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Kuyper, J., The influence of temperature on the respiration of the higher plants, in:
KNAW, Proceedings, 12, 1909-1910, Amsterdam, 1910, pp. 219-227

Botany. — *"The influence of temperature on the respiration of the higher plants."* By J. KUYPER. (Communicated by Prof. F. WENT.)

In 1905 Miss MATTHAEI [1]) carried out some investigations on assimilation in the leaves of PRUNUS Laurocerasus. The figures thus obtained led BLACKMAN [2]) to some theoretical considerations entitled: "Optima and limiting factors."

According to these views there arises in the curve representing the variation of a physiological process with temperature an optimum, in consequence of a harmful influence at higher temperatures, which influence increases with the temperature. If the process were to follow the laws of a chemical reaction completely, then the rule of VAN 'T HOFF-ARRHENIUS would hold good for any temperature interval of 10°; the figures show, however, that in the case of assimilation this rule only applies between 0° and 20°—25°. If by this rule the theoretical values are calculated for higher temperatures, they prove to be much higher than those found experimentally. At the same time these values decrease, in proportion as the objects have been exposed for a longer time to the higher temperature. According to BLACKMAN the calculated value agrees with that found by exterpolation to zero time from the series of figures found by observation in successive equal time intervals at constant temperatures.

As a corollary of this view it follows, that an optimum is not an absolute point but changes with the duration of the observations.

The influence which the process undergoes after a length of time at a higher temperature acts as "limiting factor". These limiting factors are discussed in detail in BLACKMAN's paper.

I have investigated the extent to which this theory is applicable to the normal respiration of seedlings and in the following pages I propose to give a preliminary account of the results obtained.

I used as measure of respiration the liberation of CO_2, which was estimated according to PFEFFER's method [3]). The temperature was kept constant within 0.2° C.; in order to determine the time required by the objects to attain the constant temperature, the course of the temperature was followed thermo-electrically in a few cases; it was not possible to do this continually in the botanical laboratory.

The seedlings were placed, as free from each other as possible, on aluminium plates arranged round an axis in the respiration vessel;

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[1]) G. L. C. MATTHAEI, Philosophical Transactions, vol. 197 B, p. 47, 1905.

[2]) F. F. BLACKMAN, Annals of Botany, vol. XIX, p. 281, 1905.

[3]) W. PFEFFER, Untersuchungen aus dem botan. Institut zu Tübingen, Bd. 1, p. 636—645, 1885.

in this vessel there were always also two little basins of water, as humidity was found to have a great influence.

The titration of the baryta water was carried out with HCl, with phenolphthalein as indicator.

Generally I made observations at intervals of 5°; in most cases an experiment lasted 6 hours. A difficulty, which cannot be obviated, is that, when seeds are kept for a long time, the respiration is very different at different periods. The figures thus become much less comparable; in the following table I therefore give a series of experiments which were made within as short an interval as possible.

Most of the experiments were made with Pisum sativum; these will be considered in greatest detail. For every experiment 100 seedlings were used, which had germinated for one day in water and for two days in saw-dust.

Temp.	mgr. CO_2 liberated during						Average per hour
	1st hour	2nd hour	3rd hour	4th hour	5th hour	6th hour	
0°	4	4	3.6	4	3.8		3.9
5°	6.7	6	5.6	5.7	5.8		6.1
10°	12	11.2	11.1	11 4	11.4	11.3	11.4
15°	18.6	19	19 4	19.4	20	20.2	19.4
20°	28.6	30.3	30.3	30.6	30.4		30
25°	43.3	42.4	42.2	41 7	40.7	40.9	42
30°	51 7	50.9	52.2	53.6	53.5	53 5	52.6
35°	68.7	62.8	60.1	61.7	60 9	60.9	
40°	73.3	55 2	49	45.3	43	41 2	
45°	73.5	48.4	41.9	35.9	31.9	28 6	
50°	74	38.8	17.8	12	8	5.9	

It is already clear from the averages between 0° and 20° that the proportion for any rise of temperature of 10° lies between 2 and 3; from the mean of all the observations I find the following relation: [1])

$$\frac{A_{10}}{A_0} = \frac{10.3}{4.3} = 2.4 \quad \frac{A_{15}}{A_5} = \frac{18.5}{5.9} = 3.1 \quad \frac{A_{20}}{A_{10}} = \frac{29.1}{10.3} = 2.8 \quad \frac{A_{23}}{A_{13}} = \frac{40.3}{17.8} = 2.2.$$

The rule of VAN T' HOFF-ARRHENIUS holds good therefore up to 20°,

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[1]) A_0 means respiration at 0°, etc.

with a coefficient of about 3. The observations at 0° are the least reliable, for here the quantity of CO_2 is smallest, so that the error of the apparatus, which amounts to about 0.7 mg., has the greatest influence. I have, however, not thought it advisable to make a correction for this error, as the individual differences of the plants used are much greater.
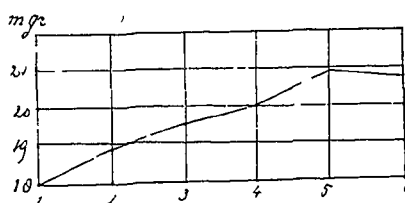

Fig 1. Respiration at 15° C.

It is evident from the figures that at 0°, 5° and 10° the respiration is constant in successive hours; between 15° and 20° something of a rise may frequently be noted. (Fig. 1).
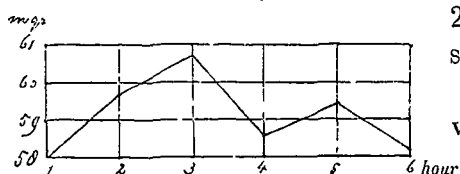
The curves at 25° and especially at 30° show an irregular course; the figures quoted in the table for 25° decrease somewhat; others show the irregularity more.

Fig. 2. Respiration at 30° C.

Fig. 2 represents this irregular variation at 30°. We may here remark that at 30° growth is optimal and can for instance be readily detected with the naked eye after 6 hours.

At 35° respiration falls off pretty rapidly during the first hour and afterwards continues to oscillate more or less; on the other hand the falling off persists at 40°, 45° and 50°; the curves somewhat resemble logarithmic ones (fig. 3) although, as far as I have been able to ascertain, they do not satisfy such a condition mathematically. The absolute and the percentage decline becomes larger with rise of temperature. Between 35°—50° therefore a harmful factor makes its appearance, so that at 25° and 30° there is neither a rise nor a decline whereas a rise may be detected at 15°—20°.

Notwithstanding BLACKMAN's theory, there is some point in investigating the optimum of respiration, because it has been a point of dispute between various observers. The principal records are those of KREUSLER [1]) and of CLAUSEN [2]).

KREUSLER found no optimum for branches of Rubus; the respiration rises to the temperature limit of life, and this is the view which has been accepted in most text books. The highest temperature observed was 46°.6 C.

CLAUSEN found for Lupinusluteus an optimum at 40°. I wish to

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[1]) U. KREUSLER, Landwirtsch. Jahrbücher, Bd. 16, p. 711, 1887.
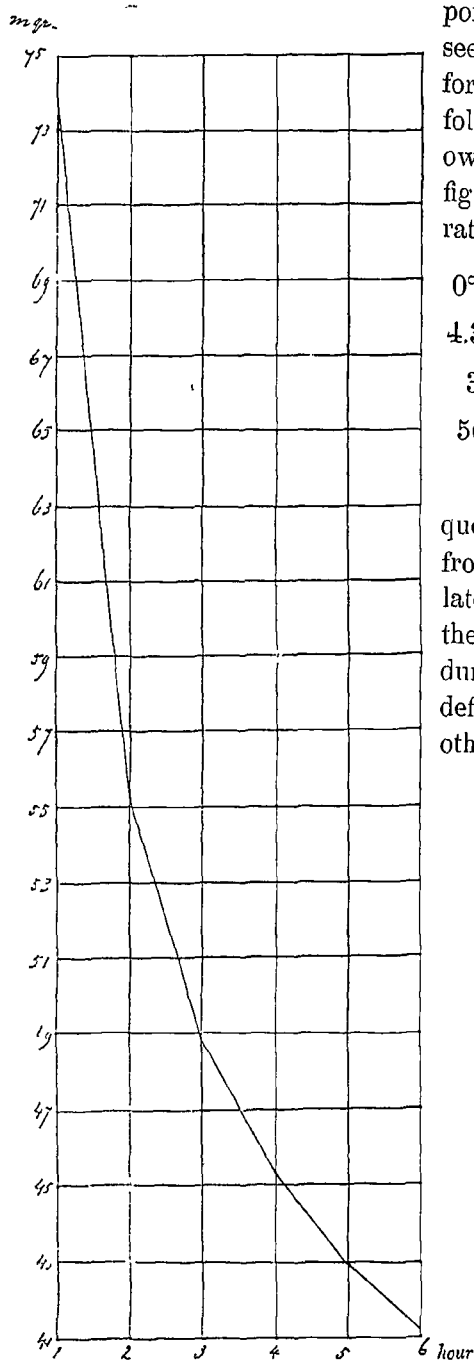
[2]) H. CLAUSEN, Landwirtsch. Jahrbücher, Bd. 19, p. 893, 1890.
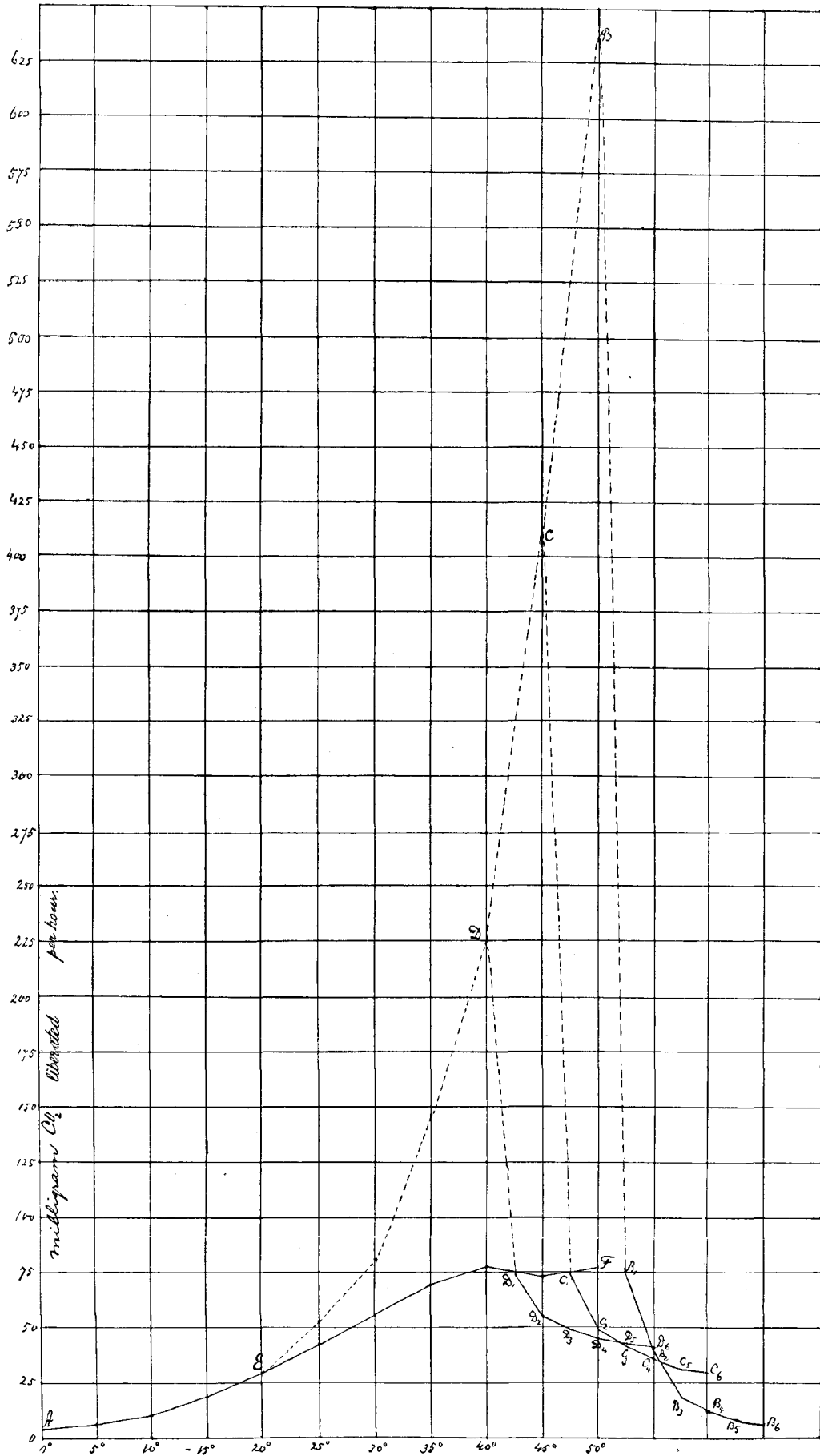
Fig. 3. Respiration at 40° C.

point out that CLAUSEN kept his seedlings for 2 hours at 50° before making an observation. The following series results from my own observations, using the figures for the 1st hour at temperatures of 35°—50°:

0°	5°	10°	15°	20°	25°
4.3	5.9	10.3	18.5	29.1	39.5

30°	35°	40°	45°	50°
56.1	68.9	77.7	73	76.4.

Thus there is obviously no question of a definite optimum; from 40° upwards the values oscillate somewhat. As is evident from the table on p. 220 the observations during the 2nd hour give a very definite optimum at 35°; on the other hand the following table, in

Temp.	CO_2 liberated per hour in mg. calculated according to observations of		
	1 hour	1/2 hour	1/4 hour
40°	77.7	79.2	82
45°	73	82	91.6
50°	76.4	92.6	100

which the respiration at 40°, 45° and 50° has been calculated from observations of the 1st half hour and 1st quarter of an hour, shows

- 6 -

mgr

22
21
20
19
18
17
16
15
14

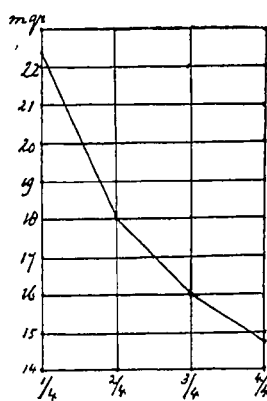$\frac{1}{4}$ $\frac{2}{4}$ $\frac{3}{4}$ $\frac{4}{4}$ hour

Fig. 4.
Respiration at 45° C. in
successive quarters of an hour.

clear an optimum which coincides with the maximum. The observations during 4 successive quarters of an hour very clearly indicate the logarithmic course of the falling-off, as is shown by fig. 4.

We see from these figures that BLACKMAN's view as regards the optima, is also completely applicable to the respiration of Pisum.

It remains to be considered whether BLACKMAN's theory can be applied still further, i.e. whether the value calculated according to the rule of VAN T' HOFF-ARRHENIUS, agrees with that found by exterpolation.

Fig. 5 gives a representation agreeing completely with that of BLACKMAN [1]). The abscissa indicates the temperature, the ordinate the mgr. CO_2 liberated per hour. The line AF gives the figures found experimentally during the first hour of observation, while AB has been drawn by taking 2.8 as coefficient for a 10° temperature interval and considering the figures for 10°, 15° and 20° as standards. The relation between the amount of CO_2 and the time would have to be indicated in a second plane at right angles to the abscissa. This plane has been imagined folded over to the right, for 40° over the line drawn at 40° perpendicular to the abscissa, and further for every temperature over a subsequent line, as the points D, C, and B always have an abscissa $= 0$ in this new system. From the point 40° onwards the abscissa indicates the time after which each observation was made.

The values D_1-D_6 etc. have been taken from the table on p. 220 The lines BB_6, CC_6 and DD_6 are not smooth curves, so that the points B, C, and D may not be regarded as obtainable by exterpolation. On the other hand the greater or less inclination of the intervals BB_1, CC_1, and DD_1 agrees with the greater or less inclination of the intervals B_1B_6, C_1C_6, and D_1D_6.

The general impression which this diagram gives, is, in my opinion, that BLACKMAN's view holds good. Nevertheless, I consider that an important deviation is found in the impossibility of deducing the theoretical points from the other figures by exterpolation. A better analysis of the whole process by which CO_2 is set free, will perhaps some day explain this deviation.

As was pointed out above, a falling-off is noticeable from 35°

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1) BLACKMAN, l.c. p. 284.

onwards, and this must be attributable to some harmful influence. I supposed that this influence was already observable at 30° and therefore tried to show it in another way. I made a series of experiments in which I first observed the peas at 20°, then warmed them to a higher temperature and again observed them at 20°. The observation times were of course chosen in such a way that the peas could properly regain the temperature; first of all it was ascertained whether a change of temperature as such had any influence, by making experiments at 5°—25°—5°. No such influence was found; my results agree completely with those of ZIEGENBEIN[1]) in contradistinction to those of ZALENSKI[2]) and PALLADIN[3]), who ascribe a powerful influence to changes of temperature.

Now in these experiments I found a falling-off, in consequence of the harmful effect of heating to 40° and higher; this falling-off was very small after warming to 35°, so small that the effect was doubtful; an exposure to 30° did not produce any decline at all. In this way also therefore no conclusion could be reached. It was indeed found by warming for various periods to 43°, that the decline for 15 min., $^1/_2$ hour, 1 hour and $1^1/_2$ hours, when plotted, gave a logarithmic curve. The slowing of the respiration by warming to 40° was found to have disappeared completely after 8 hours.

After this I extended the experiments to Triticum vulgare and to Lupinus luteus. I only investigated the respiration in successive periods at temperatures of 0°—50°. The seedlings were treated as in the case of Pisum; they were, however, left one day longer on saw dust.

For Lupinus luteus I obtained the following results for 100 seedlings. (See following table p. 225).

It results from these figures:

That the coefficient for a temperature interval of 10° is 2.6; on determining the ratio $\dfrac{A_{25}}{A_{15}}$ by taking for A_{25} the respiration in the first hour, we find 2.4; by taking the mean of my other data this even becomes 2.5. The rule of VAN 'T HOFF-ARRHENIUS seems to apply here up to 25°. At 25° a certain decline is already noticeable, and at 40° this shows a logarithmic curve.

In general Lupinus is less resistant to a high temperature than Pisum; after 6 hours at 45° the turgescence of the roots had partially disappeared. As regards BLACKMAN's theory, Lupinus gives the same general result as Pisum.

[1]) E. ZIEGENBEIN, Jahrbücher für wissensch. Botanik, Bd. XXV, p. 563, 1893.

[2]) W. ZALENSKI, Abstract in Bot. Centralblatt, Bd. 95, p. 251, 1904.

[3]) W. PALLADIN, Revue générale de Botanique, t. XI, p. 241, 1899. ·

Temp.	mgr. CO_2 liberated during						Average p. hour
	1st hour	2nd hour	3rd hour	4th hour	5th hour	6th hour	
5°	5.2	5.4	5	4.5	4 5		4 9
10°	8	7 8	7.8	8.2	8.5	8.2	8 1
15°	11.2	12.2	13.4	13 4	13.6	13.2	12.9
20°	20.9	21.9	22.9	22.5	21.1	21.5	21.8
25°	30.5	31.6	30.5	29.9	28.3	27.9	
30°	37.9	37.1	34.7	34.6	32 4	31.8	
35°	43.8	43.3	42.1	41 4	41	39 3	
40°	5S	49.7	45.1	41.8	42.3	42.1	
45°	57.1	42.3	35.8	34.9	34	31.4	
50°	49.9	12	5.7				

I here append the figures obtained for Triticum vulgare, with 50 grams of 4 days-old seedlings.

Temp.	mgr. CO_2 liberated during						Average p. hour
	1st hour	2nd hour	3rd hour	4th hour	5th hour	6th hour	
0°	4.4	4.4	,				4.4
5°	7.6	7.2					7.4
10°	11	11.2					11.1
15°	21 3	22	22	22 9	22.4	22 4	22.1
20°	26.9	27.3	27.1	28.1	28.7		27.1¹)
25°	36.4	36.4	36.4	39 2	40 8	40.8	36.4
30°	45.7	46.1	47.3	50.3	49.7	50.5	
35°	48.2	44 G	49.7	46.2	47.7	46.8	
40°	51.8	45.4	42.2	38.2	36.4	35.8	
45°	48.7	40.4	33.7	29.7	26.7	24.8	
50°	42.2	22	12.4	10	9.2	8.8	

From *all* the available figures I find:

¹) The averages for 20° and 25° have been calculated from the first three hours.

$$\frac{A_{10}}{A_0} = \frac{11.4}{4.4} = 2.6 \qquad \frac{A_{15}}{A_5} = \frac{20.2}{8.2} = 2.5 \qquad \frac{A_{20}}{A_{10}} = \frac{27}{11.4} = 2.4.$$

Hence the coefficient is here on the average 2.5. If we consider the course at every temperature, we find that up to 30° a very distinct rise is observable; I attribute this partly to the increase of respiration with the advance of the period of germination of the plant. This increase was already observed by RISCHAVI[1]; I myself found at 20° for instance after 4 days' germination 28 mg., after 5 days in the same plants 36 mg.

At 35° the curve is very irregular, while at a higher temperature the logarithmic decline again shows itself.

In this case also the general aspect is the same as that presented by Lupinus and Pisum. The difference between the three plants is in the temperature at which the rise, the oscillations and the decline occur.

		Lupinus	Pisum	Triticum
Rise	observable at	15°—20°	20°	30°
Oscillations	„ „	20°—25°	30°	35°
Decline	„ „	25°—30°	35°	40°

It will be seen that in this respect the three plants form a series.

I imagine that this different behaviour is caused by, or is at least closely connected with the reserve food which the plant has at its disposal. There is found for instance in:[2]

	Lupinus	Pisum	Triticum
as reserve food	no starch protein 37 %	starch 54 % protein 22 %	starch 74 % protein 12 %

If follows from these figures that the temperature at which the harmful effect arises, is higher when the starch content is higher, and lower in proportion as the protein content is higher. Probably there is here an indication that the course of respiration depends on the presence of proteolytic or diastatic enzymes; the falling-off at a

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[1] L. RISCHAVI, Landwirtsch. Versuchsstationen, Bd. 19, 1876.

[2] These data have been taken from HARZ, Landwirtschaftliche Samenkunde, 1885.

lower temperature in the seeds with a higher protein content is perhaps connected with the fact that the optimum for proteolytic generally lies lower than for diastatic ones.

In conclusion I mention a few experiments with capitula of Crepis biennis. I only made observations from 30°—50°; at each of the temperatures employed a falling-off was observable, which was very marked and gave an almost straight line. The experiments are too few in number to allow of a definite conclusion being drawn but the marked decline is in this case also most probably influenced by a want of respiratory material. According to the observations the respiration increases during the first hour right up to 45°, while the temperature limit of life is only a very little higher; after a 6 hours' exposure to 45° the flowers were dead.

My results are therefore as follows:

1. the theory of BLACKMAN is also applicable to respiration to the extent that:

    a. the rule of VAN 'T HOFF-ARRHENIUS holds good from 0° to 20°—25°.

    b. the optimum may be displaced with the time of observation.

    c. the falling off at 40°, 45°, and 50° has a logarithmic course in seedlings.

2. the course of respiration depends very much on the nature of the reserve food.

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Chemistry. — "*On retrogressive melting-point lines.*" By Prof. A. SMITS. (Communicated by Prof. J. D. VAN DER WAALS).

(First Communication.)

Applying the method indicated by VAN DER WAALS [1]) we find for the melting-point line under the vapour pressure the following equation:

$$\frac{dx_L}{dt} = -\frac{1}{T}\left(\frac{\partial x_L}{\partial p}\right)_T \frac{(x_L - x_q)\{(V_q - V_L)(Q_m + Q_{SL}) - (V_L - V_S)Q_{LG}}{(V_q - V_L)\{x_L - x_g\}V_S - (x_S - x_q)V_L + (x_S - x_L)V_g\}}$$

in which $Q_{SL} =$ mol. heat of melting of a compound of the concentration x_S;

    Q_m = differential mol. heat of mixing of the melted compound with a solution of the concentration x_L;

    $Q_{LG}=$ mol. heat of evaporation of a solution of the concentration x_L.

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[1]) Versl. Kon. Akad. v. Wet. 28 Febr. 1885 and Rec. Trav. chim. 5, 336 (1886).