SOME RELATIONS OF MAINTAINED TEMPERATURES TO GERMINATION AND THE EARLY GROWTH RATE OF WHEAT IN NUTRIENT SOLUTIONS.

By W.F.Gericke

Dissertation submitted to the Board of University Studies of the Johns Hopkins University in conformity with the requirements for the degree of Doctor of Philosophy.

Baltimore, 1921.

SOME RELATIONS OF MAINTAINED TEMPERATURES TO GERMINATION AND THE EARLY GROWTH RATE OF WHEAT IN NUTRIENT SOLUTIONS.[1]

Contents.

(1) Botanical contribution from the Johns Hopkins University, [illegible].

SOME RELATIONS OF MAINTAINED TEMPERATURES TO GERMINATION AND THE EARLY GROWTH OF WHEAT IN NUTRIENT SOLUTIONS.

INTRODUCTION.

In the autumn of 1918, the Committee on the Salt Requirements of Certain Agricultural Plants, of the United States National Research Council, inaugurated a cooperative study of the growth of wheat plants in nutrient solutions.(2) This prospective cooperation was to involve the carrying out of comparative experimental tests with a large number of nutrient solutions, these solutions differing according to a regular scheme. For a beginning, several different, somewhat arbitrarily selected developmental phases of the wheat plant were to be studied. It was realized that a nutrient solution might be well suited for good growth during one phase of the plant's development and not so for another phase. All cooperators were to use seed from the

(2) Livingston, Burton E. (Editor). A plan for cooperative research on the salt requirements of representative agricultural plants, prepared for a special committee of the Division of Biology and Agriculture of the National Research Council. 2nd Ed. 54pp., Baltimore, 1919.

same lot and all were to follow the same general methods, so that their results might be relatively comparable.

The aim of the cooperation was to find out what salts, salt proportions, and total concentrations of the media, might generally produce the best growth of the standard plant for each of the developmental phases employed, and what ones might give good growth for certain kinds of aerial environments. The "Marquis" variety of spring wheat was selected as the test plant. Four phases of development were outlined for study:

(1) Germination phase, from beginning of soaking till the shoot is four centimeters high, measured from seed to the tip of the shoot. (2) Seedling phase, from the end of phase 1 for a period of five weeks, without regard to the size of the plant. (3) Vegetative phase, from the end of phase 2, until the first appearance of flowering in the controls. (4) Reproductive phase, from the end of phase 3 until maturity is reached by the best five cultures.

The solutions to be tested were planned on the basis of the scheme suggested by Livingston and Tottingham[3],

[3] Livingston, B. E., and Tottingham, W. E. A new three-salt solution for plant cultures. Amer. Jour. Bot. 5:337-346, 1918.

following the general outlines worked out by Schreiner and Skinner[4] and other writers, for the experimental study of different proportions of the same salts as such differences influence plant growth. The Livingston-Tottingham scheme embraces what they call six types of solutions, each being characterized by the three main salts employed. All solutions were to have a trace of iron as ferric phosphate, the amount of this salt used for unit volume of solution being always the same. The three main salts for each

(4) Schreiner, O., and Skinner, J.J., Ratio of phosphate, nitrate and potassium on absorption and growth. Bot. Gaz. 50:1-30. 1910.

Idem. Some effects of a harmful organic constituent. U.S. Dept. Agric. Bur. Soils. Bul. 70. 1910.

Tottingham, W.E. A quantitative chemical and physiological study of nutrient solutions for plant culture. Physiol. Res. 1:133-245. 1914.

Shive, J.W. A study of the physiological balance in nutrient media. Physiol. Res. 1:327-397. 1915.

McCall, A.G. The physiological balance of nutrient solutions for plants in sand cultures. Soil Sci. 2:207-253. 1916.

Idem. The physiological requirements of wheat and soy beans growing in sand media. Proc. Soc. Prom. Agric. Sci. 1916:46-59. 1916.

Hibbard, R.P. Physiological balance in the soil solution. Mich. Agric. Exp. Sta. Tech. Bul. 40. 1917.

Shive, J.W. A study of physiological balance for buckwheat grown in three salt solutions. N.J. Agric. Exp. Sta. Bul. 319.

McCall, A.G. and Richards, P.E. Mineral food requirements of wheat plant at different stages of its development. Jour. Amer. Soc. Agron. 10:127-134. 1918.

Shive, J.W. and Martin, W.H. A Comparison of salt requirements for young and for mature buckwheat plants in water cultures and sand cultures. Amer. Jour. Bot. 5:186-191. 1918.

Idem. A Comparative study of salt requirements for young and mature buckwheat plants in solution cultures. Jour. Agric. Res. 14:115-175. 1918.

Schreiner, O., and Skinner, J.J. The triangle system for fertilizer experiments. Jour. Amer. Soc. Agron. 10:225-246. 1918.

of the six types are shown below:

Type I	Type II	Type III	Type IV	Type V	Type VI
KH_2PO_4	K_2SO_4	KNO_3	K_2SO_4	KNO_3	KH_2PO_4
$Ca(NO_3)_2$	$Ca(NO_3)_2$	$Ca(H_2PO_4)_2$	$Ca(H_2PO_4)_2$	$CaSO_4$	$CaSO_4$
$MgSO_4$	$Mg(H_2PO_4)_2$	$MgSO_4$	$Mg(NO_3)_2$	$Mg(H_2PO_4)_2$	$Mg(NO_3)_2$

Twenty-one different sets of proportions of the three salts were to be tested for each solution type, these sets of salt proportions being conveniently shown by the uniform arrangement of twenty-one points on a triangular diagram, such as was first used in this sort of work by Schreiner and Skinner. The plan defined the several solutions of each type in terms of molecular proportions of the three main constituent salts. The solutions are designated by convenient symbols referring to the serial number of the row of the diagram in which any solution is represented (always counting from below upward), and to the serial number of the solution as represented in the row (always counting from left to right. Thus R1S2 denotes the second point in the first (lowest) row of the diagram, which represents an equilateral triangle with one side horizontal and at the bottom. A Roman numeral prefixed to one of these symbols denotes the serial number of the solution type as above defined. If the three salts are always considered in the same order, according to their cations, the twenty-one different symbols (representing the different sets of salt

proportions may be defined in terms of the relative molecular proportions of the salts and the same table of symbols and proportions is equally applicable to all six solution types. These symbols and the corresponding sets of salt proportions are shown below:

Solution symbol.	Molecular proportions.		
	Potassium salt	[illegible] salt	[illegible] salt.
R1S1	1	1	6
R1S2	1	2	5
R1S3	1	3	4
R1S4	1	4	3
R1S5	1	5	2
R1S6	1	6	1
R2S1	2	1	5
R2S2	2	2	4
R2S3	2	3	3
R2S4	2	4	2
R2S5	2	5	1
R3S1	3	1	4
R3S2	3	2	3
R3S3	3	3	2
R3S4	3	4	1
R4S1	4	1	3
R4S2	4	2	2
R4S3	4	3	1
R5S1	5	1	2
R5S2	5	2	1
R6S1	6	1	1

The following are illustrations of the reading of the above table. Solution R2S3 is characterized by having two-eighths of all its salt molecules added in the form of the potassium salt, three-eighths in the form of the calcium salt, and two-eighths in the form of the magnesium salt. Solution R2S1 has two molecules of the potassium salt, one of the calcium salt and five of the magnesium salt. In reading these symbols, it may be remembered that the number following "R" tells how many eighths of all the salt molecules in any volume of the given solutions are in the form of the potassium salt, while the number following the "S" tells how many eighths are in the form of the calcium salt. The difference between the sum of these two numbers and 8 gives the number that have the form of the magnesium salt.

It was planned that work should begin by employing solutions having a total salt concentration such as would give in all cases a calculated osmotic value of about 1.00 atmosphere of osmotic pressure at 25°C. Other total concentrations were to be tested in later work.

For further details regarding this series of 126 different three-salt solutions, the reader should refer to the plan cited above. The experiments to be reported in the present paper were planned as a part of the cooperation just

considered. It was decided to confine attention [illegible] to the germination phase. This was to be a study of the influences of certain sets of environmental conditions on the germination and early growth of "Marquis" wheat.

Since the wheat seed contains a considerable supply of salts, the general plan of the cooperation was modified two ways for this study. (1) The total concentration of every solution was fixed as equivalent to 0.1 atmosphere of osmotic pressure, the solutions being thus one-tenth as concentrated as those considered in the "Plan." (2) No iron was used, on the supposition that if this element was needed for germination, the seeds contained sufficient amounts of it to suffice for the germination phase of growth.

On account of the fact that the germination phase, as above defined, comprises only physiological processes that go on satisfactorily in the absence of light, it was possible to perform all these tests in darkness. Temperature control was thus possible, and it seemed advantageous to introduce the temperature factor with this study in a quantitative way. This was done by using seven different maintained temperatures [illegible].

This study thus comprised the testing of the 126 solutions, each with seven different maintained temperatures, giving altogether [illegible] different environmental complexes. It [illegible], [illegible] given temperature, [illegible] salt combination [illegible], [illegible]

solution) would produce germination and growth results noticeably different from those of other salt combinations, and that the same salt combination would produce noticeably different results according to the temperature employed. As it turned out, the salt combinations, as such, were apparently without any clearly and easily indicated influence upon the growth phase studied, for any of the seven temperatures tested (although the study yielded several suggestions as to salt influence), but the temperatures tested showed a marked ~~temperature~~ influence on the germination and early growth of this wheat.

The experimentation here reported was performed in the Laboratory of Plant Physiology of the Johns Hopkins University, with financial aid from the National Research Council and with the personal guidance and cooperation of Professor Burton E. Livingston, director of the laboratory. The experimental work was begun in the fall of 1918 and completed the following August. The numerical data obtained were studied by the writer upon his return to the University of California, where the present paper was prepared. The appreciative thanks of the writer are due to Professor Livingston, not only for the facilities of the Laboratory of Plant Physiology of the Johns Hopkins University, but also for his advice and criticism during the progress of the experimentation and later while the present paper was in preparation.

EXPERIMENTATION.

Materials and Methods.

The wheat used was a spring wheat, of the "Marquis" variety, crop of 1918, purchased by the Committee on Salt Requirements of Agricultural Plants, from the University Farm, University of Wisconsin. The seeds were not as uniform as work of this kind requires, and hence all seeds used in this investigation were selected by hand and eye for apparent normality and uniformity. Even with this precaution, considerable variation was encountered, not only in the percentage ~~of~~ viability of the seed, but also in the growth rate of the shoots. It was thought, however, that the selected grains probably exhibited no greater variability (differences in internal conditions) than is generally shown by agricultural seed wheat of this variety.

The distilled water used for the nutrient solutions was obtained from the Barnstead still of the Laboratory of Plant Physiology of the Johns Hopkins University.

The salts used for the nutrient solutions were of the grade of Baker's Analyzed Chemicals, C.P.

The nutrient solutions used all agreed in having a total concentration corresponding to about 0.1 atmosphere of osmotic pressure. They are, therefore, to be classed as relatively dilute. The six solution types differed in regard to the three salts used in each, as has been shown above, but all six types agreed in containing the six

inorganic chemical elements that (together with iron, which was not included), constitute the inorganic elements essential for plant growth in general.

The twenty-one different solutions of each type differed from one another in their molecular salt proportions, as shown above. The solutions were made up thirty (or, in some cases, ten) times as concentrated as they were to be needed, and the stock concentrated solutions thus obtained were properly diluted whenever culture solutions were required.

Nine single-salt solutions, each representing one of the nine salts, were first prepared, these having the following volume-molecular concentrations: KH_2PO_4, 1.0 mol.; KNO_3, 1 mol.; K_2SO_4, 0.4 mol.; $Ca(H_2PO_4)_2$, 0.1 mol.; $Ca(NO_3)_2$, 1.0 mol., $CaSO_4$, .014 (saturated solution at room temperature); $Mg(H_2PO_4)_2$ 0. 1 mol.; $Mg(NO_3)_2$, 1.0. mol.; $MgSO_4$, 1.0 mol. The 126 concentrated stock nutrient solutions were each prepared by mixing proper volumes of the proper three single- salt solutions with distilled water in requisite volume, care being exercised to prevent precipitation.

For solution types I, II, III and IV (without $CaSO_4$), the concentrated stock nutrient solutions were thirty times as concentrated as those actually used for the culture tests. For solution types V and VI (with $CaSO_4$), the concen-

trated stock nutrient solutions were ten times as concentrated as those actually used.

The oxygen and carbonate-dioxide contents of the nutrient solutions used for the tests were assumed to be alike; this feature of nutrient solution experimentation has not yet attracted the serious attention of physiologists but the assumption here made was probably safe, especially in view of the fact that the very early stages of growth here dealt with gave no clearly defined differences in growth that might be related to the chemical properties of the solutions.

The cultures were arranged as follows: Glass tumblers (capacity about 300 c.c.) were prepared, each with a tightly stretched cover of thoroughly washed mosquito netting (cotton thread, with open meshes about 2 mm. square) tightly sealed to the outside of the wall of the tumbler by means of paraffin. Each of these net- covered tumblers was filled with the proper nutrient solution and twenty-five selected seeds were distributed uniformly over the netting (the area being about 78 sq.cm.). All seeds were in contact with the solutions, but they were not submerged. This simple method was adopted as the best of several methods that were compared in preliminary tests.

Each single series of cultures involved but one type of solution; it comprised twenty-one different solutions,

each represented by seven cultures. Each set of seven like cultures was distributed throughout the seven different temperatures tested, so that a single series comprised twenty-one cultures for each temperature. All of the twenty-one nutrient solutions of any one solution type were thus simultaneously tested for each of the seven temperatures, and each culture series comprised 147 cultures. The completed study involved all six types, or 882 cultures. Each of the six series, excepting those for the lowest temperatures, was repeated once, so that 1638 tests were made. The nutrient solutions were all renewed after each 24-hour period, for four renewals, the cultures being discontinued on the fifth day.

The temperature controls used were those of the battery of chambers for temperature control at the Laboratory of Plant Physiology of the Johns Hopkins University, which has been described in its essentials by Livingston and Fawcett[5]. The seven different temperatures employed in these tests were as follows: 35°, 31°, 28°, 25°, 21°, 17°, and 13° C. Variations from these values were never as great as one degree. No

[5] Livingston, B.E. and H. S. Fawcett. A battery of chambers with different automatically maintained temperatures. Phytopathology 10:336-340, 1920.

attempt was made to control or measure the chemical makeup of the air of the chambers. It may be said, however, that the air humidity approached that of saturation for the given temperature in each chamber. Light, as already stated, was excluded.

Measurements and Results.

Introduction. As has been stated, each culture solution was removed and replaced by a fresh one on the second, third, and fourth day of the culture period, the cultures being discontinued on the fifth day. These renewals of the solutions did not occur, however, at exactly 24 hour intervals and the total length of the culture period was always less then 5 days. The variation from the time schedule was not great in any case and all cultures of any series (21 solutions of a single solution type, with each of the seven temperatures used) were subjected to the same time periods between renewals, and to the same total period. On the third day of the period, all seedlings with shoots 1 cm. or more in length were counted and recorded. On the fourth day, each shoot 1 cm. long or longer was measured, and record was made showing the number of seedlings in each culture that were 1, 2, 3, etc., cm. high. All shoots were again measured on the fifth day, when the cultures were discontinued. To avoid much disturbance, measurements made prior to the final one were only approximately correct, about to a precision of 1 cm., but the fifth-day measurements were carefully made, to a precision of 1 mm., each seedling being removed from the solution for measurement. These two measurements may be termed

the first and second; they occurred after about 86 and 110 hours, respectively, with variations that will be noted below. The numerical results obtained for each culture are as follows:

(1) Number of seedlings with shoots 1 cm. or more high after about 86 hours.

(2) Approximate total shoot elongation after about 86 hours.

(3) Number of seeds germinated after about 110 hours.

(4) Total shoot elongation after about 110 hours.

(5) Total shoot elongation for the last 24 hours (obtained by subtracting 2 from 4, above).

The number of seeds germinated at the end of the whole period (3, above) may be taken to represent the viability for any culture; if this number be multiplied by 4 the product represents the percentage of germination, since each culture had 25 seeds.

Each total-shoot-elongation value (2 and 4, above) divided by the corresponding number of seedlings measured, gives the average length of shoot for the seeds that germinated in the culture in question. This quotient represents the average growth per seed in each case, omitting the seeds that failed to germinate. Finally, since the time periods were not exactly the same for all

series, the quotient just mentioned is to be divided by the exact number of hours elapsed since the starting of the cultures in each case, thus giving the mean hourly rate of shoot elongation for the given culture. Subtracting the total elongation value for the shorter period (2, above) from the corresponding value for the longer period (4, above) gives a number representing the total shoot elongation for the last portion (about 24 hours) of the whole culture period.

Each of the six different series (each series corresponding to one of the six solution types and each including the seven different temperatures) was repeated once, excepting in the case of the lowest temperature, so that the data obtained refer to the first or second test for each series, excepting those for 13° C.

Viability, growth rate, and solution composition.

Forty-two tables of data were obtained from these 6 solution types, tested at 7 different maintained temperatures. Only table I, giving the results obtained from the solutions of type I tested at 31° C, is given in this paper. It is presented as an illustration of the results obtained at the end of the culture period (3 and 4, above.). The two halves of the table represent the two like tests for the solutions of type I and for 31° C. The solutions or sets of salt proportions, are designated by the symbols in the first column, these being repeated for the second test as the data are here tabulated. Each mean hourly rate of shoot elongation is obtained

TABLE I.

Mean Hourly Shoot Elongation for Solutions of Type I,

Temperature, 31° C.

Sol. No.	Total elongation mm.	First Test. No. of seedlings	Mean hourly rate for period of 114 hours Actual mm.	In terms of average.
R1S1	1600	22	.64	1.00
R1S2	1463	23	.56	.88
R1S3	1153	16	.63	.98
R1S4	1459	19	.67	1.05x
R1S5	1784	24	.65	1.02
R1S6	1179	18	.58	.91
R2S1	1229	20	.54	.84
R2S2	1639	21	.58	.91
R2S3	1026	14	.64	1.00
R2S4	900	17	.46	.72
R2S5	1091	18	.53	.83
R3S1	1623	20	.71	1.11x
R3S2	1545	20	.68	1.06xx
R3S3	1567	20	.69	1.08xx
R3S4	1264	18	.62	.97
R4S1	1269	18	.62	.97
R4S2	1429	20	.63	.98
R4S3	1118	18	.54	.84
R5S1	1360	18	.66	1.03x
R5S2	1423	18	.69	1.08xx
R6S1	1119	16	.61	.95
Average	----	--	.64	1.00

TABLE I (Cont.)

Second Test.

Sol. No.	Total elongation mm.	No. of seedlings	Mean hourly rate for period of 114 hours: Actual mm.	In terms of average.
R1S1	1605	22	.65	.93
R1S2	1889	23	.77	1.10x
R1S3	1738	21	.76	1.09x
R1S4	1676	21	.71	1.01
R1S5	1423	18	.71	1.01
R1S6	1483	18	.74	1.06x
R2S1	1866	23	.72	1.03x
R2S2	1802	24	.67	.96
R2S3	1194	16	.67	.96
R2S4	1335	19	.63	.90
R2S5	1568	21	.67	.96
R3S1	1615	22	.65	.93
R3S2	1529	17	.80	1.14xx
R3S3	1776	22	.72	1.03xx
R3S4	1593	20	.71	1.01
R4S1	1580	22	.64	.91
R4S2	1703	22	.69	.99
R4S3	1621	19	.76	1.09x
R5S1	1754	23	.68	.97
R5S2	1716	21	.73	1.04xx
R6S1	1670	21	.71	1.00
Average	----	--	.70	1.00

by dividing the total elongation by the corresponding number of seedlings. The 21 hourly rates are averaged for each test and each rate is expressed in terms of the average of its own test.

Inspection of these sample data brings out several points generally apparent throughout the entire mass of data for all six types and for all temperatures tested. In the first place, no relation is discovered between the solution composition (indicated by the solution symbol in each case) and the number of seeds that germinated. The percentage of germination was not evidently influenced by the salt proportions. For the first test, the number of seedlings obtained from 25 seeds ranged from 14 to 24, for the second test this range is from 16 to 24, and the table shows very little agreement between the numbers of seedlings obtained with the same solution in the two like tests. This state of affairs holds for all the series in about the same way, so that it became apparent that the germination percentage could not be considered, on the basis of this study, as influenced by the salt proportions. It is also true that this percentage was not apparently influenced by the temperature. (Of course, germination was more rapid with some temperatures than with others; reference is here made merely to the number of seeds that had

germinated after [illegible] at 11 [illegible].) The differences in the number of seedlings produced [illegible] 2. [illegible] apparently largely due to internal differences in the seeds themselves. At any rate, the individual variation [illegible] the several groups of 25 seeds [illegible] greater than any possible differences in viability that may have been related to salt proportions or temperature; if there were any such differences they were [illegible] by individual variation. With these points in mind, we may [illegible] the topic of percentage of germination as a characteristic of these seeds that was not appreciably influenced by either the kind of solution used, or the temperature employed. In this connection, it may be mentioned that all the solutions used were relatively very dilute so that there could have been no significant influence exerted in the osmotic way.

Turning to the mean hourly rates of shoot elongation for the entire culture period, as illustrated by the data of table I, the first test of these solutions with a temperature of 31° C. gave an average rate of .[illegible] mm. and the second test gave an average rate of .7[illegible] mm. In the first test, the mean rates ranged from 23 per cent below the average (relative rate, .7[illegible]), to 11 per cent above it (relative rate, 1.11), [illegible] a total range of [illegible] per cent of the average. The solutions that gave [illegible] above the average in this first test might be [illegible] as

better than others, but comparison of the relative rate values for the two tests brings out the fact that some solutions showing mean rates above the average in one test showed rates below it in the other test. The solutions that gave mean rates more than 2 per cent above the average rate are marked with an X at the extreme right of table I, and only three of them (marked with a double X) are thus designated for both tests. These three solutions (R3S2, R5S2, and M5S2) might be considered as definitely better than the others of this type and temperature, but there is no apparent relation between this apparent "goodness" of the solutions and the corresponding salt proportions. Two of these are in row 3 and the other is in row 5 of the triangular diagram, so that they are not adjacent as to the potassium salt. Two are second in the row, the other being third, so that the former two have two-eighths of their salt molecules in the form of the calcium salt, and the latter has three-eighths in this form. The intervening solution with two-eighths of its salt molecules in the form of the calcium salt (M4S2) gave a value somewhat below the relative value 1.00 in both tests. Finally, one of these exceptionally "good" solutions has three-eighths of its total number of salt molecules in the form of the magnesium salt, another has two-eighths, and the third has but one-eighth in that form. It therefore seems that the exceptional "goodness" of these three solutions is not clearly related to the salt proportions employed.

A thorough study of [illegible] led to a similar conclusion for the other seed[illegible]. No consistent evidence was anywhere clearly discernable between small proportions and the mean hourly growth rate for the entire culture period. Several suggestions of certain relations between growth and the composition of the nutrient solutions were encountered, (6) but careful study of the numerical data and the extent of the variability encountered with this seed leads to the conclusion stated above. This conclusion of course applies only to the tests here considered, dealing with the very first

---

(6) In a preliminary paper, the author reported on one of these suggestions, interpreting the data to show that nutrient solutions having a relatively high potassium-ion proportion were relatively poorer growth media for these wheat seedlings at high temperatures than they were at low temperatures; and that, at low temperatures, nutrient solutions high in potassium-ion proportion were relatively better for growth than they were at high temperatures. It was subsequently found that a more rigid method for defining the "best" solutions (as shown in Table II of this paper) resulted in the elimination of some of the solutions reported as "best" in the preliminary paper. The suggestion here considered has proved to be of value, however, and it has led to further and more comprehensive experimentation along this line, but with longer growth periods. Selected solutions of the six types were tested, each one in a set of at least ten like

phases of growth, [illegible] used. [illegible] culture periods were employed, the material contained in the seed may have played a considerable part in determining the results, preventing any influence by the salt contents of the very weak solutions used. Without doubt, solutions of higher total concentration would have shown considerable differences in growth with regard to salt proportions, and probably the weak solutions here used would have shown definite salt influences with later phases of growth or with less variable seed.

cultures (for the statistical interpretation of the data) and with both a high and a low temperature. Definite solution-growth effects and solution-temperature-growth effects were obtained, which support the suggestion mentioned above. Since the culture periods for these later experiments were much longer than those for the tests of this study, thus including later growth phases, the later results are to be reported in another paper. The present report deals only with the tests described in the text. For the preliminary paper, see: Gericke, W.F. Influences of temperature on the relations between nutrient salt proportions and the early growth of wheat. Amer. Jour. Bot. 8:59-62. 1921.

Because of the conclusions [illegible] below, it is unnecessary to present the detailed [illegible] of the [illegible], and [illegible] for 21° C. and table I, for the whole culture period (table I), may suffice as an illustration. The most interesting points of the omitted tables for the whole culture period are presented, however, in tables II and III, in summarised form. Table II gives a list of apparently best solutions for shoot elongation for each temperature (excepting the lowest, for which only one single test was made) and for each solution type. The solutions listed include only those which agrees for both tests in giving mean hourly rates (for the whole culture period) that are more than 2 percent above the average for the series in which they occur, and for which the difference between the corresponding rates for the two tests is .11 mm or less. Of the three solutions marked with a double X in table I, as giving growth values more than 2 per cent above the average for their series in both tests, the first (1.3S2) is omitted from table II because the value for the first test is .68 mm. and that for the second is .80 mm., the difference being more than .11 mm. By this somewhat arbitrary scheme those solutions are listed as apparently best that showed fair agreement in the actual average hourly growth rates of the two tests and that showed growth rates, for both tests, more than 2 per cent above the series average.

Three growth values are given opposite each culture symbol in table II, these being separated by colons; the first

values [illegible] the first test, [illegible] second test, and the [illegible] in the [illegible] best. Thus, for type I, 11° [illegible] (see Table I), [illegible] have been found, [illegible] first [illegible] .[illegible] by the first test and .77 [illegible] by the second test, the average for both tests [illegible] .7[illegible]. [illegible] no [illegible] given in Table II for any temperature of type II it appears that no solutions fulfill the requirements here taken as defining the best solutions.

TABLE II.

SUMMARY OF APPARENTLY BEST CULTURES FOR SHOOT-GROWTH, ENTIRE PERIOD.

(See text for explanation.)

Sol. type	Temp. 35°C.	Temp. 31°C.	Temp. 28°C.
I.	R3S2,57:60:64	R5S2,69:71:73	R1S3,71:72:73
	R3S3,68:68:68		R1S4,71:73:74
			R3S2,70:71:71
			R4S1,72:72:72
			R4S2,70:74:77
II.	R2S5,58:55:57	R1S3,72:74:76	R1S2,70:73:75
	R4S1,61:61:60	R1S4,77:80:82	R1S3,71:73:75
	R4S3,52:56:59	R1S5,72:69:70	R1S4,80:80:79
		R2S1,69:73:76	R2S1,84:77:70
III.	R1S5,60:58:55	R1S1,78:74:70	R1S4,78:75:69
	R2S2,64:64:64	R1S2,77:75:72	R1S5,78:75:69
	R3S4,70:66.61	R1S3,77:75:73	R2S1,82:86:89
		R1S4,76:75:74	R2S2,77:80:82
		R1S5,70:72:73	
		R3S3,78:76:73	
IV.	R1S3,65:65:64	R1S1,75:79:83	R1S4,87:86;84
	R1S5,62:60:57	R2S1,78:78:78	R1S5,94:89:84
	R2S5,62:62:61	R2S5,76:75:74	
		R5S2,73:77:81	
V.	R2S1,59:61:62	R1S2,76:71:66	R1S4,79:74:69
	R2S2,54:58:61	R1S3,72:75:77	
	R4S2,60:61:61	R1S4,73:75:77	
	R5S2,58:57:55	R2S1,74:74:73	
		R3S2,75:71:67	
		R4S2,69:69:68	
VI.	R5S1,52:56:60	R1S1,77:71:65	R1S3,76:75:74
	R5S2,56:59:61	R1S3,78:73:68	R3S4,76:73:69
	R6S1,54:53:52	R3S1,79:75:70	R4S2,77:76:74

TABLE II. (Cont.)

Sol. type.	Temp 25° C.	Temp. 21° C.	Temp. 17° C.
I.	R1S4,56:58:60	R3S1,46:49:52 R4S2,46:49:52	R4S3,22:25:27 R5S1,21:25:29
II.		R1S3,44:40:36 R4S1,46:42:37 R5S2,46:42:37 R6S1,47:42:37	R4S3,28:25:21 R5S2,26:24:22
III.	R2S4,66:62:58 R2S5,68:64:59	R2S5,49:44:39	R2S2,34:30:26 R3S4,29:27:25 R5S1,32:30:27
IV.	R1S2,56:58:60 R1S5,62:61:59 R1S4,55:57:59 R2S1,61:59:57 R2S2,56:58:60	R1S3,39:42:44 R4S2,41:43:44	R5S1,25:26:26 R5S2,23:25:26
V.	R1S4,77:72:67 R4S2,71:67:62	R1S3,63:58:58 R2S1,59:58:57 R5S1,59:57:55	R5S2,44:39:34
VI.	R1S4,65:61:56 R4S2,63:62:60 R5S1,64:63:62 R6S1,60:60:59	R5S1,45:45:44 R5S2,48:49:49 R6S1,48:48:48	R3S4,23:27:30 R4S3,23:27:30 R5S1,24:27:30 R6S1,26:28:30

Table III is somewhat like table II, but it reports the apparently poorest solutions for shoot growth instead of the apparently best ones. The solutions shown in this list are those whose growth values are among the <u>four lowest</u> of their respective series, for both tests, and for which the growth values for the two like tests show differences of .11 mm.. or less. Otherwise, the notation follows the scheme of table II.

TABLE III.

SUMMARY OF APPARENTLY POOREST CULTURES FOR SHOOT-GROWTH, ENTIRE PERIOD.

(See text for explanation.)

Sol. type.	Temp. 35° C.	Temp. 31° C.	Temp. 28° C.
I	R1S1,44:48:53		
II	R1S2,38:38:40 R3S1,41:44:48	R1S1,57:54:52 R4S3,55:56:57	R2S4,55:51:48 R2S5,55:51:47 R3S4,57:53:49 R5S1,46:51:46
III	R5S2,42:41:41	R3S2,61:58:55 R4S2,49:53:58 R4S3,52:54:55 R6S1,60:62:64	R3S2,53:54:56 R5S2,62:58:54
IV		R3S4,62:60:58 R5S1,60:59:58	R2S3,53:56:59 R5S2,53:52:51
V	R1S5,38:41:45	R5S2,47:46:46	R6S1,63:60:57
VI	R1S6,48:44:40	R2S1,63:60:58 R2S2,66:64:61	R1S5,57:57:57

TABLE III (Cont.)

Sol. type	Temp. 25° C.	4 Temp. 21° C.	Temp. 17° C.
I.	R2S2,45:48:51	R2S2,36:40:44	R1S2,18:22:25
		R3S3,~~33~~:42:41	R1S3,18:20:22
		R3S4,36:40:44	R1S4,19:21:22
		R4S3,35:40:44	R2S2,17:21:25
II.	R4S3,50:46:42	R2S3,33:31:29	R1S4,22:20:18
		R3S2,37:32:28	R3S1,22:20:18
III.	R4S2,53:49:46		R1S3,26:23:20
	R6S1,47:46:46		R4S3,20:20:20
			R5S2,21:19:18
IV.	R2S4,48:49:50	R2S2,34:36:39	R1S6,20:20:21
	R5S2,48:46:44	R2S3,32:35:38	R2S1,20:19:19
		R3S3,34:35:36	R2S3,20:19:19
		R5S2,33:35:37	R2S4,18:18:19
		R6S1,33:34:36	R3S2,18:19:20
			R3S4,18:19:19
V.	R5S2,50:49:48	R3S4,44:42:41	
VI.	R1S5,49:48:47	R2S3,34:35:36	R1S1,19:20:22
	R1S6,55:50:46	R2S4,38:39:40	
		R3S2,33:35:38	

Tables II and III place on record, for use in future studies and comparisons, the sets of salt proportions that gave, respectively, the best and poorest growth rates for each solution type and temperature, for about 110 hours from the beginning of germination. If the seed had shown less variability, it may be that such summaries as these might have shown some clear and unmistakable relations between the make-up of the solution and its physiological effect. As has been said, perhaps because of the extent of the unexplained variability encountered in this study a consideration of the data here presented leads to the conclusion that no clear and consistent evidence is here given for holding any solution better than any other of the ones tested, for these temperatures, for this seed, for the length of the test period, and for the other details of these tests as reported.

It seems somewhat inconsistent to make mention, on the one hand, of the "apparently best" and the "apparently poorest" solutions, in each group, thereby suggesting that differences are apparent and related to the chemical properties or salt proportions of the solutions, and, on the other hand, to state that all the solutions tested are to be considered as essentially alike with respect to germination and early growth of the wheat used. This seeming inconsistency disappears, however, upon careful consideration.

The "apparently best" and "apparently poorest" solutions shown in tables II and III are all, the ones that gave, individually and empirically, respectively, better and lower growth rates than the averages in the several series. One group of solutions (tableII) were poor, by actual test. Had the whole series of 126 solutions been selected at random, without reference to the physico-chemical scheme of the triangular diagram, then the list of good solutions would have to be taken at its face value, as showing which solutions had been found best by test. But the solutions of this study were not selected at random, they represent a certain definite series of different sets of salt proportions and different salts. Within the limits set by the chosen total concentration and by the nine salts used, the series is so selected as to be equally distributed throughout the entire range of possibilities. They are somewhat like a set of soil samples secured one from each of a number of stations frequently and equally spaced over a broad terrain comprising many kinds of soil. This being the case, it follows that evidence for any significant influence exerted by the makeup of any given solution should be shown not only by that particular solution itself but also by the solutions adjacent to it on the triangular diagram. A study of the salt proportions of the "apparently best" solutions and of the growth rates given by the adjacent solutions fails generally, in the present study, to bring forth any evidence that one set of salt

proportions proved definitely better than others for the same solution type, or that one type turned out clearly better, for any set of salt proportions than another. It is the logical relations between the "apparently best" or "apparently poorest" solutions and the other solutions, as these relations are visualized by means of the diagrams, that finally leads to the conclusion that their "goodness" or "poorness" is only apparent and is not clearly shown as related to salts and salt proportions. There is no doubt at all that the "apparently best" solutions were actually the best in these tests, but the logically necessary collateral evidence is uniformly lacking to show this "goodness" as related to salts and salt proportions.

Growth-Temperature Relations.

The considerations presented in the preceding pages led to the suggestion that all the mean growth rates for each separate series might be averaged to give a single average rate for the given test and series, that these averages for the corresponding tests with the same temperature might be themselves averaged to give a single value representing the growth rate for the given temperature and solution type, and that all the six type averages might be averaged for each temperature to give a single growth index for each temperature considered. The logical basis for this mode of treatment may be stated as follows: Since the data at hand do not establish any relation between solution composition and growth rate for any temperature, all solutions may be treated as though they were physiologically alike, within the limits of precision set by the innate variability of the seed used, etc.

An inspection of the 42 tables obtained for the 6 solution types tested with 7 different maintained temperatures, for the entire culture period, as well as for the two partial periods (of which table I is an example), brought out very clearly the fact that the temperature influence on growth rate was pronounced and consistent, in spite of the general individual variations of the seedlings and quite without regard to the make-up of the solutions used. In the following pages the

temperature-growth relations shown in these tests [illegible] [illegible] modified/ through the cultures of [illegible] [illegible] [illegible] with exactly the same medium. The average growth for each of the mean temperatures, as calculated treating all of the 100 solutions as if they had been quite the same, and these temperature-growth indices were employed as the basis for a study of the relation of temperature to shoot growth shown in these tests.

<u>Temperature Relations for the Entire Culture Period (About 110 Hours).</u>

Table IV presents the series, type, and temperature averages for the entire culture period, being a summary of the temperature relations shown by the 42 tables, of which Table I is a sample and from which tables II and III were derived. In each case the minimum and maximum are given, as well as the average, the three values (in hundredths millimeter per hour of shoot growth, for periods ranging from 108 to 114 hours) being given consecutively, separated by colons, in the serial order: <u>minimum, average, maximum.</u> For example, referring to table I, the average for all solutions of the first test is .64 mm., the minimum is .53 mm., and the maximum is .71 mm. Hence, the summary of the first part of table I may be represented by the formula 53:64:71. In like manner, the summary for the second part of table I is 63:70:77. The averages for the several pairs of like tests (excepting for the lowest temperature, for which only one test was made) are shown in the next to the last column of table IV and the grand average for each temperature is given in the last column. The grand averages bring out very clearly the facts that the highest rates of shoot elongation were obtained with the maintained temperatures 28° and 31° (the values being about alike), that temperatures

25° and 35° gave rates that are markedly lower than those for 28° and 31°, and that temperatures 21°, 17° and 13° gave still lower rates, these being progressively lower with lower temperatures. These grand averages will receive attention below.

TABLE IV.

SUMMARY OF AVERAGE RATES OF SHOOT ELONGATION FOR THE EN-
TIRE CULTURE PERIOD AND FOR ALL SERIES.

Temperature	Solution type	Length of period 1st test hrs.	Length of period 2nd test hrs.	Min. Ave. and Max. hourly rate* mm. 1st test .01mm.	Min. Ave. and Max. hourly rate* mm. 2nd test .01mm.	Ave. of 1st & 2nd tests .01mm.	Grand Ave. for given temp. .01 mm.
35°	I	114	112	38:53:70	47:61:70	57	
	II	108	110	23:47:61	40:51:60	49	
	III	110	112	25:57:71	37:52:61	55	
	IV	112	110	47:60:78	37:51:64	56	53
	V	108	114	36:49:59	34:52:67	51	
	VI	108	110	43:51:59	41:48:65	49	
31°	I**	114	112	50:64:71	63:70:77	67	
	II	108	110	50:63:77	52:67:82	65	
	III	110	112	49:69:78	53:67:78	68	
	IV	112	110	54:68:78	52:68:83	68	66
	V	108	114	47:66:76	46:64:77	65	
	VI	108	110	63:74:85	54:62:70	68	
28°	I	114	112	52:64:73	55:68:78	66	
	II	108	110	55:63:84	45:58:79	61	
	III	110	112	53:70:86	49:63:89	67	
	IV	112	110	52:64:94	47:67:84	66	66
	V	108	114	61:74:98	55:67:78	71	
	VI	108	110	57:70:84	50:63:75	67	
25°	I	114	112	43:50:61	48:57:66	55	
	II	108	110	48:54:65	39:45:49	50	
	III	110	112	43:59:68	43:53:62	55	
	IV	112	110	48:53:62	41:54:60	54	55
	V	108	114	50:67:79	44:57:67	62	
	VI	108	110	48:58:65	38:52:62	54	

*The first value given is the minimum, the second is the average, and the last the maximum.

**Detailed data for 31°, type I, are given in Table I.

TABLE IV (Cont.)

Temperature	Solution type	Length of period hours. 1st test	2nd test	Min., Ave. and Max. hourly rate (.01 mm.) 1st test	2nd test	Ave. of 1st & 2nd tests	Grand Ave. for given temp. (.01 mm.)
21°	I	114	112	32:38:46	37:46:52	42	
	II	108	110	33:41:47	27:33:39	37	
	III	110	112	40:48:53	22:34:42	41	
	IV	112	110	32:36:42	36:43:49	40	42
	V	108	114	44:57:67	35:46:57	51	
	VI	108	110	33:44:70	22:42:52	43	
17°	I	114	112	14:20:23	21:25:29	22	
	II	108	110	19:24:30	13:19:22	22	
	III	110	112	20:28:35	18:23:27	26	
	IV	112	110	12:20:25	19:23:26	21	25
	V	108	114	32:39:47	17:25:33	32	
	VI	108	110	16:21:26	20:25:30	23	
13°	I	114		04:06:07			
	II	108		04:07:20			
	III	110		03:04:06			
	IV	112		04:06:08			07
	V	108		06:10:13			
	VI	108		04:06:07			

Temperature Relations of Cultures in Distilled Water.

A series of cultures was carried out with distilled water instead of nutrient solutions, and the mean hourly rates of shoot elongation obtained for a 110 hour period and for the seven different maintained temperatures, are given in table V. Corresponding data for the nutrient solution cultures are given in that table for comparison.

TABLE V.

TEMPERATURE RELATIONS OF SHOOT ELONGATION FOR DISTILLED WATER CULTURES AND NUTRIENT SOLUTION CULTURES, FOR ABOUT 110 HOURS FROM THE BEGINNING OF GERMINATION, VALUES BEING MEAN HOURLY RATES IN TERMS OF HUNDREDTHS OF A MILLIMETER.

Maintained temperature	Distilled water cultures.	Nutrient Solution Cultures		
		Highest rate obtained (See Table III.)	Lowest rate obtained (See Table III.)	Grand Average for given temperature. (See Table IV.)
35°	30	68	38	53
31°	33	80	46	67
28°	36	86	51	66
25°	31	72	46	55
21°	22	58	13	42
17°	16	30	18	25
13°	7	13	3	7

The rates for the distilled water cultures show the same general temperature relations as those shown by (1) the highest rates, (2) the lowest rates and (3) the grand averages, for the nutrient solution cultures. In all cases the rates for 28° and 31° are the highest and about alike, those for 25° and 35° are lower and about alike, those for 21°, 17° and 13° are progresively stilllower.

The distilled-water value is markedly lower, however, (in every case excepting that for 13°), than is the corresponding highest rate or the corresponding grand average value from the nutrient solution cultures. Furthermore, the distilled-water value is somewhat lower than even the lowest rate from the nutrient solution cultures in all cases, excepting that for 13°. It appears from table V that the cultures with distilled water generally gave mean ratesabout half as great as the corresponding rates obtained with nutrient solutions. ~~In~~ the lowest temperature tested (13°), the distilled-water cultures gave a rate just equal to the grand average for this temperature with nutrient solutions. All of the solutions tested were of about the same osmotic value (equivalent to about 0.1 atm. of osmotic pressure), so that the one feature by which all soluions agreed among themselves and yet differed from distilled water, is with regard to osmotic value. The solutions differed

from water, and agreed among themselves in that they all contained the six kinds of inorganic atoms or atomic groups (potential ions) known to be needed for plants in general, but---as has been made clear -- they did not contain these atoms and groups in the same proportions. It is clear that the presence of a slight osmotic value due to the salts used, or the presence of a small amount of the essential atoms and atomic groups in the solutions, greatly improved the water for the growth phases here dealt with. Since the solutions differed markedly in salt and salt proportion and at the same time were all essentially alike in their influence on the plantlets, it seems probable that any lower total concentration of any of these solutions (between 0.1 atm. of potential osmotic pressure --the solution concentration used-- as in the case of water) would have shown growth rates more like those secured with water than like those obtained from solution actually tested, but still alike among themselves for the solution series. It is practically certain that if the solution concentration had been ~~greater~~ (with an osmotic value greater than 0.1 atm. of potential pressure) they would have shown some relations between shoot growth and salt composition, even with seed as variable as that here used. With what total concentration value this might occur is of course not predictable without experimentation.

To the conclusions thus far reached may now be added these, that all these solutions used are much better

suited to the germination and growth of this wheat than is distilled water. It is safe to state that distilled water is not at all suitable for a germination medium when solution cultures are being prepared, unless sickly plantlets are required.

The unsuitability of distilled water for seed germination, etc., has been emphasizes and discussed by several authors(7) and the reason for this need not be dealt with here. It may be mentioned, however, that the water of the Johns Hopkins Laboratory of Plant Physiology is generally free from direct toxic influences (due to impurities) and that the injurious effect here shown was probably due to outward diffusion of substances from the seed and seedlings. This conclusion follows the discussion of True and Bartlett(8) and True (9), for some what similar experiments.

(7) A rather complete resume of the literature on the physiological properties of distilled water, up to the time of its publication, is given in the following paper: Livingston, B.E., et al. Further studies on the properties of unproductive soils. U.S. Dept. Agric., Bur. Soils, Bul. 36, 1907. See also, True and Bartlett, cited just below.

(8) True, Rodney H., and Bartlett, H.H. Absorption and excretion of salts by roots, as influenced by concentration and composition of culture solutions. U.S. Dept. Agric., Bur. Plant Ind. Bul. 231. 1912.

(9) True, R.H. Harmful action of distilled water. Amer. Jour. Bot. Vol. 1:255-273. 1914.

Temperature Relations for the last 24 Hours of the Culture Period.

Table VI presents a summary of the growth-temperature data for all series, for the last 24 hours. It was realized that the data for the entire culture period (table IV) refer to actual shoot elongation only in part; in the earlier part of the culture period shoot elongation had not yet begun. In a very general way, the data for the last 24 hours may be regarded as referring primarily to seedling enlargement, while those for the first portion of the period refer largely to the preliminary processes generally considered as seed germination. ~~Doubtless~~, it is for this reason that the average rates shown in table VI are so much larger than those shown in table IV.

The notation of table VI is self-explanatory, being somewhat simpler than that of table IV.

TABLE VI.

SUMMARY OF AVERAGE DATA ON SHOOT ELONGATION FOR THE LAST 24 HOURS OF THE CULTURE PERIOD FOR ALL SERIES.

Tempera-ture.	Solu-tion type	Mean Hourly Rate 1st test .01mm.	Mean Hourly Rate 2nd test .01mm.	Average 1st and 2nd tests. .01mm.	Grand ave. for given temperature .01mm.
35°	I	118	126	122	
	II	121	137	129	
	III	123	118	121	
	IV	134	114	124	124
	V	128	131	129	
	VI	121	121	121	
31°	I	143	149	146	
	II	148	165	152	
	III	156	140	148	
	IV	162	145	153	153
	V	153	158	156	
	VI	165	156	161	
28°	I	151	149	150	
	II	158	158	158	
	III	160	156	158	
	IV	154	152	153	157
	V	166	158	162	
	VI	162	160	161	
25°	I	140	140	140	
	II	135	137	136	
	III	138	124	131	
	IV	140	124	132	137
	V	153	141	147	
	VI	130	138	134	
21°	I	104	126	115	
	II	126	110	118	
	III	101	96	99	
	IV	108	101	105	112
	V	120	115	118	
	VI	104	123	114	

TABLE VI (Cont.)

Temperature.	Solution type	Mean Hourly Rate 1st test .01mm.	Mean Hourly Rate 2nd test .01mm.	Average 1st and 2nd tests. .01mm.	Grand ave. per given temperature .01mm.
17°	I	72	84	78	
	II	90	91	90	
	III	83	75	79	
	IV	75	--	75	82
	V	100	--	100	
	VI	---	87	87	
13°	I	27	--	27	
	II	31	--	31	
	III	24	--	24	
	IV	26	--	26	30
	V	40	--	40	
	VI	27	--	27	

Temperature Relations for the First Part (About 86 Hours) of the Culture Period.

Table VII presents a summary of the growth-temperature data for all series for that part of the entire culture period that preceded the last 24 hours. The notation is the same as that for table VI. No data are available for the lowest temperature (13°C.).

TABLE VII.

SUMMARY OF AVERAGE DATA ON SHOOT ELONGATION FOR THE FIRST PART (ABOUT 86 HOURS) OF THE CULTURE PERIOD FOR ALL SERIES.

Temperature.	Solution type	Mean Hourly Rate 1st test .01mm.	Mean Hourly Rate 2nd test .01mm.	Average 1st and 2nd tests. .01mm. h.)	Grand Ave. for given temperature (.01mm. h.)
35°	I	35	41	38	
	II	27	25	26	
	III	38	34	36	
	IV	36	32	34	31
	V	26	27	27	
	VI	28	26	27	
31°	I	40	47	44	
	II	40	34	37	
	III	44	47	46	
	IV	43	44	44	42
	V	38	37	38	
	VI	46	37	42	
28°	I	41	46	44	
	II	34	33	34	
	III	40	36	38	
	IV	38	40	39	40
	V	44	40	42	
	VI	41	37	39	
25°	I	30	33	32	
	II	31	23	27	
	III	38	33	36	
	IV	31	33	32	32
	V	38	32	35	
	VI	35	28	32	
21°	I	20	23	22	
	II	17	13	15	
	III	29	29	29	
	IV	18	23	21	[illegible]
	V	33	23	28	
	VI	24	20	22	

TABLE VII.(Cont.)

Tem-pera-ture.	Solu-tion type	Mean Hourly Rate 1st test .01mm.	Mean Hourly Rate 2nd test .01mm.	Average 1st and 2nd tests. .01mm.	Grand Ave. for given temperature (.01mm.)
17°	I	7	9	8	
	II	5	-	5	
	III	12	9	11	
	IV	8	-	8	9.5
	V	16	-	16	
	VI	9	-	9	

The general temperature relations shown in tables IV and VI are seen to hold also for table VII. The mean hourly rates given in the last table are, of course, much lower than the corresponding ones for the last 24 hours (table VI)and they are notably lower than those for the entire period (table IV). The next section will be devoted to a comparison of these three sets of growth-temperature data by means of graphs.

GRAPHS OF THE GROWTH-TEMPERATURE RELATIONS.

It has been stated above that all three series of grand averages (for the whole period, for the last 24 hours, and for the first part of the period) agree in showing the highest growth rates for the maintained temperatures, 28° and 31°, and that the average rates for these two temperatures are nearly alike in all three cases. Referring to tables IV, VI and VII (or to the graphs of Fig. 1), it is seen that the rate for 31° is 2.5 per cent lower than that for 28°, for the last 24 hours of the culture period. For the entire period the rate for 28° is 1.5 per cent lower than that for 31° and for the first part of the culture period the rate for 28° is 4.7 per cent lower than that for 31°. It is probably safe to regard these differences as insignificant, considering the general nature of the entire study, and to state that the data here considered indicate that the optimum temperature for the germination of these seeds and the early growth of the seedling shoots lies between 28° and 31°.

A growth-temperature graph was prepared for each of the three sets of grand averages and a study of these graphs will bring out some additional information. The three graphs are shown in figure 1. The actual values are shown by the circles and the lines represent smoothed graphs drawn to fit the distribution of the circles in each case. They may be taken as indicating a close approximation to the indications

LEGEND FOR FIGURE 1

Figure 1. Graphs showing mean hourly rates of shoot elongation in solution cultures, for the entire culture period (about 110 hours), for the last 24 hours of the period, and for the first part of the period (about 86 hours), and lso in distilled-water cultures for the entire period, as these rates are related to maintained temperature. Temperatures are shown by abscissas and growth rates by ordinates.

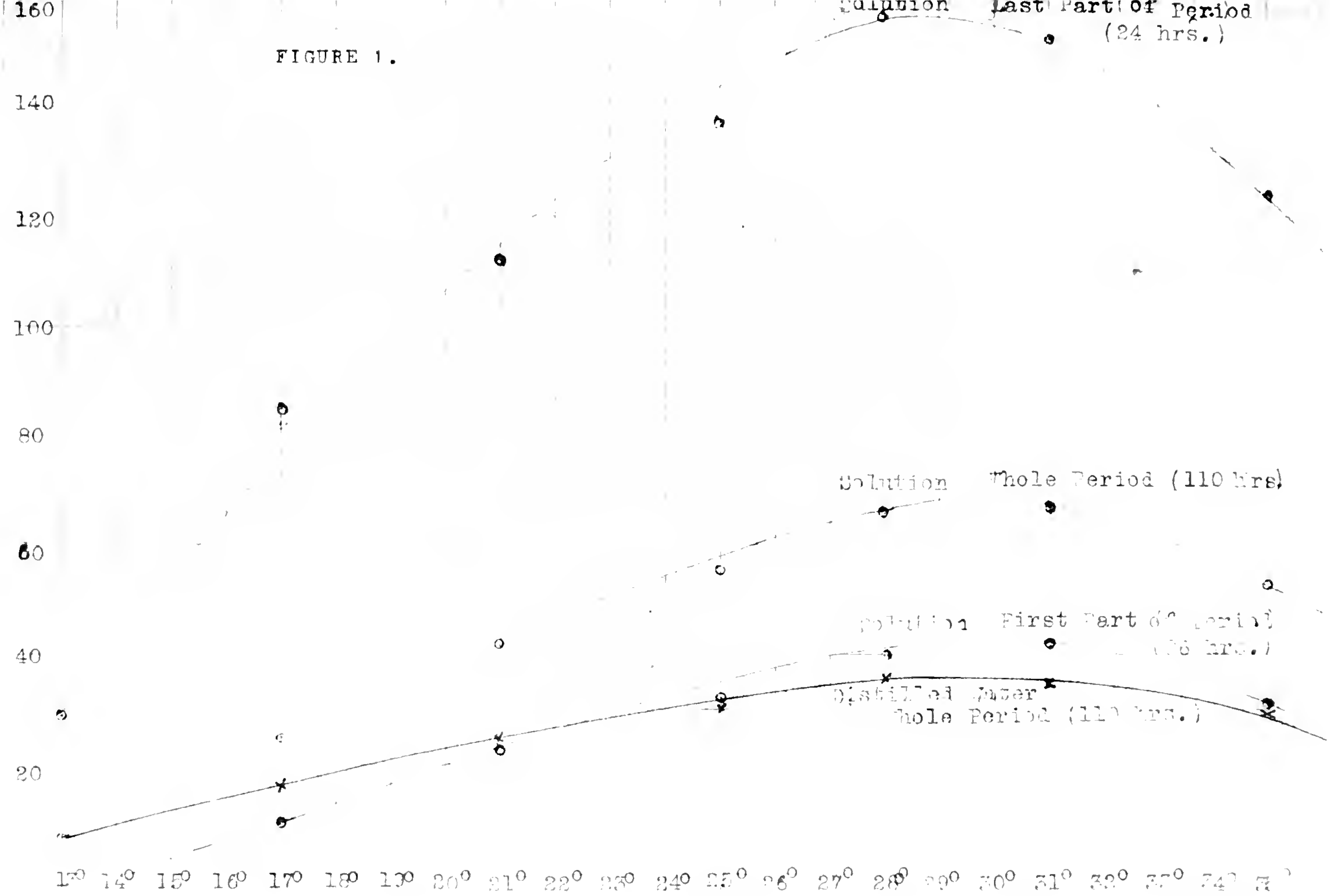

Last Part of Period
(24 hrs.)
Solution
Whole Period (110 hrs)
First Part of
Distilled
Whole Period
160
140
120
100
80
60
40
20
14°
15°
16°
17°
18°
20°
21°
22°
24°
26°
27°
28°
30°
31°
32°

FIGURE 1.

of the data in each case. A similar graph for the distilled water cultures, entire period (table V), is also shown in figure I.

The graphs substantiate the conclusion that the optimal temperature for these tests lay between 28° and 31°, almost surely not above 31° nor below 28°. Furthermore, the form of the curve indicates that the optimum temperature in every case lies about midway between the two limiting temperatures just mentioned. It may, therefore, be stated that the optimum temperature for these wheat seeds, for the periods considered, for the array of solutions used in these studies, and also for distilled water, surely lies between 28° and 31°, with the probability that it is between 29° and 30°.

In the preparation of wheat seedlings for water culture experiments (if the most rapid shoot elongation is desired), it is recommended that a temperature between 29° and 30° be employed, and that if the temperature is not maintained, its fluctuation should not greatly exceed the range between 28° and 31°. It must of course be borne in mind that this recommendationis based on these particular tests. Other temperature relations may well hold for other lots of wheat seed or for other media than the series here used. It is especially worthy of note that these same sets of salts and salt proportions (or any one of them) might exhibit

[illegible]
with suitable [illegible].
lower total [illegible], the [illegible]
growth relation [illegible] the same temperature
optimum as the one shown by the three solution graphs of Figure
I, since the distilled-water graph for the (entire period) agrees
with the others in this respect. With sufficiently different
total concentrations from those tested - either higher or lower
- the details of graph curvature would probably be significantly
different from those for the solution graphs shown in Figure I.
With sufficiently higher total concentrations even the temperature
optimum might be different from the one here indicated, and, -
as has been noted - the different sets of salts and salt propor-
tions tested in this study would then probably show marked dif-
ferences among themselves, so that they could not all be treated
as alike.

Attention should be called to the fact that the recom-
mendation just stated may introduce a modification in the "Plan
for Cooperative Research". On page 13 of that publication, it is
recommended that the temperature used for seed germination should
be 25° - 30°. If the most rapid shoot elongation is desired, the
higher temperature range here recommended should surely be used,
[illegible] similar to the ones here
tested. But it may not always be desirable, [illegible]
for these cultures, [illegible] length of shoots.

Before leaving [illegible] the temperature
relations shown by the [illegible] 1, [illegible]

to [illegible] 1, [illegible] the [illegible] temperature [illegible], [illegible] the solution graphs together indicate that the optimum-temperature graph tends to become less flat in this region as the seed-lings become older. The graph for the last 24 hours is ap-parently more pointed above than that for the whole period, and this, in turn, is less flattened than that for the first part of the period. For the very first stages of germination, it appears that the organism is not so sensitive to temperature differences as it is for later stages. This is in general agreement with many physiological observations.

Another interesting point brought out by these graphs is that each curve is very nearly symmetrical about the vertical axis, that represents its maximum (optimum temperature), as far as these data show. This does not appear to be generally true in growth and other biological processes; in many cases reported in the literature (see Lehenbauer, cited just below, for example) the upward slope of this sort of graph is more gradual than the downward slope.

Temperature Coefficients for Shoot Elongation.

Probably the most satisfactory method for characterizing the temperature relations of any process is that employing temperature coefficients.(10) The temperature coefficient for a given process and for a given temperature interval is the quotient obtained by dividing the rate for the higher temperature by that for the lower. The interval is conveniently taken as 10° C, and the symbol for the coefficient is generally expressed as Q_{10}. The values for Q_{10} were obtained for shoot elongation in these seedlings for the entire period, for all the 10-degree intervals available. The upper graph of figure 1 was used for determinng the approximate hourly rate for each temperature from 13° C. to 35° C. The rate for 13° is .29mm. and that for 23° is 1.30 mm., so that the Q_{10} (13°-23°) is 1.30 divided .29, which is 4.5. The values of Q_{10} obtained for all the 10-degree ranges are presented in table VIII which is self-explanatory.

(10) For ~~references to~~ the literature on this subject see the following, and the references there given: Livingston, B.E. and Livingston, G.J. Temperature coefficients in plant geography and climatology. Bot. Gaz. 56:349-375.1913.

Lehenbauer, P.A. Growth of maize seedlings in relation to temperature. Physiol. Res. 1:247-286.1914.

Kanitz, Aristides, Temperatur und Lebensvorgänge. Heft 1:9-175. Berlin. 1915.

Fawcett, H.S. The temperature relations of growth in certain parasitic fungi. Univ. Calif. Pub. Agri. Sci. 4:183-232. 1921.

TABLE VIII.

TEN-DEGREE TEMPERATURE COEFFICIENT (Q_{10}) FOR SHOOT ELONGATION FOR THE ENTIRE CULTURE PERIOD

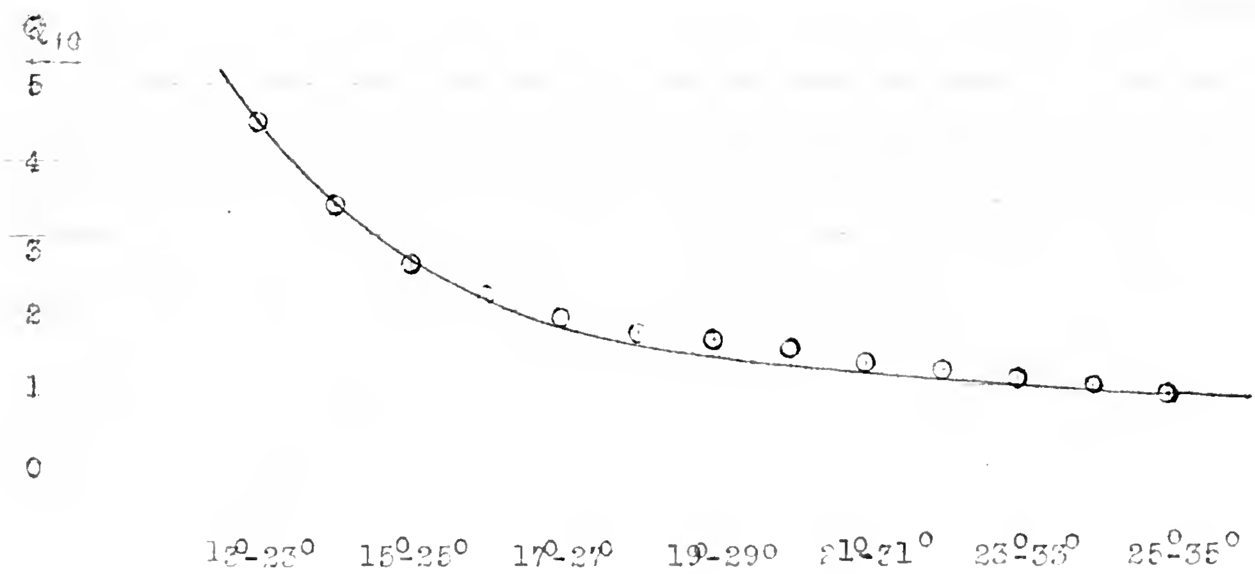
(ABOUT 110 HOURS.)

Temperature interval Degrees C.	Hourly rate for higher temperature .01mm.	Hourly rate for lower temperature .01mm.	Q_{10}
13-23	130	29	4.5
14-24	137	40	3.4
15-25	143	54	2.6
16-26	149	67	2.2
17-27	152	79	1.9
18-28	157	90	1.7
19-29	159	99	1.6
20-30	158	107	1.5
21-31	153	115	1.3
22-32	148	123	1.2
23-33	148	130	1.1
24-34	134	137	1.0
25-35	124	143	0.9

[illegible] ude, [illegible] infinit[illegible] [illegible] similar [illegible] just how this variation occurs. [illegible] considered [illegible] [illegible] Figure 2, [illegible] temperature [illegible] [illegible] [illegible] low temper- ature intervals [illegible] infinite, [illegible] is zero. The intervening values ([illegible] ow [illegible] Fig. 2.) [illegible] (15° - 25°) to [illegible] (25°-35°). [illegible] principle, like all other [illegible] ([illegible]), [illegible] root growth [illegible] the value of [illegible] is about [illegible]; [illegible] from 15° [illegible]. [illegible] 15° [illegible]

LEGEND FOR FIGURE 2.

Figure 2. Graphs of 10-degree temperature coefficients (Q_{10}) for shoot elongation for entire culture period. The different temperature intervals are indicated on the axis of abscissas and the values of Q_{10} are shown by the ordinates.



[illegible] Q_{10}, [illegible] a number [illegible] [illegible]. If [illegible] values of the Q_{10}'s are [illegible] considered [illegible] (the range from [illegible] to [illegible], for example), [illegible] that [illegible] represents 10 - degree temperature intervals between about 15° and 27.5°. For intervals including temperatures below about 15° the coefficient value is greater than 2.0 and for intervals including temperatures above 27.5° the value is less than 2.0. It is interesting to note that the coefficient has a value of unity for the 10 - degree range from 24° to 34°, and that the center of this range is 29°. This is additional evidence that the optimum temperature for these tests is about 29°, the coefficients show that 10-degree ranges centering below 29° give Q_{10}'s greater than unity, while those centering above 29° give Q_{10}'s less than unity.

Conclusions.

One of the aims of this study was to obtain evidence as to what set of salts and salt proportions and what temperature might give the most rapid germination of wheat, and most favorable early growth of the seedlings, so that definite recommendation might be made for the preperation of seedlings for solution cultures such as those outlined in the "Plan for Coöperative Research." As far as the results of these tests bear on the question, it may be said that of the 126 different solutions tested, no one is clearly and definitely more promising than any other, for the total concentration here used (equivalent to about 0.1 atm. of osmotic pressure) and for the first four or five days after the dry — seed is placed in contact with the medium. Within the limits set by the innate variability of the seed used, it must be concluded that the percentage of germination and the rapidity of shoot elongation were not measurably influenced by the solution type or the salt proportions in these tests. This appears to mean that, with seed such as this and with the total solution concentration here used, all of the 126 solutions tested must be regarded as about alike, within the ordinary temperature range for wheat growth, in their suitability for promoting the development of seedlings 4 — 5 cm. high,

although for later growth some of these sets of salt proportions are undoubtedly very poor and others are much better.

It therefore seems safe to continue using Shive's solution R5C2 (0.1 atm.) in preparing seedlings for solution cultures, as recommended in the "Plan", or to use any set of salt proportions lying in the middle portion of the triangular diagram. Shive's R5C2 is IR3.8S1.1 on the diagram used in the present ~~studies~~, that is, 3.8 eighths of all the salt molecules placed in the nutrient solution are KH_2PO_4 , 1.1 eighths are $Ca(NO_3)_2$, and 3.1 eighths are $MgSO_4$. Such simple solutions as IR3S2 or IR3S3 (both 0.1 atm.) may therefore be expected to give results about as good as any other. The salts used for solution type I are relatively satisfactory from both the physical and chemical points of view, and it may be stated that, so far as this study is concerned, they are just as promising as any of the others.

It should be kept in mind also, that the solution used for the preliminary preparation of wheat seedlings for solution cultures ought to have a considerable total concentration. Distilled water was markedly less efficient than any of the solutions used in these tests. It seems safe to recommend a total concentration at least as great as that here used. Perhaps a still higher concentration might give even better growth, but no evidence with regard to this question is available.

ith regard to temperature, the results reported in this paper indicate that any maintained temperature between 28° and 31° C. may be expected to give about the maximum rate of shoot elongation for such seeds as these.

For a very rapid rate of germination and subsequent growth of shoots until the latter are 4-5 cm. long a temperature of 29° C. may be selected with a solution, as for example, I:3S2 (0.1 atm.). Under these conditions, it should require about 25 hours to obtain (from seed like that here used) seedlings having a shoot length of 4 cm. after the shoot has broken through the seed-coat, and about 95 hours after the dry seed has been placed in contact with the solution.

These recommendations are based on the supposition that it is desirable to secure about the most rapid development of shoots during their germination phase. If a slower development is requisite, probably most physiologists would agree that it would be better to retard growth by using a temperature somewhat below the optimum rather than above it. From the graphs of figure 1. a maintained temperature may readily be chosen, such that any desired rate of shoot elongation may be approximated. hether it is desirable, in preparing seedlings for solution cultures, to allow germination to occur under nearly optimal conditions, cannot be stated.

Nevertheless, for the sake of subsequent comparisons, it is surely desirable that all the seedlings used in any comparative study should have been subjected to the same germination conditions, whether these be optimal or sub-optimal. It may often be most satisfactory to employ for germination the same temperature conditions as are to be used for later phases of growth. It is not, however, the purpose of the present paper to enter into any discussion of this fundamental question; such a discussion would require experimental evidence that has not yet been secured.

SUMMARY.

Before proceeding to summarize the results of this study, it may not be out of place to emphasize the application, in this case, of certain fundamental principles sometimes seemingly neglected. These points emphasized in this paper are based primarily on the results of the experiments of this particular study. No attempt is made to make the statements of this summary applicable to all plants, nor to all wheat seed, nor even to all "Marquis" wheat seed. They refer simply to this lot of wheat seed in these tests and to the first phase of development, about 110 hours from the beginning of the soaking of the seed. Similarly, they refer only to the maintained temperatures here employed, to the total concentration (equivalent to about 0.1 atm. of osmotic pressure) of the solutions used, to the 126 different salt compositions outlined in the "Plan for Cooperative Research," to the absence of light from the culture chambers, and to the various other details that may have been effective in controlling the results of this experimentation. The present paper is simply a report on the results secured from these tests and on the relations that obtain among them. Whether other seed might exhibit different relations for this same physiological phase of development and for these treatments is of course not predictable

from the present results. From the work of many earlier writers, and also from other results obtained by the present writer in other connections, it is safe to say that later growth phases of this seed or other salt combinations or total concentrations, would give very different indications from those here brought forward. The complexity of the internal and environmental control of developmental and growth processes should be borne in mind when reading the following statements, and it should not be forgotten that the particular lot of seedused, in spite of an effort to secure uniformity (a highly desirable feature in a study of this kind), nevertheless manifested a low degree of uniformity, that is, the seedlings were characterized by a marked degree of internal variation.

The main points brought out in the preceding sections of this paper are summarized below:

(1) Within the limits set by the 126 different solutions used, no significant relation between the composition of the medium and percentage of germination of the seed was apparent.

(2) Similarly, no relation was apparent between the percentage of germination and the temperature at which germination occurred. The rapidity of germination was,

of course, influenced by temperature, and in a marked way, though this relation was not quantitatively studied.

(3) No significant relation between the salt composition of the medium was clearly apparent. What ever influence might have been exerted by these environmental features was masked by the influence of the relatively large internal variation shown by the several lots of 25 seeds. For later developmental phases, or perhaps for these early stages of growth, with this same kind of seed if its internal variability were much lower, relations between growth rate and the composition of the medium may be expected to become manifest.

(4) For all temperatures, excepting the lowest here used ($13^\circ C.$), distilled water as a medium appeared to give rates of shoot elongation for the entire culture period (about 110 hours) that were only about half as large as those given by the nutrient solutions. Although the kind of solution was apparently without significant influence on the elongation rates of these shoots, and any solution must therefore be regarded as just as promising as any other in this respect, yet any one of these solutions was

apparently better as a germination medium than was distilled water. For the lowest temperature used (13°), however, distilled water is indicated as just as satisfactory as the solutions.

(5) Despite the great degree of internal variation in the seed used, the usual temperature influence was clearly brought out with regard to the rate of shoot elongation. The influence of maintained temperature was so great that it far surpassed the influence of internal variation. All the solutions used with any temperature were treated as if they had been just alike, and an average hourly rate of shoot elongation was obtained for each of the seven temperatures used. These average hourly rates are as follows in terms of hundredths of a millimeter:—

	Temperature, Centigrade.						
	13°	17°	21°	25°	28°	31°	35°
For first part of period. (about 86 hours.)	---	9.5	23	32	40	42	31
For last 24 hours of period.	29	85	112	137	157	153	124
For entire period	7	25	42	55	66	67	53

The optimum temperature, as shown by these averages, lies between 28° and 31°, probably between 29° and 30°.

(6) The growth-temperature graphs are uniformly flat at the top, which indicates that there is a consider-able range of temperatures, all of which are about alike in their suitability for producing the highest elongation rates. Any temperature between 28° and 31°, inclusive, may be regarded as practically optimum, as far as the results show. The graph for the last 24 hours is more pointed at the top than that for the whole culture period, and the one for the whole period (about 110 hours) is more pointed than that for the first part of the period (about 86 hours). [illegible]

(7) The growth-temperature graphs are all very nearly symmetrical about the vertical line representing approximately 29.5° as far as the results show. According to the smoothed graphs, a maintained temperature of 25° may be expected to give sensibly the same growth rates (under the conditions of these tests) as does one of 35°.

(8) The ten-degree temperature coefficient for the rate of shoot elongation for the entire culture period (about 110 hours from the beginning of the soaking of the seeds) follows the general law that has been worked out by earlier students in this field. Its value is 4.5 for the temperature interval from 13° to 23°, about 2.5 for the interval from 15° to 25° and 1.0 for the interval from 24° to 35°. The last point [illegible] that the [illegible] is to be considered as about [illegible].

Literature Cited.

(1) Bartlett, H.H. See True, R.H. and Bartlett, H.H.

(2) Fawcett, H.S. The temperature relations of growth in certain parasitic fungi. Univ. Calif. Pub. Agri. Sci. 4:183-232. 1921.

Idem. See Livingston, B.E. and Fawcett, H.S.

(3) Gericke, W.F. Influences of temperature on the relations between nutrient salt proportions and the early growth of wheat. Amer. Jour. Bot. 8:59-62. 1921.

(4) Hibbard, R.P. Physiological balance in the soil solution. Mich. Agric. Exp. Sta. Tech. Bul. 40. 1917.

(5) Kanitz, A. Temperatur und Lebensvorgänge. Heft 1:9-175. Berlin, 1915.

(6) Lehenbauer, P.A. Growth of maize seedlings in relation to temperature. Physiol. Res. 1:247-286. 1914.

(7) Livingston, B.E. (Editor). A plan for cooperative research on the salt requirements of representative agricultural plants, prepared for a special committee of the Division of Biology and Agriculture of the National Research Council. 2nd Ed. 54 pp. Baltimore, 1919.

Idem. Further studies on properties of unproductive soils. U.S. Dept. Agric. Bur. Soils Bul. 36. 1907.

(8) Livingston, B.E., and Livingston, G.J. Temperature coefficients in plant geography and climatology. Bot. Gaz. 56:349-375. 1913.

(9) Livingston, B.E., and Fawcett, H.S. A battery of chambers with different automatically maintained temperatures. Phytopath. 10:336-340. 192. 1920.

(10) Livingston, B.E., and Tottingham, W.E. A new three-salt solution for plant cultures. Amer. Jour. Bot. 5:337-346. 1918.

(11) Martins, W.H. See Shive, J.W., and Martin, W.H.

(12) McCall, A.G. The physiological balance of nutrient solutions for plants in sand cultures. Soil Sci. 2:207-253. 1916.

Idem. The physiological requirements of wheat and soy beans growing in sand media. Proc. Soc. Prom. Agric. Sci. 1916:46-59. 1916.

(13) McCall, A.G. and Richards, P.E. Mineral food requirements of wheat plant at different stages of its development. Jour. Amer. Soc. Agron. 10:127-134. 1918.

(14) Richards, P.E. See McCall, A.G. and Richards, P.E.

(15) Schreiner, O. and Skinner, J.J. Ratio of phosphate, nitrate, and potassium on absorption and growth. Bot. Gaz. 50:1-30. 1910.

Idem. Some effects of harmful organic constituents. U.S. Dept. Agric. Bur. Soils Bul. 70. 1910.

Idem. The triangle system for fertilizer experiments. Jour. Amer. Soc. Agron. 10:225-246. 1918.

(16) Skinner, J.J. See Schreiner, O. and Skinner, J.J.

(17) Shive, J.W. A study of the physiological balance in nutrient media. Physiol. Res. 1:327-397. 1915.

Idem. A study of physiological balance for buckwheat grown in three-salt solutions. N.J. Agric. Exp. Sta. Bul. 319. 1917.

(18) Shive, J.W. and Martin, W.H. A comparison of salt requirements for young and mature buckwheat plants in water cultures and sand cultures. Amer. Jour. Bot. 5:186-191. 1918.

(19) Tottingham, W.E. A quantitative chemical and physiological study of nutrient solutions for plant culture. Physiol. Res. 1:133-245. 1914.

Idem. See Livingston, B.E. and Tottingham, W.E.

(20) True, R.H. Harmful action of distilled water. Amer. Jour. Bot. 1:255-273. 1914.

(21) True, R.H. and Bartlett, H.H. Absorption and excretion of salts by roots, as influenced by concentrations and composition of culture solutions. U.S. Dept. Agric. Bur. Plant Ind. Bul. 231. 1912.

VITA.

The writer was born on a farm near Fremont, Nebraska, August 30, 1884, the son of Charles L. and Fredericka Meiersausen Gericke. He attended the district schools in his boyhood. In November, 1909, he entered Iowa State College by examinations, and was enrolled as a regular student in January, 1910. During the summer of 1911 he attended the University of Chicago. He was graduated, with the degree of Bachelor of Science in Agronomy, from Iowa State College in June, 1912. He was then appointed instructor in Soil Chemistry and Assistant Soil Chemist in the Experiment Station of the University of California. In 1915 he received the degree of Master of Science from the University of California, and in 1916 he was appointed Assistant Professor in Soil Chemistry in the same University. In 1918 he was granted leave of absence to study at the Johns Hopkins University. He was a Fellow by Courtesy in the Johns Hopkins University for the academic year 1918-19. He devoted his attention at the Johns Hopkins University to Plant Physiology, as major subject, and Physical Chemistry and Physiological Chemistry as first and second subordinate subjects, respectively. He remained at this University

and continued his experiments throughout the summer of 1919, returning to the University of California in October of the same year.