The Relation between Temperature and Growth in the Roots of Lepidium Sativum

by

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INTRODUCTION.

The publication of Blackman's [1]) „Optima and Limiting Factors" was the cause of many new investigations to be made of the relation between temperature and the rate of physiological processes.

Whereas before 1905 the experimentators beleived the optimumcurve to be the right form to express the connection between temperature and reaction-velocity Blackman lays stress on a new point of view and comes to the conclusion that a timefactor, until then neglected, comes into play: if it were possible to make an observation at different temperatures during a time zero, there would appear to be no optimum at all and the curve, calculated at infra-optimal temperatures, would gradually mount without any falling off taking place, so that van 't Hoff's rule on reaction-velocity of chemical processes which increases two—to threefold for every 10° C. rise of temperature might also be applied in biological processes. The optimum hitherto found is to be regarded as a point of the curve changing its place with the time of experiment.

[1]) F. F. Blackman. Annals of Botany. Vol. XIX. 1905. p. 281.

Miss Matthaei's experiments on the influence of temperature on assimilation led him to this theory.

The results of investigations of the relation between temperature and reaction-velocity of the various physiological processes after 1905 could not prove this theory although its possibility remains.

These experiments were made to find out if the same can be said about the lengthgrowth of plants; while they were being made another publication on the same subject appeared about which more will be said in Chapter III.

CHAPTER I.

Method.

Material.

The experimental object was the root of Lepidium Sativum.

The way of growing the roots.

The seeds were soaked on hygrophil gauze tightly stretched over glass rings floating on water in a glass basin at a temperature of 20° C.; the seeds germinated in ± 24 hours and were ready for the experiments: the root had broken the seedcoat and had become visible. Then glass plates, bent at the ends in such a way as to stand vertically, were covered with gray filterpaper, tied firmly over it and 9—10 seedlings were put with their roots along the filterpaper whose tops grew vertically downwards: the glass plates being vertical the roots grew straight downwards; 4 to 5 glass plates were put together in a glass basin with $^1/_2$ cm. of water in it in order to keep the paper moist.

The sides and the covering were covered with filterpaper leaving enough room to allow fresh air to come in. The seeds kept their first position because the slime secretion of the seedcoat in the moist atmosphere enabled me to fix them. Except for a few all the seeds germinated; most of the roots growing straight but not all of them vertically; probably the opening of the seedcoat caused some shifting. The white roots showed clearly against the dark filterpaper.

Pringsheim [1]) gives a distinct photo of it.

For each experiment I took ± 20 objects because of the individual variations.

The cultivating took place in the dark in boxes covered at the in- and at the outside with black cloth. The glass plates were put horizontally during a very short time necessary for measuring the length of the roots; therefore I repeatedly observed if any geotropical incurvations took place; but no such incurvation could be observed.

The way of measuring.

The measuring has been done in a dark room by red light. Each plant has been exposed to this light during such a short time that there were no incurvations which should be attributed to phototropy or thermotropy.

The roots have been marked with a little brush soaked in Indian ink, all the hairs of which had been cut away except six in the centre. Putting a small piece of millimeter paper along the root I was able after some training to put marks on their tops, about one millimeter from each other; when making the marks I measured with the help of a magnifying glass exactly their distances; the meaning of the signs — and + in the tables is that the length is somewhat less or more than the number denoting the mm.

The velocity of growth.

This value is found by measuring the increase of the

[1]) E. G. Pringsheim. Zeitschrift für biologische Technik und Methodik. 1911. Band II. no. 3.

distance from a certain mark on the root to its top after a certain time.

Duhamel[1]), Ohlert[2]), Wigand[3]) but especially Sachs[4]) demonstrated in their publications that only the top grew.

To make it possible to compare the growth at different temperatures two questions had to be answered first:

1⁰. what is the length of the growing zone?

2⁰. is its length variable with the temperature?

Determination of the length of the growing zone.

Wigand says in his publication that this zone for Lepidium Sativum is less than 2 mm.; with my objects it was always more than 3 mm.

Sachs measured the root without the kalyptron; as for Lepidium Sativum the limit between root and kalyptron was not always clearly perceptible there; therefore I included the Kalyptron in my data.

On the top of the roots five marks were put and the zones were numbered in Sachs' way: zone I being next to the top.

At a moment their lengths were measured and 7 hours afterwards again. The result was (see table I) that zone I, II and III had always grown, IV several times, but never more than $^1/_2$ mm., while V always kept its original length, even if the experiment was continued, which was necessary, for it might have been possible that during 7 hours the lengthening had been too slight to be observed.

1) M. Duhamel Du Monceau. La Physique des Arbres. 1e Partie. Paris. 1758. p. 83.

2) E. Ohlert. Linnaea. 1837. B. XI. p. 609.

3) A. Wigand. Botanische Untersuchungen, Braunschweig. 1854. p. 159.

4) Sachs. Arbeiten des Botanischen Instituts in Würzburg. B. I. 1864. Heft 3. p. 413.

The growth of zone II was always greatest, while the limits of I, II and III after the experiment were sometimes hardly distinguishible.

This is in agreement with the results of Sachs and the investigators before him, among others Müller[1]).

Sachs does not mention in his publications that the length of the growing zone depends on temperature.

Askenasy[2]) and Popovici[3]) do not agree with him; they come to the conclusion that it is greater at low than at high temperatures.

Popovici moreover finds that if his plants remain during a long time at a subminimal temperature the zone shortens again, but probably his experimental objects were not in a good condition as he complains of bacteria appearing in his cultures. As for Lepidium Sativum I found at every temperature the same length of the growing zone. Only at very high temperatures, which Popovici did not make use of and to which it is impossible to expose the objects during so many hours, and at very low temperatures the growth was so small, that it was only to be observed in two zones; but, if observations had been made microscopically lengthening of zone III, maybe IV, would probably have been found; at least there is no reason to suppose that this would not have been the case.

In table I "initial length" means the distance from the top of the root to the tangent of the seedcoat that is at right angles with the root.

1) N. J. C. Müller. Botanische Zeitung. 1869. p. 389 and Bot. Zeit. 1871. p. 693.

2) E. Askenasy. Berichte der Deutschen Bot. Gesellschaft: VIII. 1890. p. 61.

3) A. P. Popovici. Botanisches Centralblatt LXXXI—LXXXII 1900. p. 33.

Table I.

Initial length.	Temperature.	Numbers of the zones.	Length of the zones at the beginning at the experiment.	Growth in 7 hours.
13	21°	I	1	1+ }
		II	1	$4^1/_2$ }
		III	1	$^1/_2$
		IV	1	+
$13^1/_2$		I	1	$3^1/_2$
		II	1+	$2^1/_2$
		III	1−	$^1/_2$
		IV	1	0
$14^1/_2$		I and II	2	$5^1/_2$
		III	1−	1−
		IV	1	+
15		I and II	2−	6
		III	1	1−
		IV	1	+
16		I	1	$^1/_2$
		II	1	4
		III	1	$1^1/_2$
		IV	1	$^1/_2$
$16^1/_2$		I and II	2−	5+
		III	1	1+
		IV	1+	0
13	28°	I and II	2+	6
		III	1+	2+
		IV	1	0
15		I and II	2− }	7+
		III	1+ }	
		IV	1	$^1/_2$
$15^1/_2$		I	1 }	6
		II	1 }	
		III	1	2
		IV	1	0

Initial length.	Temperature.	Numbers of the zones.	Length of the zones at the beginning of the experiment.	Growth in 7 hours.
17½		I	1+	4½
		II	1—	
		III	1+	2+
		IV	1	½
18		I, II and III	3+	8
		IV	1	0
14	27°	I and II	2—	7
		III	1½	1
		IV	1—	0
16		I and II	2+	6½
		III	1	1½
		IV	1	½
16½		I and II	2	8
		III	1	
		IV	1	0
17		I and II	2	7½
		III	1—	1
		IV	1+	½
18		I	1+	8½
		II	1	
		III	1	
		IV	1	0
18½		I and II	2+	7½
		III	1—	1—
		IV	1—	½
13	30°	I	1	5—
		II	1	
		III	1	1½
		IV	1	½
15		I and II	2+	6
		III	1	1½
		IV	1—	0

Initial length.	Temperature.	Numbers of the zones.	Length of the zones at the beginning of the experiment.	Growth in 7 hours.
15 1/2		I	1 — }	7 —
		II and III	2 }	
		IV	1	1/2
17		I, II and III	3	7 1/2
		IV	1	0
18		I	1	3
		II	1	2 1/2
		III	1	1
		IV	1 —	1/2
18		I, II and III	1 +	7 1/2 —
		IV	1	0

After having answered these two questions only one mark at a distance of ±5 mm. from the top was required; in this way a very short time passed between the beginning of the marking and the moment when the plants were put in the thermostat.

Arrangement of the experiments at high temperatures.

The space in the thermostat being too large the plants after having been marked were put in a zinc basin with a covering, lined with filterpaper; this basin was put at the bottom of the thermostat.

In order to avoid curvature of the roots I had put into this basin some water to a height of 1 1/2 cm. and just above the surface of the water I had two holes made on either side in the wall of the basin in order to allow CO_2 to stream out and fresh air to come in so that there was no accumulation of this gas. The thermostat described in the dissertation of Rutgers[1]) was used.

[1]) A. A. L. Rutgers. The influence of temperature on the geotropic presentation-time. Recueil des Travaux Botaniques Néerlandais. Vol. IX. Livr. 1.

With the exception of the first two series all the experiments were made in the room for constant temperature. As these first two series are less accurate because they could not be made in it and furthermore as the results can be found in the „Proceedings of the Koninklijke Academie van Wetenschappen te Amsterdam" [1]) no more will be said about them.

The room for constant temperature has thick stone walls, floor and ceiling. A double door makes it possible to enter and to leave the room without any light entering. Good ventilation is taken care of.

For the heating and the regulation of the temperature electricity has been made use of. Along the walls of the room electric stoves are placed which are connected with a switch; the switch is connected with the metallic thermoregulator; when the latter makes contact the current for the stoves is interrupted and the heating stopped. When the current is interrupted by the regulator the switch makes the current go through the stoves and heating takes place.

The metallic thermoregulator was planned and made by the amanuensis of the Botanical Laboratory. See Fig. I and II.

It points to $^1/_8$° C. exactly. On a board of wood, *P*, strongly fixed on the wall, is fastened a broad bar, *A*, unmovable at one end, *b*; this bar consists of two metallic parts, lying on each other, made of different metals: zinc and iron, the upper, thinner part being iron. The other end of the bar is movable and provided with a strong curved thread, *d*, which pushes the short end of the lever, *B*, downwards at *e*. This lever, also consisting of two kinds of metal, zinc and iron, (but here the upper layer is made

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[1]) E. Talma. The influence of temperature on the growth of the roots of Lepidium Sativum. Proceedings K. A. v. W. A. Vol. XIX no. 1.

Thermoregulator, seen from aside

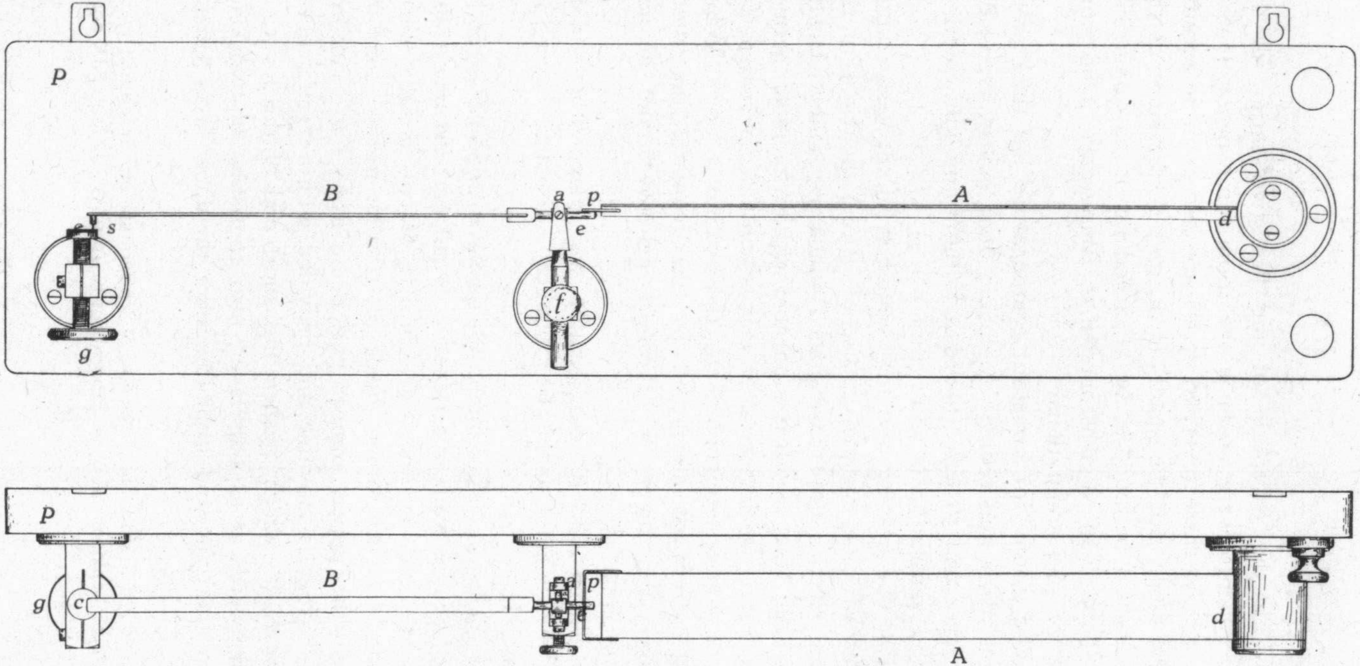

Fig. I and II.

The same seen from above.

of zinc in order to enlarge the bending) turns on a spindle which can be moved up and down by a screw, *f*. At the end of the long arm of the lever a little platine bar, *s*, is fastened, which can be brought in contact with a little disk, *c*; this disk can be moved up- and downwards by a screw, *g*. This thermoregulator is also connected with the switch.

When, at a certain temperature, while the stoves are burning, the little bar, *s*, is not in contact with the disk, the rising temperature will raise the thick end of the bar, *A*, and the iron thread bending likewise the shorter arm of *B* will rise; accordingly the longer arm of *B* is falling and contact will be made with *C*; thus the stoves cease heating and the temperature falls. The falling temperature causes the bar *A* to stretch itself: then the contrary takes place.

A thermograph proved the temperature to be the same and constant in different places in the room. Thus cultivating and measuring could be done at the same temperature, and all the plants had assumed the same temperature before the starting of the experiment; in this way the influence of temperature during the experiment can be demonstrated most clearly. In literature many examples are known of the experimental objects but slowly assuming a sudden falling or rising of the temperature of their surrounding. In the publications by Sachs this fact is most evident; table III and IV [1]) show how the curve of the rate of growth follows but slowly the curve which represents the rising and falling of the temperature. Askenasy observes that during the first interval of 12 hours plants, cultivated in a warm room, grow much more than those cultivated in a cold room.

Therefore a difference of some degrees at the beginning

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[1]) Arb. d, Bot. Inst. i. Wurzburg. B 1. Heft 2. Taf. III a. IV.

of two different experiments may be of great influence on the rate of growth during those experiments.

All this makes it clear that the use of a room of constant temperature is required for investigations of this kind.

Very shortly before I began to measure the thermostat had been brought to the temperature at which the experiment was to be done. The roots were quickly measured and put in it. No more than 20 minutes were wanted to close the thermostat and to put in action the stirrers and the water- air-pump, and to bring the water in the thermostat to the final temperature.

At the end of the experiment the roots were taken from the thermostat and measured within 10 minutes.

Only macroscopical experiments were made, for which reason they lasted $3^1/_2$, 7 or 14 hours.

Moreover several experiments have been made at high temperatures during $1^1/_2$ hours. Having remained for $1^1/_2$ hours at those temperatures, the objects were put in the room at 20.5° C. I wanted to know whether they would recover from the harmful influence of the high temperatures and if so after how many hours.

Arrangement of the experiment at low temperatures.

The way of getting a constant temperature up to 15° C. wants a special description.

It was easy enough to get temperatures from 13°—15° C.; on a day when the temperature without was a little below 13°—15° C. The electrical stoves were put out and the door giving way into the hall was opened until the room had reached the experimental temperature.

For the experiments at 10° C. the same method was followed; only now water of 10° C. was streaming between the inner and the outer wall of the thermostat in order to keep the temperature constant; therefore water of the aquaduct, which appeared to be of constant temperature was made use of.

Ice had to be applied to this water for the experiments at the temperatures up to 10° C. These experiments were when it was freezing without; it was possible to keep the temperature at $^1/_4$° C. exactly. Several hours before the starting of the proof the plants had been brought into the room.

The experiments at 0° C. could not be taken in the laboratory; a room artificially cooled was required; the great kindness of the Director of the Abattoir enabled me to make some observations there in one of the refringerators which were provided with a double door and thick stone walls exactly like the dark room in the laboratory. They could be cooled some degrees below zero. Moreover I could dispose of ice to cover the zinc basin with the plantlets at all sides.

In this way it was possible to keep the temperature of the roots at 0° C. constant during many hours; a maximum-minimum thermometer and a thermograph demonstrated that indeed the temperature in the basin was constant.

To be sure that the roots had assumed the experimental temperature at the beginning of the experiment I put the basin before starting the measuring during 2—3 hours in the refrigerator, and I covered it with ice.

Three hours afterwards I measured them again to control whether they had grown perceptibly; if this had been the case I should have been obliged to leave them a longer time before starting the proof. It appeared that they hat not grown.

During the whole night and a part of the following day they remained at this temperature.

While at the temperatures above 30° C. several curvatures occurred, at the low temperatures all the roots grew straight downwards. No other cause could be thought of than a lack or a variation of humidity of the atmosphere; in order to keep the objects as moist as possible at the high temperatures I put filteringpaper on the glass plates: in fact the number of curvatures diminished remarkably: beneath 36° C. there were hardly any.

The experiments at low temperatures are not absolutely comparable with those at higher temperatures, because the objects had already been at the experimental temperature for several hours before measuring took place, whereas this was not the case with those at higher temperatures; more will be said about it when the sources of error are further discussed.

Sources of Error.

The first difficult question to be answered was to fix the moment for the starting of the experiment. There appeared to be two possibilities: 1° the moment when I began to measure; 2° the moment when the thermostat was closed. In both ways inevitable mistakes are made. I preferred the first method, because then two errors occurred, neutralizing each other, which does not happen to be the case in the other way; measurable growth took place between the beginning of measuring and the closing of the thermostat; but it takes some time before the plants have assumed the temperature of the thermostat; therefore during the first period the rate of growth is less than agrees with the temperature of the thermostat; at least this holds good for those temperatures up to the optimum but above 20° C. This second error reduces the first though it is not possible to say in which degree.

As for the temperatures higher than the optimum: here the error will be greater, because it takes some time before the roots assume the harmful temperatures; before this moment they pass exactly that part of the curve where the rate of growth is the greatest. Also for temperatures up to 20° C. the error is worse, the objects coming from a higher temperature and keeping for some time a greater rate of growth than agrees with the experimental temperature. Again nothing can be told about the importance of the error.

If the glass plates and the paper had not to assume the experimental temperature the errors would probably be but small; Rutgers found the time neccessary for the mould in his vessels of zinc to reach that temperature to be 45 minutes, when the difference between the water of the thermostat and the mould was 15° C. The thin glass plates will certainly assume the temperature much sooner, especially when I put water of the experimental temperature in the zinc basin before closing the thermostat. About the plant nothing can be said; thermoelectrical determinations never can be made without wounding the roots and about their influence on the rate of growth we do not know anything at all; if such determinations were made the difficulty would only be transposed, not conquered, and the results would not be in accordance with the cost of time and electricity.

All these facts prove that it is necessary to start at the same constant temperature for all the observations. To have absolutely the right of comparing directly all the experiments at low and at high temperatures.

I might have proceeded in two different ways which it is nevertheless impossible to follow practically.

I should have invariably cultivated and measured at 0° C.; only the present state of the laboratory does not make it possible to keep the temperature at 0° C. constant for such a long time; moreover it must be doubted whether the plants would have grown under these circumstances, and whether the roots would reach a length of 13 mm.; I will return to this question when discussing the minimum.

The second way I might have followed in theory is as follows: cultivation and measuring both might have been done at the various experimental temperatures; certainly the harmful influence of the high temperatures would have prevented any further development.

I intended to make a series of observations at 25° C.—30° C., cultivating and measuring at the same temperatures, in order to investigate the influence of the cultivation-temperature; but during the war great economy in the use of electricity was prescribed and as the experiments would have required an especially great quantity of electricity I was obliged to renounce them.

Another factor makes absolute comparison impossible: it is the periodicity of growth; its influence must be perceived especially when the experimental time is long, and the more according as the temperature lies near the optimum, because under those circumstances the rate of growth is the greatest. A priori the greatest rising of the curves that represent the rate of growth at the different temperatures can be expected to be in those experiments where the roots remain the longest time in the thermostat; at least as far as we are in the raising part of the curve of growth, which happens to be everywhere in these investigations.

Finally the material introduced another error: the seeds do not germinate all at the same moment; therefore their lengths will be different at the starting of the experiment; one object will reach the great rising of the curve of growth sooner than an other and accordingly grow more during experiment. In order to avoid as much as possible the influence of the initial length I made some observations to know how great it was on the rate of growth, macroscopically measured during 7 hours.

Table II demonstrates that the rate of growth does not depend on the initial length when this last lies between 13 mm. and 23—25 mm.

Table II.

Temperature.	Initial length in mm.	Growth in 7 hours in mm.
21°	13	$5^1/_2$, 6 +, $6^1/_2$
	$13^1/_2$	$6^1/_2$, 7 —, 7
	14	7 —, 7
	$14^1/_2$	6, $6^1/_2$, 7
	15	$5^1/_2$, $5^1/_2$, 6, $6^1/_2$, $6^1/_2$, 7
	$15^1/_2$	$5^1/_2$, $6^1/_2$, 7
	16	$5^1/_2$, 6, 7
	$16^1/_2$	$5^1/_2$, 7
18°	10	4, $4^1/_2$
	11	4, 4, 5 —
	$11^1/_2$	$4^1/_2$, $4^1/_2$, 5 —
	13	$4^1/_2$, $5^1/_2$, 6 —
	14	5, 6 —, 6
	15	5, $5^1/_2$, $5^1/_2$
	$16^1/_2$	6 —, 6
	17	$5^1/_2$, $6^1/_2$
	19	$5^1/_2$, 6 —, 6
	23	5, 6, $6^1/_2$
	24	6 —, 6 +, $6^1/_2$
27°	$13^1/_2$	$8^1/_2$
	$14^1/_2$	$9^1/_2$
	15	9, $9^1/_2$
	$15^1/_2$	8
	16	9, $9^1/_2$
	$16^1/_2$	8, 8, $8^1/_2$, 9, 9, 10 —
	$17^1/_2$	$8^1/_2$, 9
	$18^1/_2$	8, $8^1/_2$, $8^1/_2$, 9
	$19^1/_2$	$8^1/_2$, 9, $9^1/_2$
	21	8, 9, $9^1/_2$
	$23^1/_2$	8, $8^1/_2$, 9, $9^1/_2$
$36^1/_2$°	$12^1/_2$	2
	13	2, 3 —
	$13^1/_2$	2 —, $2^1/_2$, 3

Temperature.	Initial length in mm.	Growth in 7 hours in mm.
	14	2, $2^1/_2$, 3
	$14^1/_2$	2, 2 +, 3 —
	15	$2^1/_2$, 3 —, 3 —, 3 —
	16	2, 3
	$16^1/_2$	2 —, 3 —, 3
	18	$2^1/_2$, 3
	19	2 +, $2^1/_2$, 3 —, 3
	22	$2^1/_2$. 3 —, 3

For these experiments use is made of only those objects which are not shorter, nor longer than 13—25 mm.

CHAPTER II.

Discussion of the Experiments.

In this chapter the experiments will be discussed; they are arranged in series according to the time they remained in the thermostat.

Whereas at the end of this publication the data of the experiments and the calculations are given separately, in this chapter they are put together in tables and in curves, constructed according to the tables. All the experiments, where the objects remained in the thermostat during the same time and at the same temperature have been put together.

When speaking in this chapter of tables we mean those which are to be discussed here, and not those, standing at the end of this paper.

Construction of the Tables and the Curves.

In the following tables the first column gives the temperature at which the experiments have been made; the second gives the lengthgrowth of the roots, expressed in the mean, the third the growth during one hour, equalled to the mean, divided by the number of hours, which expresses the duration of the experiment while supposing that during the succeeding hours the rate of growth is constant; of course this is not right, for, when the experiment lasts longer the influence of the periodicity of growth and the timefactor are greater; yet it gives a good idea of the importance of these influenccs as the discussion of the curves will explain; the fourth column gives the standarddeviation. The second column of table VI contains the growth observed after $3^1/_2$ hours, the third the growth during 7 hours, diminished with that of $3^1/_2$ hours; the fourth and fifth column give the growth during 7 hours and 14 hours, diminished by that during 7 hours; this table demonstrates the change in the rate of growth in succeeding periods of $3^1/_2$ hours.

Finally table VII relates to a series of experiments at high temperatures, the plants having been in the thermostat during $1^1/_2$ hours; after that they have been taken from these high temperatures at a constant temperature of 20.5° C.; this has been done in order to observe how many hours it took to reach an increase of 14 mm.

In the tables constructed according to these tables, the abscisses express the temperatures, the ordinates the rate of growth given in mm.

In the curve relating to table VII the abscisses express the temperature at which the plants remained during $1^1/_2$ hours in the thermostat and the ordinates the numbers of hours required before an increase of 14 mm. at 20.5° C. had been reached.

Calculation of the tables.

As for the calculation of the mean the usual method has been followed for which I can refer to Johannsen [1] 's book about heredity.

Discussion of the tables and the curves.

The following tables and curves are the results of experiments which have all been made in the room of constant temperature.

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[1]) W. Johannsen. Elemente der Exakten Erblichkeitslehre. Jena 1909. p. 33.

Series 1. Table III.

Temperature.	Growth during $3^1/_2$ hours = M.	Growth during one hour = $\frac{M}{3^1/_2}$.	σ
9° C.	0.9	0.21	0.49
14.8° C.	1.8	0.51	0.69
20.2° C.	3.5	1	0.42
27.2° C.	4.35	1.24	0.55
28° C.	5.1	1.46	0.49
29° C.	5.3	1.51	0.62
30° C.	5.4	1.54	0.54
32.5° C.	3.7	1.06	0.71
34° C.	2.3	0.66	0.35
36.6° C.	1.6	0.46	0.33
40° C.	0.5	0.14	0.23

Series 2. Table IV.

Temperature.	Growth during 7 hours = M.	Growth during one hour = $\frac{M}{7}$.	σ
4.1° C.	0.85	0.12	0.49
9.75° C.	1.85	0.26	0.47
13° C.	3.37[5]	0.48	0.55
14.2° C.	4.2	0.6	0.47
20.2° C.	6.5	0.93	0.48
22° C.	7.6	1.1	1.18
23.2° C.	8.5	1.21	0.81
25° C.	8.7	1.24	1.13
27° C.	9.5	1.34	1.22
28° C.	9.9	1.41	0.98
29° C.	10.1	1.44	0.96
30° C.	10	1.43	1.02
31° C.	8.5	1.21	0.63
33° C.	5	0.71	0.55
35° C.	2.9	0.42[5]	0.48
36.8° C.	1.65	0.24	0.35
38.7° C.	0.72	0.11	0·41
40° C.	0.5	0.07	0.24

Series 3. Table V.

Temperature.	Growth during 14 hours = M.	Growth during one hour = $\frac{M}{14}$.	σ
4° C.	1.5	0.11	0.38
6.8° C.	2.75	0.19	0.44
$9^3/_4$° C.	4.1	0.3	0.50
14.1° C.	8.34	0.58	0.53
20.2° C.	15.1	1.08	1.00
22.8° C.	18.9	1.35	0.95
25° C.	21.26	1.51	1.24
26° C.	21.8	1.55	1.24
27.2° C.	22	1.57	1.31
28.2° C.	20.2	1.44	1.14
29.3° C.	19.4	1.39	1.10
30° C.	17.95	1.28	1.25
31° C.	17.2	1.23	1.00
32.7° C.	12.4	0.88	1.08
33° C.	9.9	0.71	1.19
34.5° C.	5.2	0.40	0.47
35° C.	3.57	0.27	0.02
35.6° C.	3	0.21	0.49
37.5° C.	1.5	0.11	0.40
38.7° C.	0.5	0.03	

Some remarks must be made on the experiments at the low temperatures. It was impossible to make any observation at 0° C. within a short time; therefore the mean for the rate of growth at this low temperature is given only for an experiment during many hours; the plants remained there during $24—26^1/_2$ hours; the mean appeared to be 1 mm., from this mean those for $3^1/_2$, 7 and 14 hours have been deducted; we may suppose that the rate of growth has been constant during that long period: the means calculated are 0.13 mm., 0.27 mm. and 0.54 mm.

Before making the experiments at 4°—9° C. the plantlets have been during several hours in a surrounding of about the experimental temperature; here the mean has been calculated directly.

The means for the experiments up to 10° C. cannot strictly be compared with those for higher temperatures as they are more exact; moreover the plants have not been cultivated and measured at a temperature of 20° C.. if this had been the case as in the other experiments a greater value would probably have been found; however we may suppose that the difference would have been very small; therefore I believed to be right putting the means in the tables and in the curves.

All the other experiments have been made in the same way: cultivating and measuring taking place at 20° C. The number of objects in the experiments above $32^1/_2$° C. has been half the number of those at the other temperatures; in order to make the space of time passing between the measuring and the moment of closing the thermostat the shortest possible. If it had been possible to bring the plants immediately at the experimental temperature the growth might have been still less.

Many roots were curved when they had been exposed to a temperature of 40° C. during $3^1/_2$ hours and they could not be measured; those which were not curved were obviously turgescent because not flying back when touched lightly; after having returned to a temperature of 20° C. they grew in several days only very little; generally they could not be measured because of the many curvations.

When the objects had been exposed to a temperature of 40° C. it was difficult to say whether they were still alive; some were uncurved, maybe under the influence of the exceedingly moist atmosphere at that high temperature; nevertheless no increase could be observed after the return to a temperature of 20° C.; therefore I did not make experiments at 40° C. during 7 hours.

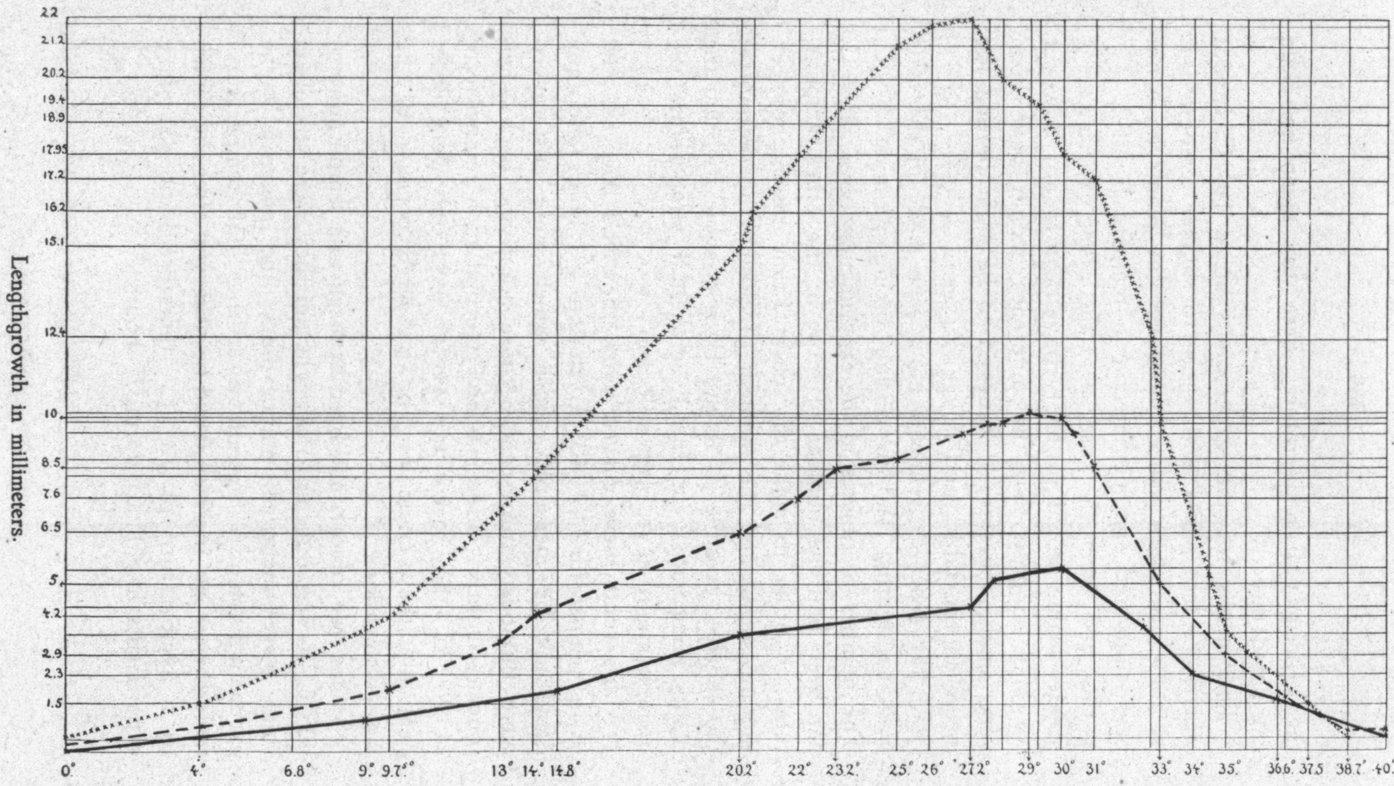
Lengthgrowth in millimeters.
2.2
21.2
20.2
19.4
18.9
17.95
17.2
16.2
15.1
12.4
10.
8.5.
7.6
6.5
5.
4.2
2.9
2.3
1.5
0°
4°
6.8°
9°
9.7°
13°
14°
14.8°
20.2°
22°
23.2°
25°
26°
27.2°
29°
30°
31°
33°
34°
35°
36.6°
37.5
38.7°
40°
Temperatures.

Fig. III.

The roots endured a temperature of 38° C. during 14 hours quite well, but at 39° C. most of them were curved; they did not fly back when touched; evidently they were dead.

Returning to the explication of the tables and curves, in Fig. III:

Curve A., the drawn line, gives the rate of growth during $3^1/_2$ hours.

Curve B., the broken line, gives the rate of growth during 7 hours.

Curve C., the crossed line, gives the rate of growth during 14 hours.

These curves, all drawn on the same scale, have in common that the first and the last part turn the convex side to the abscis, the middle part on the contrary to the concave side; this becomes more evident as the experiments last longer.

From this proceeds immediately that the temperature coefficients of the three curves are not the same. They are:

Temperature.	Coeff. for A.	Coeff. for B.	Coeff. for C.
$\frac{10°}{0°}$ C.			7.9
$\frac{15°}{5°}$ "	3.6	4.7	5.2
$\frac{20°}{10°}$ "	3.4	3.43	3.45
$\frac{25°}{15°}$ "	2.25	1.9	2.27
$\frac{26°}{16°}$ "	1.86	1.88	2.1
$\frac{27°}{17°}$ "	1.81	1.83	1.9
$\frac{28°}{18°}$ "	1.86	1.79	1.64

Temperature.	Coeff. for A.	Coeff. for B.	Coeff. for C.
$\frac{29^\circ}{19^\circ}$ C.	1.71	1.68	1.43
$\frac{30^\circ}{20^\circ}$ „	1.59	1.57	1.2
$\frac{35^\circ}{25^\circ}$ „	0.49	0.33	0.13
$\frac{37^\circ}{27^\circ}$ „	0.32	0.16	0.9
$\frac{40^\circ}{30^\circ}$ „	0.07	0.04	

The falling off of these coefficients from the low to the high temperatures is the greatest for curve C., being the smallest for C. at $\frac{37^\circ}{27^\circ}$, at $\frac{27^\circ}{17^\circ}$ for C. about as much as for A. and B. and at $\frac{15^\circ}{5^\circ}$ for C. much more than for A. and B.

The contrary applies to A., whereas the coefficient for B. lies in general between that of A. and C.

In general we can say that the coefficients up to $\frac{27^\circ}{17^\circ}$ are smaller for A. than for B., whereas those for B. are again smaller than those for C., but then the relation turns and the coefficient for A. > for B. > for C.

As to $\frac{10^\circ}{0^\circ}$ the coefficients for A., B. and C. must be compared, the values for A. and B. not being calculated directly. The cause of the changing relation between the three coefficients at $\frac{27^\circ}{17^\circ}$ is probably the influence of the great period of the growth, which will be the greatest at the optimal and infraoptimal temperatures which the roots endure without the rate of growth being harmed.

The influence of the great period becomes still more evident in Fig. IV, where the growth has been given, found in several series, divided by the number of hours expressing the duration of the experiments, according to the rate of growth calculated per hour.

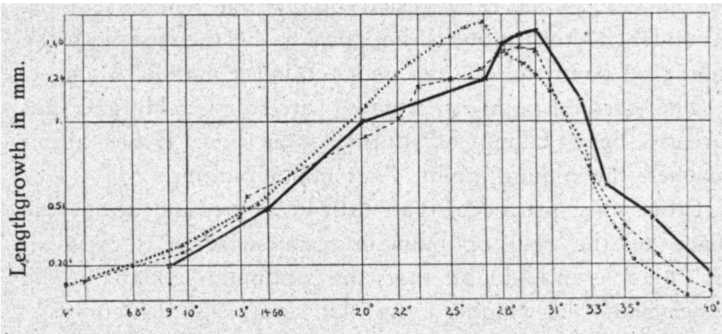

Fig. IV.

A, the drawn curve, gives the rate of growth in 1 hour for the experiments of $3^1/_2$ hours.

B, the broken curve, gives the rate of growth in 1 hour for the experiments of 7 hours.

C, the crossed curve, gives the rate of growth in 1 hour for the experiments of 14 hours.

These curves illustrate the influence of two dominating factors: the great period and the harm caused by the high temperatures.

Beforehand we may expect this to manifest itself most clearly in those experiments wich last the longest time and which have been made at those temperatures, lying next to the optimum, understanding this to be the highest value of the rate of growth. This is in accordance with the facts; C reaching the highest, A the middle, B the lowest optimum must be explained as follows: the harmful influence of the high temperature in the neighbourhood of the optimum reduces the rate of growth per hour as the duration of the experiment is greater; but it is partly neutralised by the influence of the great period, this factor fully surpassing the timefactor in observation during several hours. The further course also shows the important parts these two factors are playing; in the mounting parts of the curves, A and B lie rather equally, but generally taken, A under B; the opposite happens to be the case with the falling off parts: here C lies under, B in the middle, A above.

The turning-point is situated at 28° C. Here C has already been falling off during some time, B has about reached the highest point, A is still mounting.

From this proceeds that little can be said about the place of the real optimum in Sachs'sense; if it exists at all there is no doubt that the optimum, found in the experiments lies higher; the flat course of the curve at 26° C. proves that the two factors are competing for the first place; the relation between the increase during 14 and during 7 hours is:

for a temperature 27.2° C. $= \frac{22}{9.7} = 2.27.$

" " " 26° C. $= \frac{21.7}{9.2} = 2.36.$

" " " 25° C. $= \frac{21.2}{8.7} = 2.44.$

" " " 24° C. $= \frac{20.2}{8.6} = 2.35.$

The influence of 25° C. not being harmful it is certain that the optimum (in Sachs'sense) will be at least at that temperature; only we are not quite sure if the method for the experiments is accurate enough to set great store by such little differences of the values. Calculating likewise the relation between the increase during 7 and during $3^1/_2$ hours, we find:

for a temperature 30° C. = $\frac{10}{5.4}$ = 1.85.

„ „ „ 29° C. = $\frac{10.1}{5.3}$ = 1.9.

„ „ „ 28° C. = $\frac{10}{5.1}$ = 1.96.

„ „ „ 27° C. = $\frac{9.5}{4.35}$ = 2.18.

„ „ „ 26° C. = $\frac{9.1}{4.2}$ = 2.16.

„ „ „ 25° C. = $\frac{8.7}{4.05}$ = 2.14.

This makes it probable that the optimum lies here under 27° C.

Table VI gives the rate of growth during the first period of $3^1/_2$ hours and the first and the second period of 7 hours.

Table VI.

Temperature.	Growth in $3^1/_2$ hours.	Growth in 7 hours—$3^1/_2$ hours.	Growth in 7 hours.	Growth in 14 hours—7 hours.
10°	1	0.9	1.9	2.4
15°	1.8	2.7	4.5	4.85
20°	3.4	2.95	6.35	8.55
25°	4.05	4.65	8.7	12.6
26°	4.15	4.95	9.1	12.7
27°	4.3	5.2	9.5	12.5
28°	5.1	4.9	10	10.7
29°	5.3	4.8	10.1	9.5
30°	5.4	4.6	10	7.9
31°	4.8	3.17	8.5	8.7
32.5°	3.7	2.15	5.85	7.15
35°	2	0.9	2.9	0.85
37.5°	1.2	0.1	1.3	0.15

Fig. V shows clearly the influence of the timefactor and the great period; the values for the first and the second period differ but little, probably both factors having not yet much influence though the timefactor already comes into play; the rapid mounting of D must be attributed to the great period, which comes more to the front with increased duration of the experiment; it causes the great difference between the first and the second period of 7 hours.

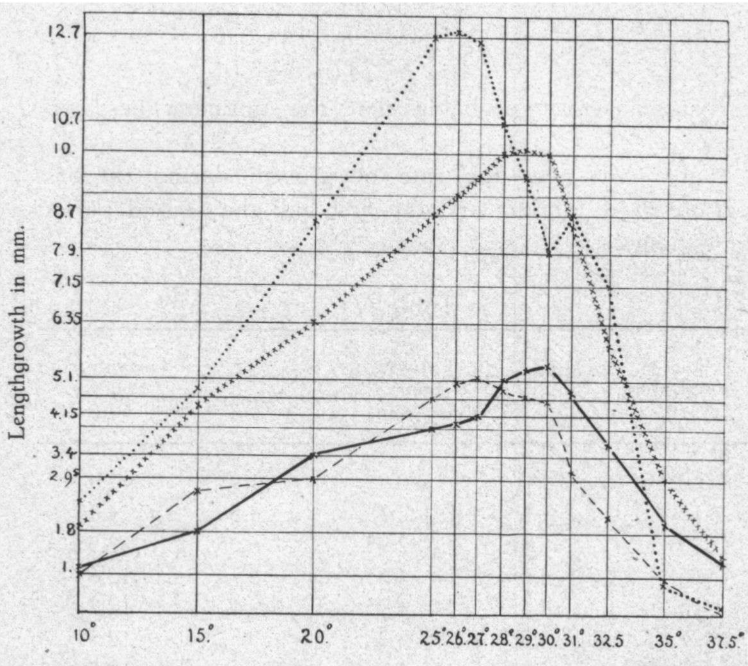

Fig V.

A, the drawn line, gives the rate of growth during $3^1/_2$ hours.

B, the broken line, gives the rate of growth during the second period of $3^1/_2$ hours.

C, the crossed line, gives the rate of growth during the first period of 7 hours.

D, the dotted line, gives the rate of growth during the second period of 7 hours.

The data of the experiments at 4°, 6.8° and $9^3/_4$° C. show that there is no reason to suppose a sudden cessation of growth.

The points of the curves representing the growth during 14 hours at 38.7° C. during 7 and $3^1/_2$ hours at 40° C., make it probable that something of this kind also applies to the maximum. After all this must be doubted, considering Fig. III, where the course of the three curves is equal between 37° and 38° C.; from this might be concluded that no growth takes place after $3^1/_2$ hours' exposure to that high temperature; it is remarkable that the plants should be alive.

The question cannot be solved in this paper, the great difficulty being that we cannot decide which part of the growth must be attributed to the coming at temperature and which part to the direct influence of the experimental temperature merely.

Probably microscopical observations would have demonstrated an increase at those high temperatures, even at 7 and 14 hours.

In the last series of experiments I tried to investigate the rate of growth of plants which have been exposed to a high temperature during $1^1/_2$ hours in the thermostat and which have been brought back after experiment to a constant temperature of 20.3° C.

With different intervals of time I measured the objects. At first I had the intention to investigate when the roots would have assumed the normal rate of growth, belonging to 20° C.; I have not been able though to avoid the influence of the great period; this might have been possible if many more experiments had been made and if I had

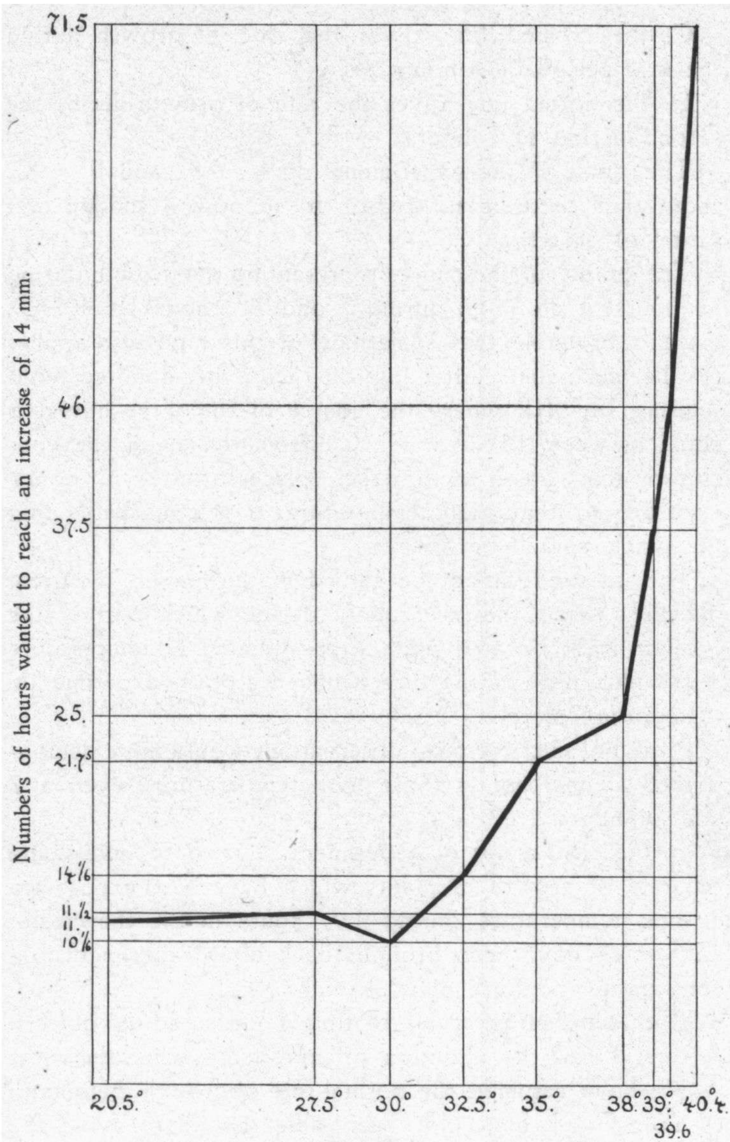

Fig. VI.

Temperatures, to which the plants have been exposed during $1^1/_2$ hours.

allowed the temperatures to have their influence during most varied experimental times, long ones and short ones. Therefore I restricted my experiments to ones series.

Table VII gives the numbers of hours the roots wanted to reach an increase of 14 mm.

It is evident that the time, necessary for this increase, is longer with the raise of the temperature to which the plants have been exposed during $1^1/_2$ hours.

If we may set value upon the little difference in hours existing between the experiments at 27.5° C. and 30° C., the temperature of 30° C. should have a favourable influence. Fig. VI relates to this series.

Table VII.

Temperature.	Numbers of hours wanted to reach an increase of 14 mm.
20.5°	11
27.5°	$11^1/_2$
30°	$10^1/_6$
32.5°	$14^1/_6$
35°	$21^3/_4$
38°	25
39°	37.5
39.6°	46
40.4°	71.5

CHAPTER III.

Discussion of the Results.

This chapter refers to the results in connection with literature. The tops of the roots of Lepidium Sativum grow in the same way as Ohlert[1]), Müller[2]) and Sachs[3]) have observed; the length of the growing zone being the same at low and at high temperatures.

Now the cardinal points will be discussed first.

The minimum.

Sachs finds that the minimum for the germination process of different species of plants lies beneath 4°—6° R.; his experimental objects are Cucurbita Pepo, Phaseolus and also small seeds as Brassica, Raphanus, which are of about the same size as Lepidium Sativum. He concludes from it that the germination-velocity increases with the rise of temperature, and believes the influence of the low temperatures to be indifferent notwithstanding the fact that the seeds do not show any further development at a temperature where germination takes place; development ceases and he supposes that this cessation of growth may be protracted ad infinitum. He supposes each phase of development to have its own minimum, the position of this point being higher for each succeeding phase; accordingly below the minimum for the germination process no development takes place at all.

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[1]) E. Ohlert. Linnaea: Bd. XI 1837.

[2]) N. I. C. Müller. Bot. zeit. 1869—1871.

[3]) J. Sachs. Arb. des Botan. Instituts in Würzburg, 1874. Ba. I· Heft 1. Heft 2. Heft 3.

This paper shows clearly that in every case growth exists at 0° C. Though Lepidium Sativum is not Sachs' experimental object it is not acceptable that it should make an exception to his rule. — Growth existing at 0° C. it would be worth while to examine if germination takes place at still lower temperatures; the practical difficulties for experiments of the kind however are very great, several publications having proved that germination at low temperatures is very slow; a low constant temperature would be required during several days, maybe weeks; moreover the seeds but germinating when moist, a liquid should be resorted to, having no chemical influence on the seeds; ice cannot be made use of, because mechanical resistance might occur at the stage of the seedcoat 's bursting (Kirchner [1]), the germinationenergy. at such low temperature being too small to conquer the resistance.

I had to leave experiments of this kind aside on account of the inadequate arrangements of the botanical laboratory. We may suppose that probably also below 0° C. germination would have been observed.

From several places in literature it appears to be a wellknown fact that growth happened to be in the earth at al low temperature, if not frozen, even in ice.

Uloth [2]) found in a dark ice- cellar seedlings of maple and wheat, lying on and between ice; the roots had penetrated into the ice; he concludes from this that the seeds had germinated at 0° C. Sachs [3]) does not admit this explaining the fact otherwise; after all the question is not solved. Kirchner observed Sinapis germinating at 0° C. and supposes other causes to be present than a low temperature which may prohibit the germination-process, for instance the resistance of the seedcoat being

[1]) O. Kirchner. Cohn's Breiträge III. 1883.

[2]) Uloth. Flora 54. 1871 p. 185.

[3]) Lehrbuch der Botanik. 1874 p. 697.

of so great a value that the turgor, providing the seeds with energy, required for the stretching-process, cannot conquer it; indeed the seedcoat having been removed, the roots of Phaseolus grew energetically; but this won't do every where, Pisum not showing any greater rate of growth at all under those circumstances.

In the very neighbouhood of zero he observed undoubtedly growth taking place.

Likewise wintercorn shows increase when covered with snow.

The resistance above mentioned may also have been the cause that Frank's [1]) roots, having been put horizontally at 0° C. did not show any geotropical curvation, but it is quite inexplicable that Hofmeister has not seen any curvation at 16° C.

As for the publications of Rutgers [2]) and Miss de Vries one would expect a cause of the kind having come into play with their objects, not exhibiting any curvation at 0° C., so much the more because perception has taken place and reaction appearing after the return to a higher temperature.

It must be doubted whether the exposure to a low temperature during a long time hurts the roots.

The plantlets of de Vries[4]) endure a temperature of 0° C. during a quarter of an hour, but no longer, whereas Sachs does not think a low temperature to have any harmful influence.

True[5]) finds that his objects after enduring a low tem-

[1]) Frank. Beiträge zur Pflanzenphysiologie. 1868. p. 37.

[2]) Rutgers l.c.

[3]) M. de Vries. Der Einflusz der Temperatur auf den Phototropismus. Recueil des Travaux Botaniques Néerlandais. Vol. XI. Livr. 3. 1914. p. 215.

[4]) H. de Vries. Diss. 1870. 's Gravenhage.

[5]) R. H. True. Annals of Botany. IX. 1896.

perature about the minimum, when returned to a higher temperature, diminish their rate of growth; only if they have been exposed to it a very short time they immediately assume, when brought back to a higher temperature the rate of growth according to this last temperature.

Askenasy [1]) is of the same opinion.

De Vries brings forward a publication of Mohl [2]) in Charpentier's name, who discovered alpine plants which have been under ice for at least four years; as the ice made only a slight evaporation possible those years they revived.

All these results show that it is an unsolved question whether an exposure to a low temperature during a long time is of any harmful influence on the rate of growth of roots.

In any case Sachs' opinion about the minimum for germination and growth lying under 4° R. is wrong.

There is no reason to accept, as far as we are able to judge from macroscopical observations, a minimum at which the growth stops suddenly; very probably the curve will fall off gradually with the temperature until a certain point where no experiment can be made any more.

Even microscopical observations will not be able to demonstrate that a minimum exists.

The maximum.

Sachs [3]) inserts in his paper many maxima, observed by serveral experimenters for most different plants, but all these data are vague and the experiments have been made inaccurately.

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1) Askenasy. Berichte der deutschen Botanischen Gesellschaft. 1890. VIII. p. 85.

2) H. Mohl. Botanische Zeit. 1843 p. 13.

3) Sachs: Flora 1864. p. 5.

Therefore he starts a new investigation with seedlings. Supposing that there does not exist one highest temperature which a plant is able to endure, but that it can support a certain high temperature during a short time, whose influence during a longer time will be mortal, he makes observations at various temperatures during various experimental times.

If Sachs had gone a little farther and if he had investigated the influence of optimale and supraoptimale temperatures at various spaces of time he might have come to the same conclusion as Blackman.

His results are that his objects can be exposed to 51° C. during 20—30 minutes without any harm; when being directly in contact with water a temperature of 51° C. during 10 minutes appeared to be of harmful influence, whereas they could endure 49°—50° C. more than 10 minutes; in all these cases his plants died when being directly in contact with water.

De Vries [1]) comes to about the same conclusions.

The roots can endure a temperature of 50°—52° C.; obviously the quantity of water is of great influence.

Both of them, Sachs and de Vries, make the observation that the plasma being dead already, the plant keeps its sound, fresh appearance, even the colour remains if only transpiration is prevented. Sachs' plants keep their turgor for several days, after having been exposed to a temperature of 50°—51 C. during 10 minutes. This makes it clear that the disappearing of the turgant state is no criterium for death, for which reason the experimenters have stated a plant to be dead when growth ceases. Pfeffer [2]) supposes that high temperature may call for-

[1]) H. de Vries: De invloed der Temperatuur op de Levensverschijnselen der Planten. Diss. 1870. 's Gravenhage.

[2]) Pfeffer: Pflanzenphysiologie II. Leipzig.

ward „Wärmestarre", which Sachs mentions to take place at high temperatures near the maximum.

Hilbrig's [1]) results about the ultramaximum, though affirming Sachs' theory of every function of life having its own maximum, is to be doubted.

As for the results with regard to the maximum in my own experiments: macroscopically measured growth seems to cease after an exposure during $3^1/_2$ hours to a temperature of 38° C., the curves relating to the experimental times $3^1/_2$, 7, 14 hours having about the same course. As said before in chapter II, it is not impossible that microscopical observations may lead to an other conclusion and may give results of the same kind as discussed when dealing with the question about the position of the minimum.

The optimum.

Sachs proves the optimum for the various physiological processes to be variable with different plants, being constant for each species. In accordance with this opinion De Vries [2]) states that the optimum for the growth of roots of Lepidium Sativum lies at 27.4° C.; the duration of his experiments is very long, 48 hours.

This view about the optimum being constant has been changed by Blackman's theory à propos of Miss Matthaei's data relating to assimilation; he holds that there would not be any optimum at all if the timefactor could be hindered from having its influence; if observation were possible after an experimental time zero.

The optimum appears to alter its position on the curve when the number of hours during which the experiment has been carried on becomes smaller; at last we would get a higher value than the so-called optimum on a curve

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[1]) Hans Hilbrig. Über den Einflusz supramaximaler Temperatur auf das Wachstum der Pflanzen. Diss. Freiburg 1900.

[2]) H. de Vries. l.c. 97.

being the continuation of the curve representing the relation between the rate of growth and the lower temperatures. In his paper be construes for the process of assimilation the hypothetic curve, but like every extrapolation this construction is rather arbitrary.

Since 1902 several publications have appeared on various kinds of physiological processes in order to control his theory. Whereas Kuyper[1]), Rutgers[2]) and Miss de Vries[3]) agree so far that in their opinion Blackman's theory may be right, though extrapolation is possible, Miss van Amstel on the contrary believes the theory to be untenable, as she considers the optimum to be primary and not secundary, but her method of extrpolation is arbitrary all the same; she has not succeeded in proving Blackman's theory to be wrong.

All these observations have one result in common: a falling off of the temperature-coefficient with the rising of the temperature. Cohen Stuart[4]) has demonstrated in his study on the subject and Kanitz[5]) likewise that this fact makes Blackman's theory the more probable, the falling off of the temperature-coefficient appearing to be of the same kind for chemical reactions. The same remark has also been made by Rutgers.

In the meantime it is clear enough that very little is known about physiological processes because the living organism must be regarded as an extremely complicated heterogen system.

1) J. Kuyper. De invloed der temperatuur op de ademhaling der hoogere planten., Diss. Utrecht. 1909.

2) A. A. L. Rutgers. l.c.

3) M. S. de Vries. l.c.

4) Cohen Stuart. Een studie over Temperatuurcoefficienten en den regel van Van 't Hoff. April 1912. Zittingsverslag Kon. Akad. van Wet. Amsterdam.

5) A. Kanitz Temperatur und Lebensvorgänge. Berlin. 1915.

As for the results which might proceed from my own investigations a priori one can say that about the optimum for the process of growth no more will be found than for other processes. Blackman states already in his publication of 1905 that internal factors, not to be controlled directly, will make indistinct the real course of the curve representing the rate of growth. He considers as limiting factors the quantity of plastic material with the exception of the time at the high temperatures; when the temperature becomes higher respiration will go so fast that within a short time there will be a lack of plastic material.

Harting[1]) already mentions something like it in his experiments with Humulus lupulus and believes that the cause of the falling off of his growth-curve (Sachs calls it periodicity of growth) is the long way the material has to go, its transport at last becoming to slow that a diminishing of the rate of growth takes place.

A question yet to be answered is whether the turgor, of course at a low temperature different from that at a high temperature, is of great influence, as Sachs supposes it to be.

All these factors may be expected to play an important part in the process of growth; but knowing their influences we shall be able to get a clear opinion about ist real being.

In every case these observations have proved that the optimum changes its position with the experimental time; the periodicity of growth however being cause that less is known about it here than in other physiological processes.

The same applies to the process of growth as to others: the falling off of the temperature-coefficient with the rise of the temperature.

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[1]) P. Harting. Tijdschrift voor natuurlijke geschiedenis en physiologie. Leiden. 1842. D. IX.

Investigations published when these experiments were already going on.

An abstract of a paper by Lehenbauer[1]) is published in the „Botanisches Centralblatt"; I tried in vain to get its original. It deals with the influence of the temperature on the growth of the roots of Zea Mays; the results he arrives at are that van 't Hoff's rule is applied from 20° C. up to 32° C., the temperature-coefficient varying from 2.40—1.88; his cardinal points are somewhat higher than those observed for Lepidium; nothing is mentioned about the minimum.

Meanwhile Miss Leitch[2]) published „Some Experiments on the Influence of Temperature on the Rate of Growth in Pisum Sativum."

She makes experiments with low temperatures of 22 hours' and half an hour's duration. Her curves have the same course for temperatures up to 10° C., but at the higher temperatures they diverge, the curve for 22 hours, calculated after the observed rate of growth for 1/2 hour, lying higher; there are irregularities in the curve demonstrating the rate of growth during the 1/2 hour's experiments; she believes that an other way of making her experiments, perhaps also the influence of the periodicity of growth, is the cause of the diverging. Nothing is said about practical difficulties and she reckons her plants to assume the temperature of the thermostat immediately, which must be doubted. Furthermore her experiments during very short periods, only for some minutes, are not convincing, exactly because her curve for experiments of 1/2 hour's duration shows many irregularities.

As for the position of the optimum, though she distinguishes an optimum and a maximum rate of growth

1) H. A. Lehenbauer. Physiol. Res. I. p. 247—288. f. 1—4. 1914. (Bot. C. 1915. No. 51).

2) J. Leitch. Annals of Botany. Vol. XXX. Jan. 1916. p. 25.

she comes to the same conclusion as all the other experimentors there being one point where the rate of the process is constant, where the timefactor is not yet in play, whereas at a higher temperature the velocity changes. She finds, like Kuyper for the process of respiration that the reactionvelocity is ranging between 30° and 35° C. Her temperature coefficients are falling off in the same way as it happens to be with other physiological processes, but she thinks van 't Hoff's rule not applying at all because the temperature-coefficients are two to three only between 10° and 29° C.

As mentioned above the studies of Cohen Stuart and Kanitz prove that this fact merely does not tell against it.

But surely we do not yet know enough about physiological processes to decide the question whether it does apply or not.

Finally I met with a paper by Groves[1]); here the temperature-coefficient is not changing, this being in contrast with all the other physiological observations. Probably we are not allowed to compare his experiments with those mentioned above because he deals with temperatures above 50° C. only, whereas in the other papers a temperature above 50° C. has never been made use of.

Therefore nothing can be concluded from it in relation to van 't Hoff's rule.

Summary of Results.

The growing zone of the root of Lepidium Sativum is 3—4 mm., its length not being variable with the temperatures.

As with all other physiological processes the optimum

[1]) J. F. Groves. The Botanical Gazette. March 1917. Vol. LXIII no. 3. p. 169.

changes its position with the observation-time. About its exact position little can be decided, because of the influence of the periodicity of growth being the greatest in its neighbourhood. Yet the experiments of $3^1/_2$, 7 and 14 hours' duration prove the optimum to be falling off at higher temperatures with increased duration of the experiment.

In this regard Blackman's theory is applicable.

The temperature-coefficient φ_{10} falls off from low to high temperature, mostly in the experiments of 14 hours' duration, which must be attributed for a considerable part to the influence of the great period of growth.

Nothing more can be said about the application of van 't Hoff's rule.

The minimum appears to lie under 0° C.; it is very improbable that in Sachs' conception growth ceases suddenly.

The maximum lies at 40° C,; for experiments of longer duration still lower.

Whether „Wärmestarre" occurs cannot be decided positively.

The observed rate of growth being about the same at 37°—38° C. tells for it; one might conclude no growth to take place anymore at that high temperature after $3^1/_2$ hours.

The course of the curve makes it probable that for the maximum the same can be said as for the minimum if it were only possible to apply a very accurate method of observation.

These experiments were made in the Botanical Laboratory at Utrecht. I wish to express my best thanks to Professor Went for his kind interest taken in the experiments I made and the liberal way in which be enabled me to carry them out.

Experiments made at 0° C.

TEMPERATURE.	DATE.	CLASSES IN M.M.	< 1	1
0° C.	1916. 18—19 Febr.	number of plants	6	8
	19—20 „		11	9
			17	17

$$A = M = 1.$$

			< 1	1
	23—24 „		8	9

$$A = 0.5\ b. = + \frac{9}{17} = 0.5.$$

$$M = 1.$$

TABLE A.

This Table relates to Table III in the text.

TEMPERATURE.	DATE.	< 1	1	σ
9° C.				0.4942
	18 Jan. 1917	10	8	
	19 Jan. 1917	13	9	
		23	17 = 40	

$$A = 0.5\,b = + \frac{17}{40} = 0.425$$

$$M = 0.9$$

TEMPERATURE.	DATE.	< 1	1 < 2	2 < 3	σ
14.8° C					0.6923
	16 Dec. 1916	4	7	11	
	17 Dec. 1916	1	9	6	
		5	16	17 = 38	

$$A = 1.5\,b = + \frac{12}{38} = 0.3$$

$$M = 1.8$$

TEMPERATURE.	DATE.				σ
20.2° C.		< 3 | 3	< 4 | 4		0.4252
	16 June 1916	1	13	5	
	17 June 1916	1	22	2	
	13 Sept. 1916	2	14		
		4	49	7 = 60	

$$A = 3.5 \quad b = + \frac{3}{60} = 0.5$$

$$M = 3.5$$

27° C.		< 4 | 4	< 5 | 5		0.5571
	10 June 1916	5	5	3	
	3 Febr. 1917	3	17		
		8	22	3 = 33	

$$A = 4.5 \quad b = -\frac{5}{33} = -0.15$$

$$M. = 4.35$$

28° C.		4 < 5 |	5 < 6	0.4989
	18 Oct. 1916	10	10	
	1 Febr. 1917	5	7	
		15	17 = 32	

$$A = 5.5 \quad b = -\frac{15}{32} = -0.4$$

$$M = 5.1$$

290° C.		< 5 | 5	< 6 | 6		0.6227
	1 July 1916	3	9	1	
	10 Juli 1916	8	10	3	
		11	19	4	

$$A = 5.5 \quad b = -\frac{8}{34} = -0.2$$

$$M = 5.3$$

Temperature.	Date.				σ
30° C.		4 < 5	5 < 6	6 < 7	0.5449
	28 June 1916	6	10	5	
	1 Febr. 1917	8	14	4	
		14	24	8 = 47	

$$A = 5.5 \quad b = -\frac{5}{47} = -0.1$$

$$M = 5.4$$

Temperature.	Date.				σ
32.5° C.		2 < 3	3 < 4	4 < 5	0.7130
	28 June 1916	2	6	4	
	13 Jan. 1917	1	6	7	
	13 Jan. 1917	3	4	4	
		6	16	15 = 37	

$$A = 3.5 \quad b = +\frac{9}{37} = 0.24$$

$$M = 3.7$$

Temperature.	Date.			σ
34° C.		< 2	2 < 3 | 3	0.3571
	10 Jan. 1917	2	8	
	11 Jan. 1917	1	9	
		3	17 = 20	

$$A = 2.5 \quad b = -\frac{3}{20} = -0.15$$

$$M = 2.3$$

Temperature.	Date.			σ
36.6° C.		1 < 2	2	0.3353
	10 Jan. 1917	7	1	
	11 Jan. 1917	9	2	
	13 June 1916	11	1	
		27	4 = 31	

$$A = 1.5 \quad b = +\frac{4}{31} = 0.1$$

$$M = 1.6$$

TEMPERATURE.	DATE.		σ
40° C.		$< {}^1/_2 \mid {}^1/_2 < 1 \mid$	0.2389
	23 Nov. 1916	4 3	
	1 Febr. 1917	5 2	
		9 5 = 14	

$$A = 0.25 \quad b = \frac{5}{14} \times \frac{1}{2} = 0.15$$

$$M = 0.4$$

TABLE B.

This Table relates to Table IV in the text.

TEMPERATURE.	DATE.		σ
4.1° C.		$< 1 \mid 1$	0.4945
	17 Jan. 1917	9 5	
	18 Jan. 1917	12 6	
		22 11 = 32	

$$A = 0.5 \quad b = + \frac{11}{32} = 0.35$$

$$M = 0.85$$

9.75° C.		$1 < \mid 2 -$	0.4786
	15 Jan. 1917	14 6	
	16 Jan. 1917	12 8	
		26 14 = 40	

$$A = 1.5 \quad b = + \frac{14}{40} = 0.35$$

$$M = 1.85$$

13° C.		$2 < 3 \mid 3 < 4 \mid 4$	0.5553
	22 Jan. 1917	4 10 2 = 16	

$$A = 3.5 \quad b = - 0.125$$

$$M = 3.375$$

Temperature.	Date.	3 < 4	4 < 5	σ
14.2° C.	26 Jan. 1917	5	9	0.4715
	27 Jan. 1917	4	9	
		9	18 = 27	

$A = 4.5 \quad b = -0.3$

M = 4.2

Temperature.	Date.	< 5	5 < 6	6 < 7	7	σ
20.2° C.	5 Dec. 1916		4	11	6	0.4865
	10 Dec. 1917		5	13	6	
	9 Jan. 1917	1	2	9	4	
		1	11	33	16 = 61	

$A = 6.5 \quad b = +\frac{3}{61} = 0.04$

M = 6.5

Temperature.	Date.	5 < 6	6 < 7	7 < 8	8 < 9	9	σ
22° C.	16 Dec. 1916	1	5	5	3	3 = 17	1.1823

$A = 7.5 \quad b = +\frac{2}{17} = 0.1$

M = 7.6

Temperature.	Date.	6 < 7	7 < 8	8 < 9	9 < 10	σ
23.2° C.	27 Oct. 1916		5	11	5	0.8112
	2 Dec. 1916	2	4	10	7	
		2	9	21	12 = 44	

$A = 8.5 \quad b = -\frac{1}{44}$

M = 8.5

Temperature.	Date.	< 7	7 < 8	8 < 9	9 < 10	10	σ
25° C.	26 Oct. 1916	2	5	9	7	1	1.13
	2 Dec. 1917	1	2	6	9	1	
		3	7	18	16	2 = 46	

$A = 8.5 \quad b = +\frac{7}{46} = 0.16$

M = 8.7

TEMPERATURE.	DATE.	7<8	8<9	9<10	10<11	11<12	σ
27° C.							**1.228**
	18 Oct. 1916	1	8	8	4	4	
	23 Oct. 1916	2	3	3	7	2	
	24 Oct. 1916	4	4	3	6	1	
		8	15	14	17	7 = 61	

A = 9.5

M = 9.5

TEMPERATURE.	DATE.	<9	9 < 10	10 < 11	11 < 12	σ
28° C.						**0.9805**
	1 Sept. 1916	2	8	6	3	
	20 Oct. 1916	4	7	7	3	
	21 Oct. 1916	3	10	9	1	
		9	25	22	7 = 63	

$A = 9.5 \quad b = + \frac{27}{63} = 0.43$

M = 9.9

TEMPERATURE.	DATE.	< 9	9 < 10	10 < 11	11 < 12	σ
29° C.						**0.9616**
	10 Juli 1916	4	2	8	3	
	3 Sept. 1916	5	10	6	4	
	7 Febr. 1917	1	6	12	5	
		10	18	26	12	

$A = 10.5 \quad b = - \frac{26}{66} - 0.4$

M = 10.1

TEMPERATURE.	DATE.	7<8	8<9	9<10	10<11	11<11	σ
30° C.							**1.0204**
	26 Juni 1916	1	3	6	7	4	
	29 Juni 1916		3	7	5	3	
	7 Sept. 1916		4	4	10	3	
	9 Sept. 1916	1	2	5	3	6	
	3 Febr. 1917		4	6	8		
		2	16	28	34	16 = 26	

$A = 10.5 \quad b = - 0.5$

M = 10

TEMPERATURE.	DATE.				σ
31° C.		7 < 8	8 < 9	9 < 10	0.6305
	6 Sept. 1916	2	13	6	
	11 Nov. 1916	5	11	3	
		7	24	9 = 40	

$$A = 8.5 \quad b = + \frac{1}{20} = 0.05$$

$$M = 8.5$$

33° C.		3 < 4	4 < 5	5 < 6	0.551
	31 Oct. 1916	1	5	6	
	1 Nov. 1916		7	8	
	8 Nov. 1916		5	5	
		1	17	19	

$$A = 4.5 \quad b = + \frac{18}{37} = 0.5$$

$$M = 5$$

35° C.		2 < 3	3 < 4		0.4841
	17 Nov. 1916	5	4	
	4 Dec. 1916	6	5	
	15 Dec. 1916	8	3	
		19	12 = 31	

$$A = 2.5 \quad b = \frac{12}{31} = 0.4$$

$$M = 2.9$$

36.8° C.		1 < 2	2 < 3		0.3502
	14 Dec. 1916	5	2	
	4 Febr. 1917	9	1	
	9 Febr. 1917	10	1	
	5 Febr. 1917	6	1	
		30	5 = 35	

$$A = 1.5 \quad b = + \frac{1}{7} = 0.15$$

$$M = 1.65$$

TEMPERATURE.	DATE.				σ
38.7° C.		< 1	1		0.4103
	19 Nov. 1916	9	1		
	20 Nov. 1916	7	2		
	11 Febr. 1917	6	3		
		22	6 = 28		

$A = 0.5 \quad b = +\frac{6}{28} = 0.22$

$M = 0.72$

TEMPERATURE.	DATE.			σ
40° C.		< ½	½ < 1	0.2466
	23 Nov. 1916	4	3	
	24 Nov. 1916	4	5	
	25 Nov. 1916	6	2	
		14	10 = 24	

$A = 0.25 \quad b = +\frac{10}{24} \times \frac{1}{2} = 0.21$

$M = 0.46$

TABLE C.

This Table relates to Table V in the text.

TEMPERATURE.	DATE.				σ
4° C.		< 1	1 < 2	2	0.3862
	18-19 Jan. 1917	1	15	1	
	19-20 Jan. 1917	2	13	1	
		3	28	2 = 33	

$A = 1.5 \quad b = -\frac{1}{33}$

$M = 1.5$

TEMPERATURE.	DATE.			σ
6.8° C.		2 < 3	3 < 4	0.449
	16-17 Jan. 1917	9	5	
	20-21 Jan. 1917	14	4	
		23	9 = 32	

$A = 2.5 \quad b = +\frac{9}{32} = 0.25$

$M = 2.75$

TEMPERATURE. DATE. σ

$9^3/_4$° C. | | 3 < 4 | 4 < 5 | | | | | 0.504
---|---|---|---|---|---|---|---
| 15-16 Jan. 1917 | 9 | 13 | | | | |
| 23-23 Jan. 1917 | 7 | 10 | | | | |
| | 16 | 23 = 39 | | | | |

$$A = 4.5 \quad b = -\frac{16}{39} = 0.41$$

$$M = 4.1$$

14.1° C.		7 < 6	6 < 9	9		0.5398
	17-18 Jan. 1917	6	16	2	
	21-22 Jan. 1917	4	12	1	
		10	28	3 = 41	

$$A = 8.5 \quad b = -\frac{7}{14} = -0.16$$

$$M = 8.34$$

20.2° C.		13<14	14<15	15<16	16<17	17	1.001
	11-12 Dec. 1917	3	3	10	1	1	
	29-30 Jan. 1917	4	3	9	2	1	
	31 J.-1 Febr. 1917	3	8	7	3		
		10	14	26	6	2 = 58	

$$A = 15.5 \quad b = -\frac{24}{58} = -0.41$$

$$M = 15.1$$

22.8° C.		16<17	17<18	18<19	19<20	20<21	0.9582
	19-20 Dec. 1917	1	2	7	5	5	
	12-13 Jan. 1917		2	10	6	1	
		1	4	17	11	6 = 39	

$$A = 18.5 \quad b = +\frac{17}{39} = 0.43$$

$$M = 18.9$$

TEMPERATURE.	DATE.	19<20	20<21	21<22	22<23	23<24	24	σ
25° C.		19<20	20<21	21<22	22<23	23<24		1.244
	10-11 Dec. 1916	4	5	2	6	2		
	1 F.-2 Febr. 1917	3	6	5	4	1		
		7	11	7	10	3 = 38		

$$A = 21.5 \quad b = -\frac{9}{38} = -0.24$$

M = 21.26

26° C.		19<20	20<21	21<22	22<23	23<24	1.245
	26-27 Jan. 1917	2	3	6	5	3	
	28-29 Jan. 1917	3	1	7	6	5	
		5	4	13	10	8 = 40	

$$A = 21.5 \quad b = +\frac{12}{40} = 0.30$$

M = 21.8

27.2° C.		19<20	20<21	21<22	22<23	23<24	24	1.3134
	27-28 Nov. 1916	1	3	8	6	1	2	
	29-30 Nov. 1916	3	0	6	5	5	1	
		4	3	14	11	6	3 = 41	

$$A = 21.5 \quad b = +\frac{21}{41} = 0.5$$

M = 22

28.2° C.		17 < 18	18 < 19	19 < 20	20 < 21	21	1.149
	2-3 Febr. 1917	1	0	6	2	7	
	3-4 Febr. 1917	1	1	9	2	4	
		2	1	15	4	4 = 33	

$$A = 19.5 \quad b = +\frac{21}{33} = +0.7$$

M = 20.2

Temperature.	Date.	16<17	17<18	18<19	19<20	20<21		σ
29.3° C.								**1.102**
	24-25 Jan. 1917	1	2	4	5	4		
	25-26 Jan. 1917	1	0	1	8	7		
		2	2	5	13	11	= 33	

$$A = 19.5 \quad b = -\frac{4}{33} = +0.1$$

M = 19.4

Temperature.	Date.	14<15	15<16	16<17	17<18	18<19	19		σ
30° C.									**1.255**[1]
	4-5 Dec. 1916	1	0	2	5	1	4		
	14-15 Dec. 1916		1	1	7	2	5		
		1	1	3	12	3	9	= 29	

$$A = 17.5 \quad b = +\frac{13}{29} = 0.45$$

M = 17.95

Temperature.	Date.	14<15	15<16	16<17	17<18	18<19		σ
31° C.								**1.003**
	30-31 Jan. 1917		1	5	6	4		
	11-12 Jan. 1917		3	1	4	3		
			4	5	10	7	= 27	

$$A = 17.5 \quad b = -\frac{7}{27} = -0.26$$

M = 17.2

Temperature.	Date.	10<11	11<12	12<13	13<14	14		σ
32.7° C.								**1.083**
	10-11 Jan. 1915	2	0	7	1	1	= 11	

$$A = 12.5 \quad b = -\frac{1}{11} = -0.1$$

M = 12.4

Temperature.	Date.	<9	9<10	10<11	11<12		σ
33° C.							**1.194**
	17-18 Dec. 1916	3	2	4	1		
	18-19 Dec. 1916	3	1	6	1		
		6	3	10	2	= 21	

$$A = 10.5 \quad b = -\frac{13}{21} = -0.6$$

M = 9.9

TEMPERATURE.	DATE.				σ
34.5° C.		4 < 5	5 < 6		0.4714
	4-5 Febr. 1917	4	6		
	5-6 Febr. 1917	3	8		
		7	14 = 21		

$$A = 5.5 \quad b = -\frac{1}{3} = -0.3$$

M = 5.2

35° C.		3 < 4	4 < 5		0.024
	15-16 Dec. 1916	6	1		
	9-10 Jan. 1917	9			
		15	1 = 16		

$$A = 3.5 \quad b = +\frac{1}{16} = 0.06$$

M = 3.56

35.6° C.		2 < 3	3 < 4		0.4991
	6-7 Febr. 1917	3	4		
	7-8 Febr. 1917	5	5		
		8	9 = 17		

$$A = 3.5 \quad b = -\frac{8}{17} = -0.5$$

M = 3

37.5° C.		< 1	1 < 2	2	0.407
	14-15 Jan. 1917	1	8	1	
	8-9 Febr. 1917		7	1	
		1	15	2 = 18	

$$A = 1.5 \quad b = +\frac{1}{18}$$

M = 1.5

38.7° C.		< 1			
	20-21 Dec. 1916	7			
	9-10 Febr. 1917	8			
		15			

M = 0.5