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Botany. — *"The influence of temperature on the presentation-time in geotropism."* By Dr. A. A. L. RUTGERS. (Communicated by Prof. F. A. F. C. WENT).

(Communicated in the meeting of Sept. 24, 1910).

§ 1. *Introductory.*

In 1905 and 1908 there appeared two papers[1]) by BLACKMAN in which he dealt with the influence of temperature on physiological processes in general, while in addition in the first of these papers he tested on a special case his new views on this subject and showed that the results arrived at by Miss MATTHAEI on assimilation as a function of temperature[2]) confirmed his theory.

One of the chief points in BLACKMAN's argument is the proposition that VAN 'T HOFF's law of reaction velocity as a function of temperature must also hold good in the field of physiology. According to this law the reaction, for certain chemical transformations increases two- to three-fold for every 10° C. rise of temperature. The connection between temperature and a physiological process is in general represented by a curve with an inversion-point, the so-called optimum curve. BLACKMAN maintains that the inversion-point owes its origin to secondary influences, that in consequence this optimum does not express a primary relation which universally holds good between temperature and a physiological process.

With the aid of the figures available for this purpose, BLACKMAN shows further that in general the law of VAN 'T HOFF applies in the field of botany for temperatures roughly between 10° C. and 27° C. Above 27° C. a quick falling off takes place, so that at higher temperatures the values obtained do not nearly reach those which might be expected, if calculated by VAN 'T HOFF's law.

BLACKMAN in his explanation of this phenomenon lays stress on a new point of view, calling attention to the time-factor which here comes into play. With higher temperatures too low a value is found in consequence of the harmful influence of such temperatures. The longer the plant remains exposed to these harmful temperatures, the greater is the damage. So also conversely the shorter the time they remain at this temperature, the less is the

1) F. F. BLACKMAN, Optima and Limiting Factors, Annals of Botany, Vol. XIX, 1905.
F. F. BLACKMAN, Opening Address of the Botanical section of the British Association, Nature, Vol 78. 1908.

2) G. L. C. MATTHAEI, Experimental Researches on Vegetable Assimilation. Phil. Trans. Series B, Vol. 197, 1905.

harm done. BLACKMAN holds that according to VAN 'T HOFF's law the theoretical value would be found, if only an observation could be made after an exposure of 0 minutes to the higher temperature. This value after time 0 cannot however be experimentally determined and so BLACKMAN has recourse to extrapolation from the curve which can be drawn through the points representing the values obtained after an exposure to the higher temperature of shorter and shorter duration. In this way by extrapolating the time curves obtained by Miss MATTHAEI for assimilation at high temperatures, BLACKMAN indeed finds values which fairly well agree with those calculated according to VAN 'T HOFF's law.

From these considerations it also follows that the optimum must vary with the time of observation. If the subject of the experiment is warmed for a short time only before the observation, the optimum will be found at a higher temperature than after longer warming.

Although the author is evidently convinced that his theories will have to apply over the whole field of plant physiology, there are nevertheless processes to which he has not yet been able to extend his conclusions, at least at the end of his second paper he says: "Finally superposed upon all this comes the first category of phenomena that we are content still to regard as stimulatory." "From our present point of view vision does not extend to the misty conceptions of stimulation upon our horizon".

In the investigation of which a preliminary account is here given, an attempt is also made to apply the ideas developed by BLACKMAN to the field of pure physiology of stimulus and to test their general validity experimentally.

§ 2. *Methods.*

In order to determine the influence of temperature in connection with the time-factor, the experimental objects (coleoptiles of *Avena sativa*) were kept before and during the experiments for a definite time at that temperature of which the influence had to be determined. After having been warmed for a certain time the oat-seedlings were stimulated for some minutes by means of gravity at an angle of 90° and were afterwards placed vertically at a temperature at 20° C. In this way the presentation-time for temperatures between 0° C. and 40° C. was determined after various periods of warming. The warming took place in a thermostat specially constructed for this purpose which was electrically warmed and kept at a constant temperature by means of an electrical regulator, so that there was no need to use gas for the experiments as it considerably impairs the power of geotropic curvature.

All the experiments took place in the excellently fitted dark room of the Botanical Laboratory at Utrecht under the direction of Prof. WENT. The most important source of error was in the difficulty of keeping the air in the laboratory quite pure and in the individual variations of the objects of experiment. Great care was bestowed on the elimination of these sources of error, in the first place by keeping the atmosphere as pure as possible and further by using for every experiment as great a number of plants as possible.

Determinations were made at temperature-intervals of 5° C. and at each temperature after warming for 1, 2, 4, 6, 12, and 24 hours, unless it was evident from the experiments that the time-factor was absent, when two determinations sufficed.

§ 3. *Results.*

The results of this investigation are summarised in the following table. The horizontal rows give the values of the presentation-times

SUMMARY OF PRESENTATION-TIMES.

Temperature.	Warming for 1 hour	Warming for 2 hours	Warming for 4 hours	Warming for 6 hours	Warming for 12 hours	Warming for 24 hours
0°	72′	—	72′	—	—	—
5°	16′	—	16	—	—	—
10°	10′40″	—	10′40″	—	—	—
15°	6′	—	6′	—	—	—
20°	4′20″	—	—	1) 4′10″	—	—
25°	2′20″	2′20″	2′20″	2′20″	—	—
30°	3′30″	3′10″	2′10″	1′50″	1′40″	1′40″
35°	2′30′	3′30″	4′	4′	2) 5′	5′
37°	9′20″	16′	—	21′40″	—	21′40″
38°	11′30″	19′10″	38′	53′	75′	347′
39°	23′	40′	—	—	—	—
40°	260′	—	—	—	—	—

1) After warming for 8 hours. 2) After warming for 18 hours.

corresponding to the temperature at the beginning of the row. The length of warming is given at the top of the vertical columns.

According to this table the presentation-time shows a clear dependence on temperature, while at higher temperatures, the length of warming is evidently of great importance.

If we now ask how far VAN 'T HOFF's law holds good, we cannot simply take the ratio of the presentation-time for the determination of the temperature-coefficient. The presentation-time is not itself a chemical process, but can serve as the measure for the perception process. If the rate of this process is greater, then the presentation time will be less, and conversely.

For the determination of the temperature-coefficient, we shall therefore be obliged to take the reciprocal values of the presentation-time, or, which comes to the same thing, instead of $\frac{K_{20}}{K_{10}}$, the reciprocal $\frac{K_{10}}{K_{20}}$.

We then find:

$$\frac{K_0}{K_{10}} = \frac{72'}{10'40''} = 6.8 , \frac{K_5}{K_{15}} = \frac{16'}{6'} = 2.6, \frac{K_{10}}{K_{20}} = \frac{10'40''}{4'20''} = 2.5 ,$$

$$\frac{K_{15}}{K_{25}} = \frac{6'}{2'20''} = 2.6 , \frac{K_{20}}{K_{30}} = \frac{4'20''}{1'40''} = 2.6 , \frac{K_{25}}{K_{35}} = \frac{2'20''}{2'30''} = 0.93 ,$$

$$\frac{K_{30}}{K_{40}} = \frac{1'40''}{260'} = 0.0064 .$$

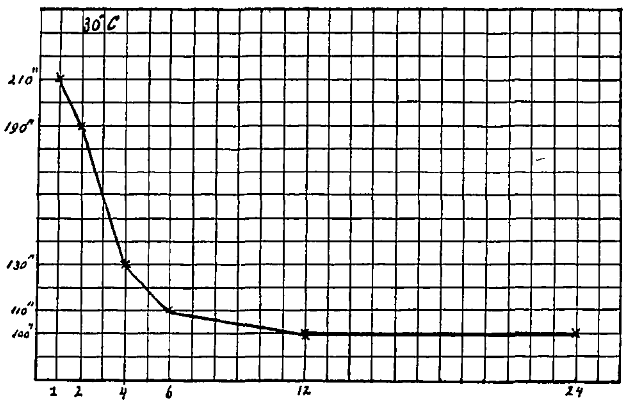
As is evident from these coefficients VAN 'T HOFF's law for the presentation-time holds good in geotropism from 5° C. to 30° C. At 0° C. we notice a sudden increase of the presentation-time, through which the temperature coefficient between 0° C. and 10° C. reaches the unusually high value 6.8. Possibly this is connected with the cessation of growth at 0° C.

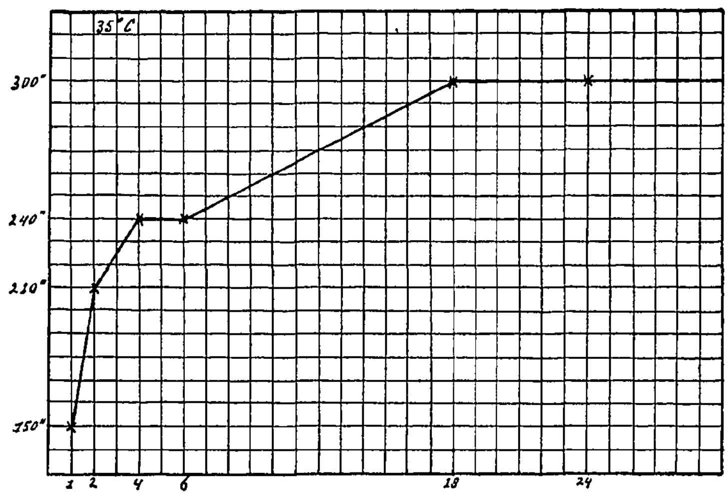
The above table also gives a very good idea of the significance of the length of the previous warming. From 0° C. to 25° C. no influence of the length of warming can be traced, at 30° C. and higher the time-factor, in BLACKMAN's sense, plays an important part.

The accompanying figures represent graphically the change in the presentation-time at 30° C. and 35° C., as a function of the time f warming. The most remarkable thing about these more or less ogarithmic curves, is the fact that the presentation-time at 30° C. ecreases and at 35° C. increases. This therefore means that at

30° C. the presentation-time decreases under the influence of the longer warming, at 35° C., however, it increases.

The temperature of 35° C. has, therefore, a distinctly injurious influence, while the favourable influence of the temperature of 30° C. appears to be a function of time.





Nevertheless there also seems to be a harmful influence acting at 30° C. This is evident when we compare the values obtained after warming for 1 hour at 30° C. with the corresponding values at 25° C. The latter is 2′20″, the former 3′30″, which means that in the first hour at a temperature of 25° C., the presentation-time fell from 4′20″ at 20° C. to 2′20″ at 25° C., and that in the first hour at a temperature of 30° C. there was only a decline from

4′20″ at 20° C. to 3′30″ at 30° C. Thus there is here clearly a harmful influence at work which was only gradually overcome by the favourable influence of this temperature.

We might represent this influence in the following way, that for the greater rate of transformation at 30° C., a greater quantity of an enzyme is required. The first effect of this temperature is the destruction of a quantity of enzyme and only gradually a sufficient quantity of the enzyme is formed, in order to accelerate the process and so to obtain a smaller presentation-time. Whether we are indeed concerned with the action of an enzyme, cannot, however, be made out.

One may readily assume that not only at 30° C., but also at higher temperatures, the favourable influence of these temperatures which expresses itself by a shortening of the presentation-time, acts only gradually. Only at 35° C. and higher temperatures this phenomenon can no longer show itself in consequence of the much stronger opposite influence of these temperatures. In one way alone can the fact still be traced that the shortening of the presentation-time at increased temperatures does not immediately occur, namely, that after one or more hours previous warming, those values which we should expect according to BLACKMAN's theory, are not found. This is indeed the case. Extrapolation from the time-curves does not here give the values for time 0, which, according to VAN 'T HOFF's law, we could calculate for it from the values found at lower temperatures. Nor can this be, if the favourable influence of the higher temperature is a function of time, for then this theoretical value after a time 0 does not exist, but the starting-point of the time-curve for a time 0 lies at a higher value of the presentation-time.

The same circumstance explains also the fact that the optimum here is only in very slight degree variable with the time of observation. After 1 hour's previous warming, we find a not very distinct optimum at 22° C., after 12 hours' previous warming it is shifted to 30° C.

The whole course of the presentation-time as a function of temperature and of time of previous warming, is represented in Plate I. The thick continuous line is the presentation-time at varying temperatures after 1 hours' previous warming.

From 30° C. upwards this line is continued by an interrupted line which connects the points calculated by VAN 'T HOFF's law, starting from the values found at lower temperatures. The above plate also gives the time-curves which, for temperatures of 30° C.

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upwards, show the connection between the presentation-time and the period of previous warming. For this purpose the abscissae axis has been taken as time axis and for each temperature the ordinate of that temperature as starting-point. The dotted lines with which these time-curves begin connect the values, found after 1 hour's previous warming, with the values calculated according to VAN 'T HOFF's law.

§ 4. *Comparison with the results of previous investigators.*

In two directions the results of this investigation lead to a comparison with previous work. In the first place we must consider to what extent earlier papers on the influence of temperature on the presentation-time in geotropism are confirmed by this investigation and in the second place the results of this inquiry must be used to ascertain the correctness of BLACKMAN's theory.

CZAPEK [1]) and BACH [2]), the former with germinating roots of Lupinus albus, the latter with seedlings of Vicia Faba,, have examined the influence of temperature on presentation-time. CZAPEK found in this way a falling of the presentation-time from 0° C. to 15° C., from 15° C. to 30° C. it was constant, after which up to 40° C. there was a rise. BACH found from 14° C. to 30° C. a continuous decrease above 30° C. a rise in the presentation-time. Thus both found in the main the same curve, because the stationary character of the presentation-time between 10° C. and 30° C. in CZAPEK's experiments must no doubt be attributed to secondary influences.

In CZAPEK's and BACH's work there are also a few indications that VAN 'T HOFF's law applies, although their observations are not complete enough to attach great value to their figures from this point of view. From CZAPEK's figures we can calculate: $\frac{K_5}{K_{15}} = \frac{45'}{20'} = 2{,}25$, and from BACH's figures: $\frac{K_{20}}{K_{30}} = \frac{7'.5}{2'} = 3.75$, values which make it appear not improbable that also with the objects of experiment used by them, if the investigation were more complete, VAN 'T HOFF's law would be found operative.

There have been only a few investigations since the appearance of BLACKMAN's first published paper, in which his above-mentioned views have been taken into account. In 1907 SMITH [3]) mentioned in a few lines that in Hydrilla verticillata the intensity of respiration

1) F. CZAPEK. Weitere Beiträge zur Kenntniss der geotropischen Reizbewegungen. Jahrb. f. wiss. Botan., Bd. XXXII, 1898.

2) H. BACH. Ueber die Abhängigkeit der geotropischen Präsentations- und Reaktionszeit von verschiedenen Aussenbedingungen. Jahrb. f. wiss. Botan.. Bd. XLIV, 1907.

3) A. M. SMITH. Respiration of Hydrilla verticillata. Proceedings of the Cambridge Phil. Soc. Vol. XIV, 1907.

rose from 7° C. to 50° C. according to VAN 'T HOFF's law with a coefficient 2.2 for every 10° C. rise of temperature.

In 1908 BALLS [1]) published figures on the growth of fungus hyphae, from which he concluded that between 15° C. and 30° C. the growth in this case followed VAN 'T HOFF's law.

In 1909 KUYPER [2]) published a detailed account of the influence of temperature on respiration and came to the conclusion that BLACKMAN's theory is only partly applicable to respiration.

Up to 10° C. the same quantity of CO_2 is expired in successive hours and from 10° C. to 20° C. there is a slight increase during successive hours, then there follows a period in which the production of CO_2 oscillates, while above 40° C. a regular decrease takes place which graphically represented gives an almost logarithmic curve. VAN 'T HOFF's law holds good for Pisum and Triticum at 0°—20° C., for Lupinus up to 25° C.; the coefficient for a rise of 10° C. of temperature lies between 2 and 3. The optimum is variable with the time of observation. Extrapolation from the time curves in order to obtain the values after 0 time, did not give the values which should be obtained if BLACKMAN's theory applied fully.

The results of the above-mentioned investigations were all more or less a confirmation of BLACKMAN's theory; there is therefore no need to discuss them in further detail. This is, however, not the case with a paper which appeared in 1910 by VAN ITERSON and Miss VAN AMSTEL [3]), in which the writers come to the conclusion that BLACKMAN's theory must be rejected. Since, on the ground of my own investigation, I have come to the opposite conclusion, I will briefly explain to what extent, in my opinion, VAN ITERSON's figures can be employed against BLACKMAN's theory.

In the determination of the influence of temperature on alcoholic fermentation the writers find the following values for the temperature coefficient at temperatures below the optimum ·

$$\frac{V_{30}}{V_{20}} = 2,3, \frac{V_{35}}{V_{25}} = 2,0, \frac{V_{40}}{V_{30}} = 1,8, \frac{V_{45}}{V_{35}} = 1,5.$$

On account of this decrease of the temperature coefficient with rise of temperature, the writers conclude: "it should thus be pointed

1) W. L. BALLS. Temperature and Growth. Annals of Botany. Vol. XXII, 1908.

2) J. KUYPER. De invloed der temperatuur op de ademhaling der hoogere planten. Diss. Utrecht. 1909. Also published in Recueil des Trav. Botan. Néerl. Vol. VII, 1910.

3) G. VAM ITERSON JR. and Miss J. VAN AMSTEL. On the temperature optimum of physiological processes. Proc. Royal Academy Sciences. Amsterdam. 1910.

out very emphatically that already on account of the course of the optimum curve below harmful temperatures the theory of DUCLAUX and BLACKMAN must be rejected."

This conclusion is not justified, because there is also the same decrease of the temperature-coefficient to be observed *in vitro*. Thus PLOTNIKOW [1]) found the temperature-coefficient 6.2 for the reaction between ethylene and bromine at — 78° C. TRAUTZ and VOLKMAN [2]), for the saponification of ethyl-acetate by baryta, give the following values for the temperature-coefficient:

$$\frac{10^\circ}{0^\circ} = 1{,}96 \quad \frac{20^\circ}{10^\circ} = 2{,}04 \quad \frac{30^\circ}{20^\circ} = 1{,}90 \quad \frac{40^\circ}{30^\circ} = 1{,}75 \quad \frac{50^\circ}{40^\circ} = 1{,}60 \quad \frac{60^\circ}{50^\circ} = 1{,}45.$$

For the saponification of propylacetate the corresponding values: 1.63, 2.00, 1.81, 1.70, 1.55, 1.43.

COHEN [3]) also points out that the temperature-coefficient in a chemical reaction is in general liable to vary with change of temperature. At high temperatures the temperature-coefficient decreases, at low ones it rises. The other ground on which VAN ITERSON believes BLACKMAN's theory to be untenable, is that the curve which represents the connection between the alcoholic fermentation and the temperature, is also a pronounced optimum-curve for a previous-warming time of 0 minutes. In my opinion, the authors have attached too great weight to this objection also. Various points can be brought forward to explain this phenomenon.

In the first place, there is the fact already mentioned, that the temperature-coefficient decreases with a rise of temperature.

Further it must be pointed out that VAN 'T HOFF's law applies less strictly in the field of botany than in that of chemistry, for the living organism may not be regarded simply as a homogeneous system.

Moreover even in this case a special factor comes into account, through which an important deviation at higher temperatures is *a priori* probable. The reaction takes place here between the zymase which is enclosed within the cell-wall and the sugar solution outside it.

Thus the transformation only takes place when the sugar diffuses inwards and the reaction products diffuse out in the opposite direction. Now, since after 10° C. rise of temperature the velocity of

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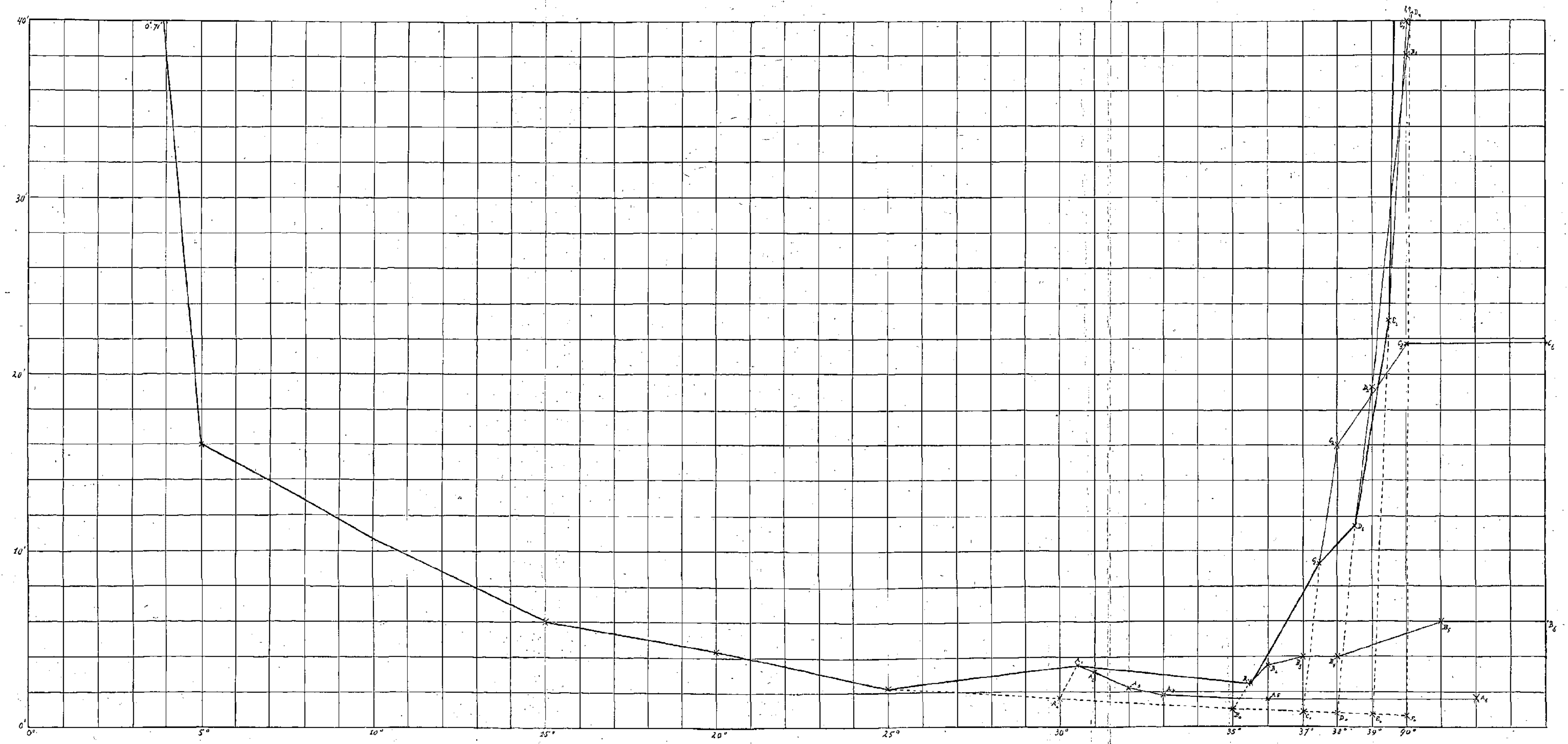
[1]) J PLOTNIKOW, Reaktionsgeschwindigkeiten bei tiefen Temperaturen Zeitsch. f. phys. Chemie LIII, 1905.

[2]) M. TRAUTZ, und K. TH. VOLKMANN, Der Temperaturkoëfficient chemischer Reaktionsgeschwindigkeiten. Zeitschr. f. phys. Chemie LXIV, 1908.

[3]) E. COHEN, Vorträge für Aerzte über Physikalische Chemie. 2e Aufl. Leipzig, Engelmann. 1907.


40'
30'
20'
10'
0'
0°
5°
10°
20°
25°
30°
35°
37°
38°
39°
40°

diffusion only rises about $20^0/_0$ [1]) and the velocity of fermentation 150—200$^0/_0$, it is to be expected that at higher temperatures the velocity of fermentation will remain considerably under the theoretical values, in consequence of the diffusion not proceeding quickly enough.

Finally, the possibility must be considered that also in alcoholic fermentation the favourable influence of higher temperatures first makes itself felt as a function of time, in the same way as was the case in this inquiry at 30° C., and that hence also there the theoretical values according to VAN 'T HOFF's law have no real existence. For if it takes a certain time for the reaction velocity to reach the value belonging to that temperature then this value will never be reached, because, before that happens the harmful influence of the high temperature will already have made its action felt.

The values obtained for the reaction velocity at high temperatures will then, especially after a short time of previous warming, be lower than ought to be the case according to BLACKMAN's theory. The values when extrapolated for time 0 will also be found too low.

Summarising our results, we can therefore say that BLACKMAN's theory in the investigation of the influence of temperature on the presentation-time in geotropism is in the main confirmed, while the investigations which have hitherto taken this theory into account, give no reason to reject it.

On the contrary, in this investigation it is clear, that also in the field of the pure physiology of stimulus the laws of physical chemistry hold.

For the perception of the stimulus of gravitation it follows from this investigation that, with reference to temperature, perception behaves as a chemical process.

Geophysica. — "*On the volcanic eruption in the island of Téon (Tijau) in* 1659". By Prof. ARTH. WICHMANN.

(Communicated in the meeting of Sept. 24, 1910).

In his criticism of RUMPHIUS and VALENTIJN as historiographers of Ambon F. DE HAAN says: "We do not intend to express by this the "desirability of publishing before long the History of Ambon (by "RUMPHIUS). VALENTIJN has plundered it in such a degree, that only "a scanty gleaning of details of little importance is left for a later

[1]) E. COHEN, Vorträge für Aerzte über Physikalische Chemie. 2e Aufl. Leipzig. ENGELMANN. 1907, p. 126.