

THE TEMPERATURE COEFFICIENT OF PHOTOSYNTHESIS.

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The temperature coefficient of photosynthesis presents an interesting problem. On the one hand is the fact that light reactions have very low temperature coefficients; while on the other hand it appears that the temperature coefficients of photosynthesis reported by various investigators¹ are as high as those of ordinary reactions. It should be noted, however, that in a recent investigation van Amstel² found a temperature coefficient of 1.26, but expresses doubt whether this really represents the correct value for photosynthesis.

The difficulties of determining temperature coefficients are great in the case of land plants, for when leaves are exposed to sunlight their temperature rapidly rises and it may fluctuate as much as 10°C. in a half hour period. For this reason the writers have employed aquatic plants which form thin layers, the temperature of which can be sufficiently controlled.

In the present investigation the plants were placed in tubes filled with solution; these were immersed in a water bath the temperature of which was kept constant within 1°C., which sufficed for the purposes of the investigation. Thermometers placed in the tubes showed that the temperature did not rise more than 1°C. above that of the bath and that it did not fluctuate more than that of the bath itself. The plant employed in these investigations forms such thin layers

¹ Cf. Matthaei, G. L. C., *Phil. Tr. Roy. Soc., B*, 1905, cxcvii, 47, and the interpretation by Kanitz, A., in *Temperatur und Lebensvorgänge*, 1915, p. 18. Also Blackman, F. F., and Matthaei, G. L. C., *ibid.*, 1905, lxxvi, 402. Blackman, F. F., and Smith, A. M., *ibid.*, 1911, lxxxiii, 401.

The results of these observers have been interpreted by Brown and Heise as showing very low temperature coefficients (Brown, W. H., and Heise, G. W., *Philippine J. Sc., C.*, 1917, xii, 1).

² van Amstel, J. E., *Rec. trav. bot. néerlandais*, 1917, xiii, 1.

(0.078 mm. thick) that its temperature quickly reaches that of the surrounding liquid. This plant is the marine alga *Ulva rigida* (sea lettuce) which was chosen because of its rapid rate of photosynthesis, its hardness under laboratory conditions, and its excellent mechanical properties.

The method³ (which seems to be more accurate than those hitherto employed) consisted in placing the plant in sea water to which an indicator had been added, the whole being contained in a tube which was immersed to a depth of 2 or 3 inches in a water bath and exposed to direct sunlight.⁴ Photosynthesis was allowed to proceed until a definite amount of CO₂ had been abstracted from the sea water, as shown by the color of the indicator. This was repeated as often as necessary. It has been shown in a previous article³ that the rate of photosynthesis is not constant from the start, but steadily increases until it reaches a constant value. It was therefore necessary to continue the exposure until the constant value was reached. After determining the constant rate the temperature was changed and new determinations were made.

Since the amount of CO₂ abstracted by the plant (and consequently the amount of photosynthesis) was always the same, the rates at different temperatures are inversely proportional to the time required for the standard amount of photosynthesis.

Since the object of the investigation was to ascertain whether the temperature coefficients are those of light reactions or of ordinary chemical processes, it was not necessary to extend the experiments over a wide range of temperature. The temperatures chosen were 17° and 27°C., which are high enough to ensure rapid photosynthesis but which do not produce the slightest injury.

The results are shown in Table I. For convenience the rate of photosynthesis at 17°C. is taken as 100 and other rates are expressed as per cent of this. Thus the rate at 27°C. is found to be 169 ± 1 .⁵

³ The details of technique are fully explained in a previous article. See Osterhout, W. J. V., and Haas, A. R. C., *J. Gen. Physiol.*, 1918, i, 1.

⁴ The tubes were inclined so as to receive the sunlight as nearly as possible at right angles.

⁵ This figure represents the average of eight experiments. The results were first expressed as per cent and then averaged.

This is designated in the table as the apparent rate of photosynthesis since it is not corrected for respiration. The correction is made by adding the rate of respiration⁶ to the apparent rate of photosynthesis. The sum gives the true rate of photosynthesis.⁷ The true rate is seen to be 150 at 17°C. and 271 at 27°C., giving a temperature coefficient of 1.81.⁸

The question arises: How can the process have so high a temperature coefficient? The answer is not far to seek. The writers have suggested in a recent paper⁹ that photosynthesis involves catalytic reactions of the type $S \rightarrow M \rightarrow P$ in which S represents a substance which, under the influence of light, breaks down to form M ;

TABLE I.
Temperature Coefficient of Photosynthesis and Respiration in Ulva.

	Temperature.		Temperature coefficient.
	17°C.	27°C.	
Apparent rate of photosynthesis.....	100	169±1.1	1.69
Rate of respiration.....	50±1	102±1.5	2.04
True rate of photosynthesis.....	150	271	1.81

Each figure represents the average of eight experiments. The rate of photosynthesis at 17°C. (which is taken as 100) represents a change from pH 8.1 to pH 8.3 in 18.1 minutes.

this in turn forms P , the amount of which is proportional to the amount of photosynthesis. If the reaction $S \rightarrow M$ is more rapid than $M \rightarrow P$ -

⁶This was ascertained by repeating the experiment with the same pieces of *Ulva* under precisely the same conditions except that light was excluded. It is expressed as per cent of the rate of photosynthesis at 17°C. (which is taken as 100).

⁷This involves the assumption that the rate of respiration is practically the same in light and in dark (as long as the temperature remains the same). There seem to be good grounds for this assumption.

⁸It is not likely that this result is affected by "limiting factors," since the light was practically full sunlight, and since the temperatures were near the optimum and the supply of CO₂ was sufficient, owing to the presence of carbonates and bicarbonates in the sea water. The effect of a limiting factor would be to make the coefficient appear less than it is in reality.

⁹Osterhout and Haas, *J. Gen. Physiol.*, 1918, i, 1.

(as is presumably the case), the speed of the process as a whole will depend chiefly on the speed of $M \rightarrow P$ (the velocity of the whole catenary process being regulated by the speed of the slowest member). It is therefore evident that when the temperature is raised its effect on the process as a whole will depend chiefly on its effect upon $M \rightarrow P$ rather than upon its effect upon $S \rightarrow M$. Hence if the light reaction $S \rightarrow M$ has a low temperature coefficient, while $M \rightarrow P$ (which is not a light reaction) has a high coefficient, the temperature coefficient of the process as a whole will be high. It is therefore not surprising to find that photosynthesis has a temperature coefficient of 1.81. Analogous cases exist in photochemistry.¹⁰

It is to be expected that similar relations will be found in heliotropic and heliotactic reactions where the stimulus is given by light and the growth or movement which follows is due to a slower process with a coefficient presumably higher than that of the light reaction.¹¹

SUMMARY.

The temperature coefficient of photosynthesis in *Ulva* (between 17° and 27°C.) is 1.81. This may be explained by assuming that the process involves a light reaction with a low coefficient followed by an ordinary reaction with a high coefficient.

¹⁰ Cf. Bovie, W. T., *Science*, 1913, xxxvii, 373.

¹¹ According to T. Nybergh (*Ber. bot. Ges.*, 1912, xxx, 542) this is the case for the oat seedling, but this is disputed by Marie de Vries (*ibid.*, 1913, xxxi, 233; *Versl. wis. en natuurk. Akad. Wetensch. te Amsterdam*, 1913, xxi, 1056.) In certain cases the whole process may depend on the diffusion of a substance (produced in the light) from the point of origin to another region. The coefficient may then be that of diffusion (usually not over 1.28).