

MEDEDELINGEN LANDBOUWHOGESCHOOL
WAGENINGEN • NEDERLAND • 74-17 (1974)

ADDITIONAL NOTES ON TEMPERATURE RELATIONS IN PLANT PHYSIOLOGICAL PROCESSES

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360th Communication*

(Received 26-VII-1974).

1. *Introduction*

In a previous paper the linear relationship of several plant physiological processes with temperature has been discussed, alongside with some other temperature relationships (1).

It was pointed out that the linear relationship can be understood as an exponential relationship which, at increasing temperatures, is increasingly suppressed by the action of another limiting factor with a lower temperature increment.

It was pointed out as well that this conclusion can only be substantiated by a plant physiological analysis of the straight line obtained, in such a way that the Q_{10} (or rather Q_5)-values of the highest temperature intervals within the still 'physiological' range (e.g. 20–25°, 25–30°C) are modified by specific conditions of the plant material, its previous history or certain aspects of the environment. This type of analysis has only been made in very few cases (2). These cases definitely substantiated the type of explanation of the straight line temperature relationship mentioned above.

In the previous paper (1) it was also mentioned that straight-line relationships are characterized by smoothly decreasing Q_5 -values with increasing temperature; these values were calculated and demonstrated for several examples of straight lines from literature. Straight lines are rather spectacular, but it can easily be shown that the principal effect, the smooth decrease of Q_5 not necessarily needs to result in a straight line; the lower part may still be exponential, characterized by constant Q_5 -values, the upper part may even lie below a straight line relationship (see, e.g., 1, fig. 1, fig. 6). Experimentally produced shifts between these possibilities strengthen the basis for the interpretation (1, fig. 6, fig. 10).

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It is certainly possible and has been attempted in certain cases, to describe experimental relationships of several types by mathematical relationships adjusted by suitably chosen coefficients. Such formulae may also be set up on a theoretical basis, different from the one above (*i.e.*, the interaction of partial processes of different types, showing different Q_5 -values). In our opinion the validity of such propositions should always be tested experimentally in order to see in how far they can explain experimentally produced modifications of the (chiefly) linear relationship.

2. Discussion of some additional data

In this connection, we would like to discuss briefly some observations made a few years ago by BALDRY *et al.* (3) and subjected to theoretical analysis by

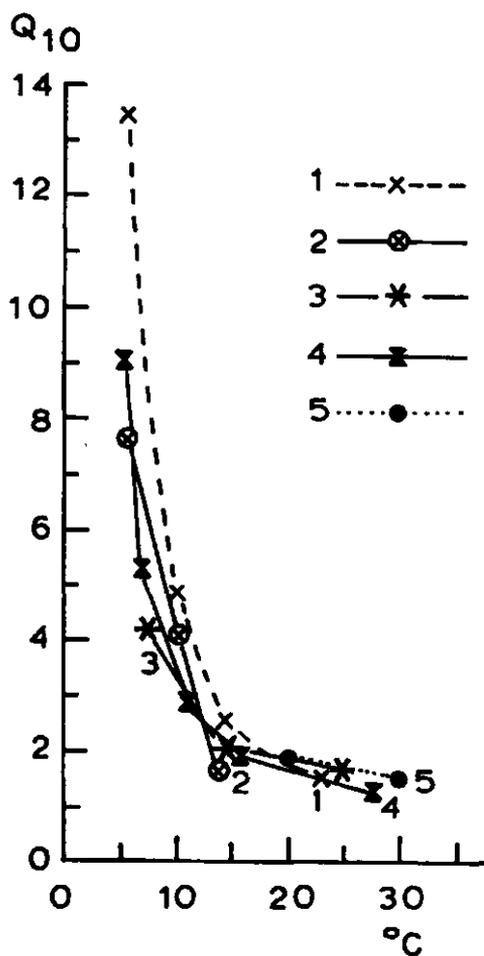


Fig. 1. Q_{10} -values of photosynthesis, as collected in (3), Table 1. Curve 1: EMERSON, *Chlorella*, 2: EMERSON and GREEN, *Gigartina*, 3: WARBURG, *Chlorella*, 4: BALDRY *et al.*, pea chloroplasts. 5: VERKROOST, *Scenedesmus*, inhibition of photosynthesis, owing to pretreatment with ozone.

SELWYN (4). They are concerned with photosynthetic CO₂-fixation by isolated chloroplasts of pea seedlings, at temperatures from 5–30°C.

The authors (3) plotted their data as log max. rate of fixation against 1/T (°K). Moreover, they compared their Q₁₀-values with some other series available in literature (3, Tab. I). In figure 1, we have plotted the latter data against the temperature scale. This figure shows a truly remarkable fit between the various series; all Q₁₀-values are within a narrow band, with a very clear general trend from (sometimes very) high values at the lowest temperatures to low ones at high temperatures. The trend reminds very much of those shown for Q₅ in ref. 1, figs. 1 and 2. *It does not suggest that temperature relationships in photosynthesis are governed by principles, strongly differing from those obtaining in other plant physiological processes.*

Table 1. Maximum rates of CO₂-fixation (in μmoles/mg chlorophyll/10 minutes, calculated from readings of graphs in (3), figs. 1–3.

Temp.	Periods read					Rate calculated	Brought together at 10°C
(3), figure 1							
	5'	10'	15'	20'	25'		
5°	–	–	"	–	"	0.58	0.59
10°	–	–	"	–	"	1.41	1.44
15°	–	–	"	–	"	2.66	2.72
20°	–	–	–	–	–	–	–
25°	–	–	–	–	–	–	–
30°	–	–	–	–	–	–	–
(3), figure 2							
5°	–	–	–	–	–	–	–
10°	–	"	"	"	–	4.07	1.44
15°	–	"	"	"	–	7.03	2.46
20°	"	"	"	–	–	9.99	3.50
25°	"	"	"	–	–	11.8	4.13
30°	–	–	–	–	–	–	–
(3), figure 3							
5°	–	–	"	–	"	0.54	0.54
10°	–	–	"	–	"	1.44	1.44
15°	–	–	–	–	–	–	–
20°	–	–	–	–	–	–	–
25°	"	"	"	–	–	5.76	5.76
30°	"	"	"	–	–	7.20	7.20

Max rate/10 min
 $\mu\text{ mol CO}_2/\text{mg Chl}$

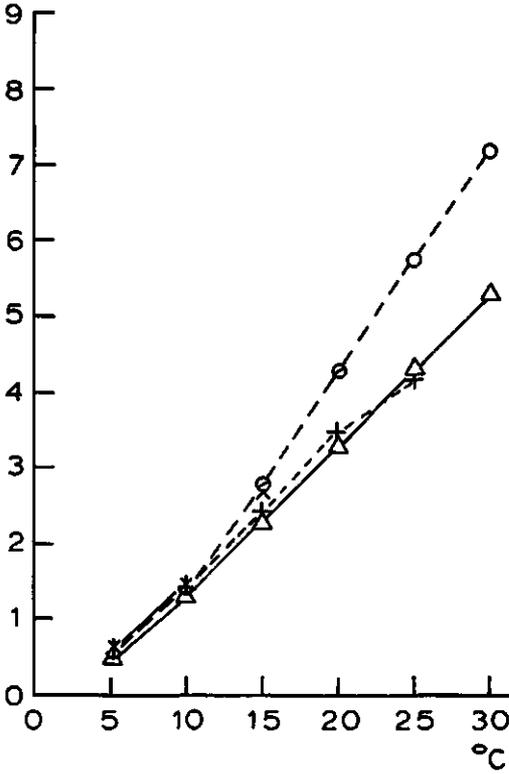


Fig. 2. Maximum rates of CO_2 -fixation in 10 minutes, at various temperatures. Compiled from (3), fig. 1 (×), fig. 2 (+), fig. 3 (○; ∅ interpolated figures).

For comparison: Rates of protoplasmic streaming in *Chara* (arbitrary units), after HILLE RIS LAMBERS (5), adapted from ref (1); ordinate 5 is about $90 \mu/\text{sec}$ (△).

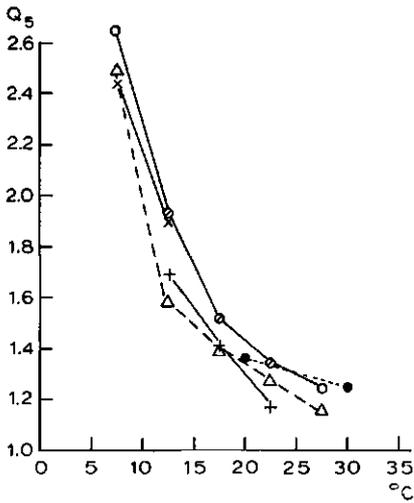


Fig. 3. Q_5 -values derived from the data collected in fig. 2. Explanation, see fig. 2. ● Derived from Q_{10} -values of fig. 1.

This observation induced us to look in some detail into the basic data of BALDRY *et al.* (3) as contained in their figures 1, 2 and 3. The difference in ordinates and the differences in absolute rates of CO₂-fixation had to be taken into consideration as well as the more or less pronounced initial lag phase. Taking all this into consideration, the rates listed in Table 1 have been derived. The data of (3), fig. 1 and fig. 3 show closely comparable activities, those recorded in (3), fig. 2 are very much higher. In order to eliminate these differences in activity, the data have been brought to coincidence at 10°C, on the value 1.44 (μmol CO₂/mg chl/10 min). The rate curves against temperature, thus obtained, have been plotted in figure 2. On the basis of the points at 5°, 10°, 25° and 30°C, derived from (3), fig. 3, (○) which, from 10° onwards, appear to form a fairly straight line, the points at 15° and 20° have been interpolated (∅). It is clear that the points derived from (3), fig. 1 (×) as far as available closely coincide with those of (3), fig. 3, whereas those derived from (3), fig. 2 (+) show a smoother slope, and a further downward trend at the highest temperature. If we remember that, actually, the material of (3) fig. 2 showed much higher actual rates of CO₂-fixation than that of (3), figs. 1 and 3, it will be seen that the result is just what should be expected on the basis of the explanation advanced in (1) and above, *viz.* with higher absolute rates one will expect that processes with low Q₅-values become rate limiting already at lower temperatures than in cases of lower absolute rates as e.g. in (3), figs. 1 and 3.

It would seem that the lines indicated in fig. 2 with × and ○ on the one hand, and with + on the other hand, may be looked upon as an incidental example of the same trend as brought about intentionally in the case represented in (1), fig. 6, by the same cause, *viz.*, differences in absolute rates of the processes studied (see also (1), fig. 9).

In fig. 3, the courses of Q₅ for the various cases have been collected. They show the strongly downward trend, variously reported in (1), smoothing out towards low values at high temperatures. Clearly, those derived from the data of (3) fig. 2 lie below those from (3), figs. 1 and 3.

In figs. 2 and 3 (of this paper), a rate curve and a Q₅-curve for the protoplasmic streaming in *Chara*, taken from (1), fig. 2, have been introduced for comparison. They show similar trends and closely corresponding values for Q₅. That the temperature relationship of protoplasmic streaming can be considered from the viewpoint forwarded above has been convincingly shown by BOTTE-LIER (2), as discussed in (1).

Thus, in our opinion, there seems no direct reason to introduce a different type of explanation for similar phenomena occurring in the field of photosynthesis.

SELWYN (4) has shown that it is possible to explain the data of (3) by considerations based on the evidence that cyclic processes (and feed-back mechanisms) are included. In order to give preference to this type of explanation above the one based on the limiting factor considerations as discussed in (1), we feel that intentionally set-up experimental procedures, specifically affecting cyclic processes should be carried out in order to see whether these produce effects to be

expected by the theory, as have been presented and discussed for the field of the limiting factor theory in (1). As long as such evidence is not available, we feel that there is no definite reason to reject the limiting factor theory specifically for the case of photosynthesis. We hope that the analysis presented in this paper will contribute to further elucidation of the problems involved.

3. *Inhibition of photosynthesis bij ozone*

One of the reasons we went to look into temperature relations in photosynthesis was in some observations of a slightly different nature made in a recent study by VERKROOST (6) on effects of ozone on photosynthesis in *Scenedesmus* species. Temperature relationships of the ozone effect were studied. In these cases the procedure was as follows: A suspension of the algae in culture medium was submitted to a treatment with a certain ozone content in air during 1, 2, 3 or 4 hours, at 15°, 25°, and 35°C, at high light intensity. These treatments inhibited subsequently measured photosynthesis to certain degrees. In all cases photosynthesis was measured at 25°C, so that a direct effect of temperature on the rate of photosynthesis was excluded. The degree of inhibition of photosynthesis owing to the preceding treatment with ozone was expressed in percentages of the activity of untreated samples at 25°C. The inhibition was both time- and temperature dependent. Therefore, calculations were made of Q_{10} for 2 regions, viz. 25/15° and 35/25° after 1, 2, 3, and 4 hours of ozone pretreatment.

It turned out that the inhibition (damaging) of the photosynthetic system at 15°C was time-saturated already after 1 hour, and remained small, whereas those at 25° and 35°C still increased considerably after 1 hour and reached much higher values of inhibition than at 15°C (see (6)).

Owing to these facts, Q_{10} for inhibition in the range 25–15°C increases considerably with time, viz. from 1.10 after 1 hour to ca. 1.90 after 4 hrs. For 35–25°C the Q_{10} values rise from ca. 1.3 to 1.6 in the same time range. Q_5 values for these regions would range from about 1.05 to ~ 1.37 for 15–25°, and from about 1.15 to 1.25 for 25–35°C. The 4-h. values have been indicated by dots (●) in fig. 1 and fig. 3 of this paper.

It should still be observed that the inhibiting – or rather damaging – effect on photosynthesis was largely irreversible.

The mentioned points in fig. 1 and 3 match very well with those from direct measurements of the temperature dependency of photosynthesis.

VERKROOST (6) also established Q_{10} values for the remaining photosynthetic activity. Obviously these show a downward trend, $Q_{25/15}$ for 1 hour to 4 hours decreasing from ~ 1.0 to 0.7, $Q_{35/25}$ decreasing from 0.90 to 0.60.

The nature of the inhibiting reaction (or rather of the process causing damage to the photosynthetic apparatus) is unknown up to now; chlorophyll is also lost to some degree, and one might speculate about deterioration of membranes.

VERKROOST (6) also studied the same effects on respiration. Here, the 15° curve lags behind still much more than in the case of photosynthesis, and correspondingly has a still lower degree of inhibition. This entails very high

Q_{10} values for the 25°/15°C range, viz. between 4 and 8 in the time range from 1–4 hours (max. at 2 h.).

Q_{10} for 35/25° shows much lower values, viz. from 2.3 to 1.5 Q_{10} values for remaining respiratory activity show much the same trends as in the case of photosynthesis (see above). For further details consult ref. (6).

4. Summary

Data on temperature relationships in photosynthesis, as presented in ref. 3, and discussed in ref. 4, have been considered from the viewpoints, developed in ref. 1, and compared with some data, presented there.

Q_{10} -values of photosynthesis, collected by various authors, show remarkably good agreement, all falling into a narrow band (cf. fig. 1). They decrease strongly with increasing temperature as also shown in other cases compiled and discussed in ref. 1. Before relating temperature dependency in photosynthesis specifically to cyclic reaction mechanisms in this process, specific relations of Q_{10} (or Q_5) with deliberately brought about changes in these cyclic mechanisms would appear required, as has been demonstrated for the limiting factor type of explanation in ref. 1 (examples see also ref. 2). So far, the data from ref. 3 do not suggest the necessity of a type of explanation, fundamentally differing from the one discussed in ref. 1.

In figures 1 and 3, some data are shown on inhibition of photosynthesis by pretreatment with ozone at different temperatures (ref. 6), they fit well into the general trends.

5. References

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