.62	6.4	7.8
18	Cp /20	12.32	4.54	1.406	10.82	7.6	7.7
19	Cp 1/	16.36	6.95	1.599	13.61	3.6	7.2
20	Cp 5/	17.62	7.06	1.760	13.22	3.2	6.4
21	CpNa	16.54	5.62	1.711	17.38	4.2	7.0

BpCa, as also by two cultures in the C block, namely CpO and Cp 1/.

Wider differences are found in the case of peas grown at lower temperature in more humid air, but the maximum growth occurs in the A block, especially with the addition of a small amount of alkali (Ap /5) and in the ApM culture, containing both monobasic and dibasic phosphates. No culture in the B block approaches the values referred to, and the same is true of the C cultures. Grown 16 days under dry conditions at a high temperature the yield of the various cultures is much reduced, and the relative values of the culture media do not remain the same as before. In this instance the B block exhibits the highest yields, especially cultures BpCa and BpK_2/10. The next higher yield is found in Ap /10. In the A block the effect of high

TABLE XIX
(Series 4, III—Peas [dry, high temperature])
SALT REQUIREMENTS AND H-ION CONCENTRATION IN RELATION TO GROWTH

No.	Culture indices	Total gr. wt. (gms.)	Gr. wt. of roots (gms.)	Total dry wt. (gms.)	Greatest length (cm.)	P_H	
						Initial	After gr.
1	ApO	7.42	3.05	.952	23.68	3.4	4.6
2	Ap /5	10.62	3.55	1.026	24.63	4.6	5.0
3	Ap /10	13.95	4.49	1.161	27.63	5.8	5.4
4	Ap 1/	3.20	1.10	.642	11.82	3.35	5.3
5	Ap 3/	6.78	2.47	.796	18.84	3.15	5.0
6	ApNa	11.22	3.60	.945	25.33	3.45	4.4
7	ApM	10.00	3.89	1.095	23.57	5.4	5.6
8	BpO	12.79	4.37	1.023	24.06	6.6	4.5
9	Bp /5	12.97	4.15	1.059	25.96	7.4	7.3
10	Bp /10	12.90	4.12	1.027	26.05	8.6	7.4
11	Bp 1/	8.64	2.15	.877	21.11	6.4	7.0
12	Bp 5/	11.95	4.27	.948	24.23	3.2	6.1
13	Bp 10/	2.97	0.75	.432	9.95	2.8	3.0
14	BpK_2 /10	14.32	4.90	1.130	27.37	7.0	7.3
15	BpCa	14.44	4.92	1.233	26.33	7.3	7.8
16	CpO	6.60	2.10	.929	16.91	4.2	6.0
17	Cp /5	11.65	3.50	1.046	21.43	6.4	6.6
18	Cp /20	5.11	1.22	.760	15.40	7.6	7.6
19	Cp 1/	10.97	3.45	.977	21.28	3.6	5.4
20	Cp 5/	5.40	1.25	.636	15.54	3.2	5.8
21	CpNa	8.75	2.45	.966	18.99	4.2	6.0

hydrogen ion concentration is marked. In general, as the conditions of evaporation are intensified it would appear that somewhat more favorable results are obtained with this plant when the hydrogen ion concentration does not approach too closely the acid limit.

It is clear, however, that the preparation of nutrient solutions with acid phosphate—even though of high grade—may mean, and often does mean, a hydrogen ion concentration either perilously near the critical region for growth, or actually inhibiting growth. This is particularly true for wheat, and it may be true for corn and other crops under any conditions which may accentuate acid injury. Pronounced diminution in growth may occur as the P_H exponent is progressively diminished from about 4.5.

For each plant in the preceding series a separate set of curves (figs. 5, 6, and 7) has been prepared; and in each figure there are

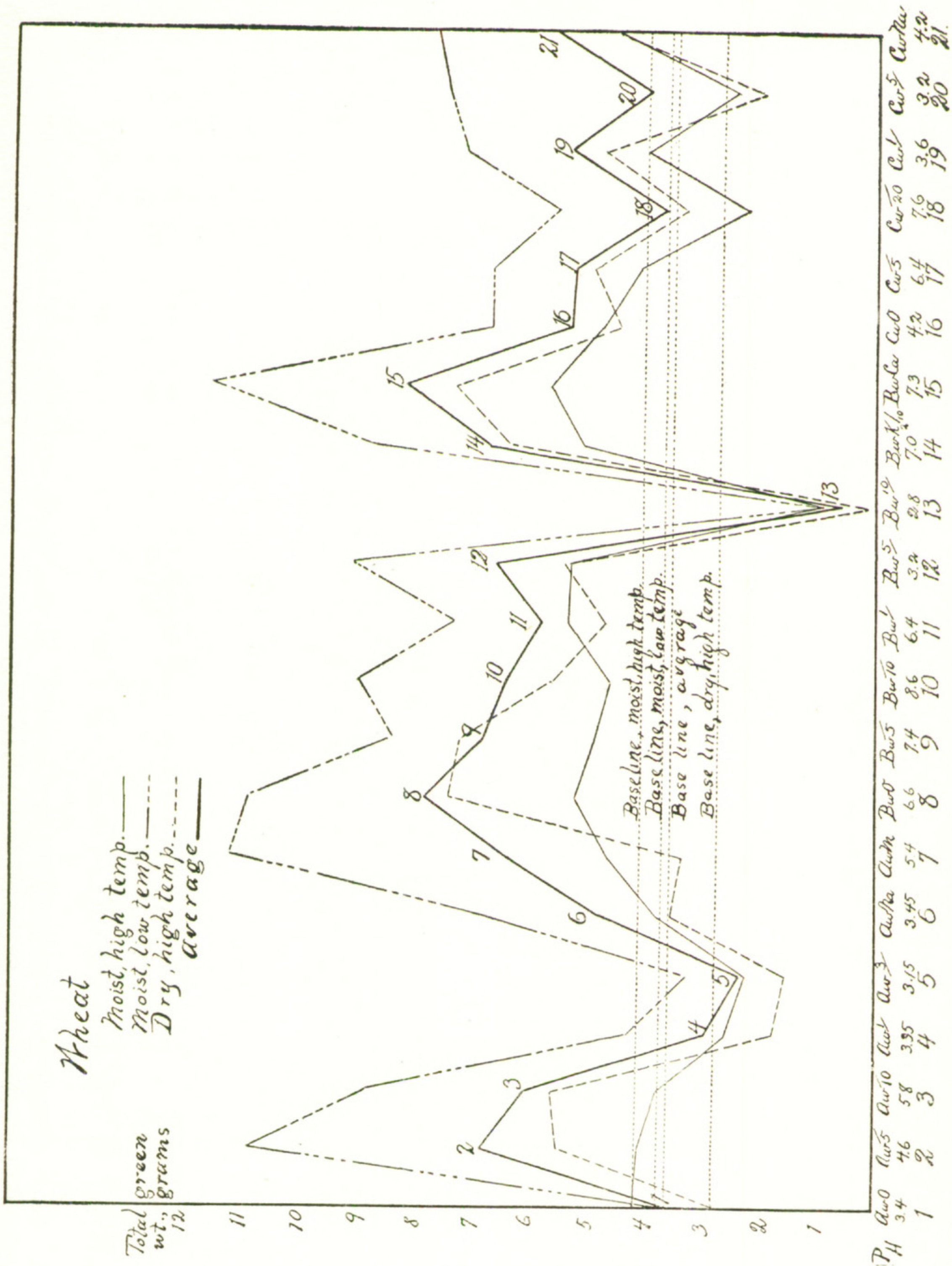

Fig. 5. Total green weight of wheat in solutions A, B, and C, with variations and under somewhat diverse external conditions, as indicated in connection with the curves.

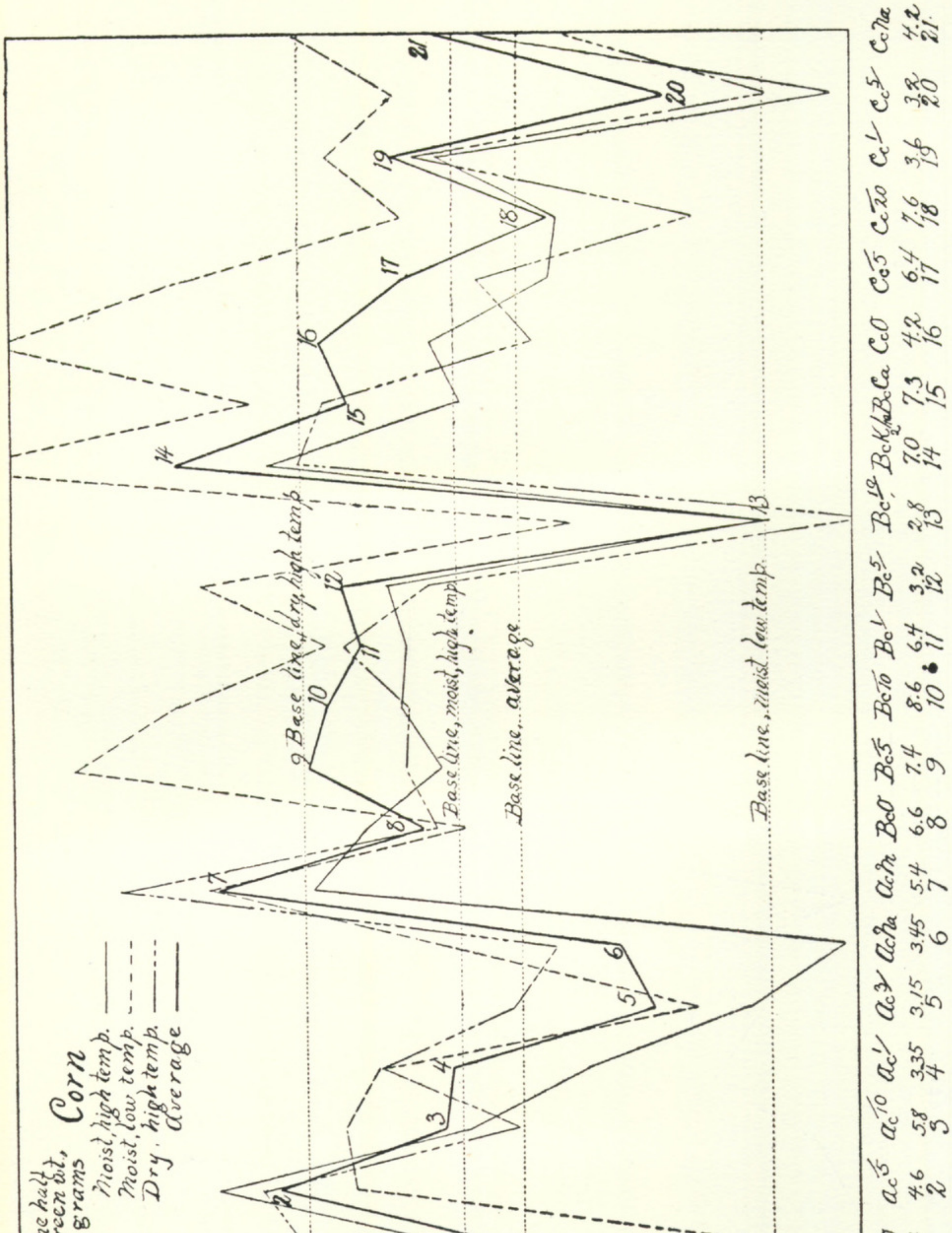

Fig. 6. One-half total green weight of corn in solutions A, B, and C, with variations and under somewhat diverse external conditions, as indicated in connection with the curves.

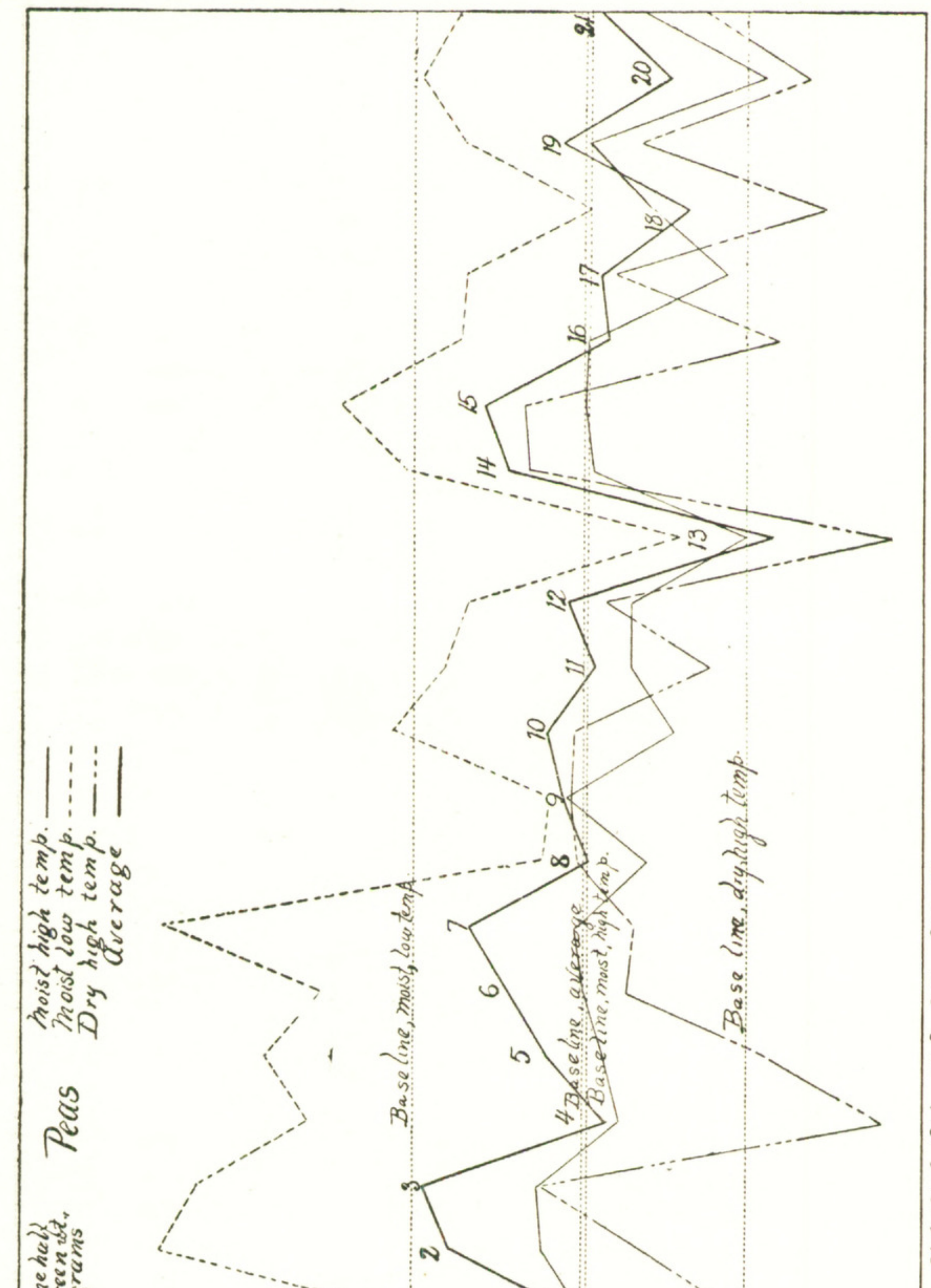

Fig. 7. One-half total green weight of Canada field peas in solutions A, B, and C, with variations and under somewhat diverse external conditions, as indicated in connection with the curves.

3 curves representing the results under the 3 combinations of conditions, as well as a fourth curve exhibiting the average of the 3 others.

General Discussion

Hoagland ('17) determined the effect of H- and OH-ion concentration on the growth of barley seedlings in an incomplete nutrient solution, omitting calcium, magnesium, and iron,—employing therefore only phosphates of potassium in some series and in others adding to these small proportions of sodium salts, including nitrate. The H-ion adjustments were made on the alkaline side with K_3PO_4 and K_2HPO_4; on the acid side there was used KH_2PO_4, supplemented in one case by H_3PO_4 and by the dibasic salt. As a result of numerous experiments he finds that a concentration of OH-ion greater than 1.8×10^{-6} was injurious, and it was extremely toxic when the concentration reached 2.5×10^{-5}. A concentration of H-ion of $.7\times10^{-5}$ was favorable to growth while $.3\times10^{-3}$ was very toxic. In these solutions there was, of course, opportunity for antagonistic effects, and since the solutions were unbalanced, the injurious effect of the potassium or sodium ions or both would require consideration.

Some of the complicated effects resulting from the addition of salts to toxic acid and alkaline solutions, especially in respect to the water relations of plants, have been dealt with by Dachnowski ('14); but inasmuch as the constituents of nutrient solutions were not involved either in control experiments or otherwise the data are scarcely applicable here.

It is difficult, if not impossible, to attempt a comparison of the toxic action of H-ions and OH-ions from the dissocation respectively of mineral acids and such hydroxides as those of sodium and potassium in distilled water with the toxic effects produced by the same ions in a culture solution containing diverse other ions, especially the cations of the salts usually employed. In the latter solutions antagonistic effects, dependent in part upon specific relations of the plant employed, must to a certain degree obscure the magnitude of the effects. It is of interest to note, however, that Kahlenberg and True ('96) found that roots of *Lupinus albus* just lived in n/6400 HCl. Nevertheless, after 5 days in n/25,600 HCl the growth rate was but little more than one-half that of similar roots in distilled water. Thus we may assume that a hydrogen ion concentration approximately P_H 4 depressed the root growth of this plant. The same seedlings survived n/400 potassium hydroxide during 24 hours, but with this reagent no growth measurements after an interval of several days, comparable to those with HCl, were made. The results of Heald ('96) also show that while roots of *Pisum sativum* survived n/6400 HCl, and those of *Zea Mays* n/1600, still in the former the growth rate was low in n/12,800 and for corn in n/3200, during an interval of 48 hours. No comparisons with distilled water were included.

Loew ('03), working with the seedlings of *Zea Mays*, and Miyake ('14), using *Oryza sativa*, have both shown a relatively greater resistance of these plants to alkali than to acid, all of which emphasizes the importance of devoting special consideration to the initial acidity of the culture solution.

Respecting the reaction of soils, there is considerable evidence indicating that acidity alone is not necessarily a limiting factor in the growth of many crops. With a method considered adequately accurate as applied to field conditions, Gillespie ('16) has examined air-dried samples of 22 crop soils and found the P_H exponent to vary from 4.55 to 7.1 in the case of 18 soils from Maine, Maryland, and Virginia, and a variation of from 8.1 to 8.7 with 4 soils from Utah and Montana. It is also reported by Gillespie and Hurst ('18) that the highest acidity (P_H 4.5) was not in the least injurious to potato culture in Caribou and Washburn loams, the two main potato-soil types in the region in which they worked.

Plummer ('18), employing the soil-suspension method, examined 68 samples of a variety of soil types of humid regions, especially of the southern states. Untreated sandy loam or clay soils exhibited a range of acidity $.1 \times 10^{-3}$ to 1×10^{-6}, while peat gave in one instance a hydrogen ion concentration $.2 \times 10^{-1}$. Evidence was gained to the effect that the surface film emphasizes the direction of the reaction, that is, in acid soils the surface film is more acid and in alkaline soils it is more alkaline. This is scarcely in corroboration of certain work of Sharp and Hoagland ('16).

In general, when the reactions of the culture solutions (such as have been employed in this work) are strongly acid, the contact with plant roots effects a change towards neutrality. The extent and rapidity of this change, however, depend somewhat upon the crop, and especially upon the composition of the culture solution. It may be noted, for instance, from tables XI–XIX that solution A never became neutral, while solution C was changed, in the extreme case, to P_H 8.6. On the other hand, it is not necessarily true that alkaline culture solutions tend to become acid, as may be seen in the case of solution C. Solution B, normally near the neutral point, may be shifted slightly in either direction.

Impelled in part by the general experience of others in field work, indicating a general tendency of cultivated soils to become acid, Breazeale and Le Clerc ('12) undertook solution-culture experiments to determine "the effect of the reaction of the culture medium on the growth of wheat seedlings and particularly on the development of the root," with a view to a possible explanation of the results obtained in practical agriculture. They regard the acid tendency as due primarily to the decay of organic matter and secondarily to the selective action of the root; the last mentioned only they proposed to investigate. Their experiments were chiefly with certain salts, particularly KCl, K_2SO_4, and $NaNO_3$, used singly and each in combination with solid $CaCO_3$. According to their results greater absorption of the K ion, when the potassium salts are used, caused the solution to become acid; while in the case of the sodium salt, the greater absorption of the NO_3 ion tended to produce alkalinity. The addition of calcium carbonate precludes the development of acid with the potassium salts. In the toxic action reported no account is taken of the lack of physiological balance in the solutions lacking Ca, and no experiments were made with KNO_3. Moreover, only a titration method (consistent with the general usage at that time) was employed in determining acidity and alkalinity.

Some time previous to this Hartwell and Pember ('07) emphasized the "marked property of the seedlings [wheat, rye, barley, and oats] of rendering the nutrient solutions alkaline—," insufficient, however, to cause precipitation. Similar observations are numerous in the literature.

Hoagland and his associates ('17, '18, '19) in a series of articles have pointed out some misinterpretations and discrepancies in the earlier work, and among other things have shown that with certain proportions of salts in solution cultures and in sand cultures having an initial acid reaction, this reaction was changed with the growth of the crops until it was approximately neutral. In certain cultures with an initial reaction approximately neutral, plants were grown to maturity without change of solution, and with the reaction remaining constant throughout. A nutrient solution strongly alkaline from the presence of K_3PO_4 became approximately neutral. Hoagland has also emphasized an important point appreciated likewise by some earlier investigators, namely, that the equivalence of positive and negative ions in the solutions is maintained, and the state of equilibrium, the recognition of which is often too vague, is of necessity kept in mind in any discussion of the absorption of ions.

In this paper it has been pointed out that there is generally a decline in growth in solutions A and C when the H-ion concentration is approximately P_H 6. This may be due to the relative insolubility of the phosphates. On the other hand, the generally more favorable growth in the B solution at or approaching neutrality may be related in part to the better distribution of phosphate ions or particles, due to the presence of certain substances in a state of greater dispersity. In this connection it will be recalled that Bonazzi ('19) and Allen ('19) have contributed interesting data on the favorable effects of shaking or agitation, on the growth of *Azotobacter chroococcum*, an organism necessarily grown in alkaline solutions.

Toole and Tottingham's ('18) results, showing increased yield with the addition of ferric hydroxide to Knop's solution, are also of particular interest in considering the data obtained in this work with solution B. At present there seems to be no basis for a final opinion on the rôle of aluminium in promoting growth in these experiments. The high adsorptive property of the compound used, together with its buffer action, may be concerned in the explanation. The maximum effect of this compound occurred with wheat, but in view of the complication of factors involved this may not be significant.

In the various series of experiments here reported there is considerable diversity in the intervals between the renewal of solutions. These intervals have varied from four days to a time interval covering the entire culture period. The results have been as consistent as might be expected, and it is believed that the value of lengthening the interval in this way is important from the standpoint of reducing the labor in the maintenance of such cultures. Trelease and Free ('17) have, however, shown that frequent changes of solution are more favorable for growth; but it also appears from their data that renewals during the first two weeks are not so important as those made later. They suggest that a continuous flow of solution through the culture is more beneficial than a daily change.

The work of Pantanelli ('15) and others has shown that after plants have been for a few hours in contact with salt solutions it may be demonstrated that there has been a different rate of absorption of the various ions. The solution, therefore, changes rapidly in the presence of abundant absorbing surfaces. Hoagland has also emphasized this point, and within a certain range of osmotic concentration he regards the initial concentration of any particular ion as practically immaterial. Nevertheless, it would be admitted by all that there must be on the one hand a true physiological balance, and that on the other hand, the concentration of no necessary ion or molecule shall become a limiting factor in growth. It is not, however, proposed to discuss in this paper the significance and final results of the interchange of ions or molecules between roots and solutions.

Discussing limiting factors in water cultures Stiles ('16) has drawn attention to the limited application of the water-culture method in physiological problems. He regards this as related to "(1) the difficulty in analyzing results due to the complex of factors not under control; (2) the difficulty of controlling in some cases even the factor whose action is being investigated; and (3) the excess of labor required to produce results which are only of a low degree of accuracy."

In a previous paper Stiles ('15) has in a measure crystallized the feeling of many investigators working with water cultures in arriving at the conclusion that it is necessary to calculate the probable error of the results in accurately evaluating the significance of differences exhibited by different sets of cultures.

In a study of probable error he grew single plants in each of 10 bottles of 1200 cc. capacity, employing uniform methods and seed of a selected strain of rye. Four concentrations of nutrient solutions were used with the different lots. Experiments conducted during the early months of the year yielded results as follows: The greatest individual variation in any one lot amounted to never less than 70 per cent. In the weakest concentration the individual variation was 333 per cent. However, the probable error of the mean in these cases was only about 3–10 per cent of the mean dry weights. Comparable differences were found in cultures made later in the spring with a pure line of barley.

That considerable variability has been found by others is evident from the examination of the tables in any case in which the data have been given in detail. Livingston and Tottingham ('18) give a table from which it appears that while the culture R_1C_3 yields only a fair growth of roots the dry weight for the entire plant is third and for tops is the highest of all in the series. This solution, however, differs from R_8C_1 in containing one-eighth the concentration of KNO_3, 3 times as much $Ca\ (H_2PO_4)_2$, and 6 times as much $MgSO_4$. R_8C_1 is regarded as "the best balanced for young wheat plants of all the nutrient solutions so far noted in the literature."

The Shive solution, on the one hand, and the Livingston-Tottingham solution, on the other, were of course designed with the idea of simplification. The 3 salts employed contain all the essential ions except iron. Theoretically, the phosphate, nitrate, and sulphate ions may be added in the form of the salts of either of the 3 bases or cations, K, Ca, and Mg. However, the relatively low solubility of Ca as sulphate may seem to render it less practicable to use this salt. There remain 7 possibilities in the selection of salts, and it might appear that in the selection of these the only important points might be, first, H-ion concentration, and second, the use of a base required in relatively low concentration with an anion which may be similarly reduced in strength.

From the emphasis in the literature, as is well known, an important consideration is an appropriate ratio between the ionic proportion of Ca and Mg. Other antagonistic relations also require consideration. An analysis of the differences between the Shive and the Livingston-Tottingham solution shows that the latter contains a relatively greater concentration of K and NO_3 ions and a lower concentration of Ca, Mg, PO_4, and SO_4. Serious typographical errors in one of their tables (table three, page 345) have led Livingston and Tottingham ('18) into error in the statement that in the R_5C_2 solution there are 2.89 times as many atoms of Ca as of K per unit volume. As a matter of fact the partial volume atomic concentration of the R_8C_1 solution of Livingston and Tottingham contains more than 10 times as much K as Ca, while R_6C_1 contains more than 8 times as much K as Ca, and nearly 6 times as much Mg as Ca. The Mg : Ca ratio of R_8C_1 is very nearly 2 : 1. In both of the best Livingston-Tottingham solutions the ionic concentrations of K and NO_3 are greatest. It seems quite probable that this factor, together with the variability in H-ion concentration of KH_2PO_4, is accountable for the better growth in these solutions.

Summary and Tentative Conclusions

The experiments reported in this paper were undertaken primarily to determine the influence of variations in hydrogen ion concentration on the yield of certain seed plants in solution cultures. As the work progressed, however, many modifications were suggested, and some of these involved in no way a consideration of hydrogen ion concentration at points which might be regarded as critical for the growth of the crops used.

The selection of several culture solutions seemed necessary in order that some diversity might be introduced in the salt proportion or composition factors. The solutions employed, and their designations, were as follows: solution A, a slight modification of one of Shive's "best" solutions; solution C, a slight modification of one of the best Livingston-Tottingham combinations; and solution B, based in part upon the Crone combination of salts, but with this essential difference, namely, that "soluble ferric phosphate" was used in place of the "insoluble" iron salt. Each of the solutions first mentioned contains a monobasic phosphate, and with theoretically pure chemicals should yield culture solutions with a P_H exponent about 4.5. Solution B may vary, in my experience, from a hydrogen ion concentration represented by P_H 5.4 to P_H 7.1; frequently, however, it is 6.6 to 7.1.

The experiments have been carried out in the greenhouse at different periods of the year, and represent, on the whole, a considerable range of environmental conditions. It has been impracticable to analyze these except in a very general way, or relatively. Wheat and corn have been employed in every series of experiments and Canada field peas in all series here reported except one.

Under the most favorable conditions, the 3 solutions mentioned above, without other modification, may all yield excellent growth. Plants grown in solution B are invariably of a deeper green, presenting a finer appearance, and the average of the growth quantities (green weight) is higher for wheat and corn than in either of the other 2 solutions. In the unmodified solutions A and C the green weight of peas averages higher than in the unmodified solution B.

Culture solutions prepared with monobasic phosphates may, however, exhibit a hydrogen ion concentration which is too high for the maintenance of the best growth under certain conditions, and especially is this true in the case of wheat.

Solutions made with monobasic potassium or calcium phosphate free from acid may, under certain conditions, yield maximum growth quantities, but there is often considerable variability in the duplicate cultures due to unknown factors. Certain grades of the phosphates mentioned—if not specially purified in the laboratory—exhibit a P_H which may be distinctly toxic. Correction of the P_H to about 4.8 or 5.2 by means of $NaOH$ or by the use, in part, of a dibasic salt generally affords increased growth.

Under extreme conditions—effecting a high evaporation rate—it becomes more important to correct to the higher P_H exponent. Wheat, corn, and peas are sensitive in the order named to high hydrogen ion concentration.

Usually, the addition to solution B of small amounts of dibasic potassium phosphate, of solid calcium carbonate, and of aluminium hydroxide has given increased yields, often considerably above that of the unmodified solution. The results in the case of the aluminium compound are notable in the case of wheat grown under the conditions described,—related in part, presumably, to adsorption and buffer action.

In general, it would seem that there may be no single "best" solution for the growth of any of the 3 plants employed in this work. In all probability a "best" solution, like the "optimum" temperature, is represented within the "optimum" concentration rather by considerable range of salt or ion proportions, influenced to a greater or less degree by environmental factors.

If the initial P_H of the culture solution is considerably less than neutrality there is generally a tendency for this to be shifted toward the neutral point, although this depends in part upon the composition of the solution and in part upon the plant grown.

Bibliography

Allen, E. R. ('19). Some conditions affecting the growth and activities of Azotobacter chroococcum. Ann. Mo. Bot. Gard. **6**: 1–44. *pl. 1.* 1919.

Bonazzi, A. ('19). On nitrification. II. Intensive nitrite formation in solution. Jour. Bact. **4**: 43–59. *pl. 1.* 1919.

Breazeale, H. F., and Le Clerc, J. A. ('12). The growth of wheat seedlings as affected by acid or alkaline conditions. U. S. Dept. Agr., Bur. Chem. Bul. 149: 1–18. *pl. 1–8.* 1912.

Burd, J. S. ('19). Rate of absorption of soil constituents at successive stages of plant growth. Jour. Agr. Res. **18**: 51–72. *f. 1–13.* 1919.

Clark, W. M., and Lubs, H. W. ('17). Colorimetric determination of hydrogen ion concentration and its applications in bacteriology. Jour. Bact. **2**: 1–34, 109–136, 191–236. 1917.

Dachnowski, A. ('14). The effects of acid and alkaline solutions upon the water relation and the metabolism of plants. Am. Jour. Bot. **1**: 412–440. *f. 1–4.* 1914.

Duggar, B. M. ('11). Plant physiology. New York, 1911. (See pp. 136–194.)

————, ('19). The micro-colorimeter in the indicator method of hydrogen ion determination. Ann. Mo. Bot. Gard. **6**: 179–181. 1919.

————, and Bonns, W. W. ('18). The effect of Bordeaux mixture on the rate of transpiration. Ann. Mo. Bot. Gard. **5**: 153–176. *pl. 10.* . 1918.

————, and Dodge, C. W. ('19). The use of the colorimeter in the indicator method of H-ion determination with biological fluids. Ann. Mo. Bot. Gard. **6**: 61–70. *f. 1.* 1919.

Gillespie, L. J. ('16). The reaction of soil and measurements of hydrogen ion concentration. Wash. Acad. Sci. Jour. **6**: 71–76. *f. 1–2.* 1916.

————, and Hurst, L. A. ('18). Hydrogen ion concentration—soil type—common potato scab. Soil Science **6**: 219–236. *f. 1–3.* 1918.

Hartwell, B. L., and Pember, F. R. ('07). The relation between the effects of liming and of nutrient solutions containing different amounts of acid, upon the growth of certain cereals. R. I. Agr. Exp. Sta., Ann. Rept. **20**: 358–380. *f. 1–2.* 1907.

Heald, F. D. ('96). On the toxic effect of dilute solutions of acids and salts upon plants. Bot. Gaz. **22**: 125–153. *pl. 7.* 1896.

Hoagland, D. R. ('17). The effect of hydrogen and hydroxyl ion concentration on the growth of barley seedlings. Soil Science **3**: 547–560. 1917.

————, ('18). The relation of the plant to the reaction of the nutrient solution. Science N. S. **48**: 422–425. 1918.

————, ('19). Relation of the concentration and reaction of the nutrient medium to the growth and absorption of the plant. Jour. Agr. Res. **18**: 73–117. *f. 1–4.* 1919.

Kahlenberg, L., and True, R. H. ('96). On the toxic action of dissolved salts and their electrolytic dissociation. Bot. Gaz. **22**: 81–124. 1896.

Livingston, B. E., and Tottingham, W. E. ('18). A new three-salt nutrient solution for plant cultures. Am. Jour. Bot. **5**: 337–346. 1918.

Loew, F. A. ('03). The toxic effect of H- and OH-ions on seedlings of Indian corn. Science N. S. **18**: 304–308. 1903.

McCall, A. G. ('15). A new method for the study of plant nutrients in sand cultures. Am. Soc. Agron. Jour. **7**: 249–252. 1915.

————, ('16). Physiological balance of nutrient solutions for plants in sand cultures. Soil Science **2**: 207–254. *pl. 1. f. 1–8.* 1916.

————, Norton, J. B. S., and Richards, P. E. ('19). Abnormal stem growth of soy beans in sand cultures with Shive's three-salt solution. *Ibid.* **6**: 479–481. *pl. 1–2.* 1919.

Miyake, K. ('14). Ueber die Wirkung von Säuren, Alkalien und einiger alkali Salze auf dem Wachstum der Reispflanzen. Sapporo Nat. Hist. Soc., Trans. **5**: 91–95. 1914.

Pantanelli, E. ('15). Über Ionenaufnahme. Jahrb. f. wiss. Bot. **56**: 689–733. 1915.

Plummer, J. K. ('18). Studies in soil reaction as indicated by the hydrogen electrode. Jour. Agr. Res. **12**: 19–31. 1918.

Schmidt, C. L. A., and Hoagland, D. R. ('19). Table of P_H, H+, and OH-values corresponding to electromotive forces determined in hydrogen electrode measurements, with a bibliography. Univ. Calif. Publ., Physiol. **5**: 23–69. 1919.

Schreiner, O., and Skinner, J. J. ('10). Ratio of phosphate, nitrate, and potassium on absorption and growth. Bot. Gaz. **50**: 1–30. *f. 1–9.* 1910.

————, ————, ('10a). Some effects of a harmful organic soil constituent. *Ibid.* **50**: 161–181. *f. 1–11.* 1910. (See also U. S. Dept. Agr., Bur. Soils Bul. 70: 1–98. *pl. 1–4. f. 1–31.* 1911.)

————, ————, ('11). Organic compounds and fertilizer action. U. S. Dept. Agr., Bur. Soils Bul. **77**: 1–31. *f. 1–5.* 1911.

————, ————, ('12). The toxic action of organic compounds as modified by fertilizer salts. Bot. Gaz. **54**: 31–48. *f. 1–5.* 1912.

Sharp, L. T., and Hoagland, D. R. ('16). Acidity and absorption in soils as measured by the hydrogen electrode. Jour. Agr. Res. **7**: 123–145. *f. 1.* 1916.

Shive, J. W. ('15). A study of physiological balance in nutrient media. Physiol. Res. **1**: 327–397. *f. 1–15.* 1915.

————, ('15a). A three-salt nutrient solution for plants. Am. Jour. Bot. **4**: 157–160. 1915.