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RELATIONSHIPS BETWEEN ACTIVITY OF ORGANISMS AND TEMPERATURE AND THE COMPUTATION OF THE ANNUAL RESPIRATION OF MICRO-ORGANISMS DECOMPOSING LEAF LITTER

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SUMMARY

A brief outline is given of the relationships between temperature and the rate of a reaction or biological activity. The use of the Q_{10} ratio is criticized and an alternative method using a computer-based curve-fitting technique is suggested. Using this technique, the total respiration of ash (Fraxinus excelsior L.) and hazel (Corylus avellana L.) litter over a period of nearly one year has been calculated and compared with the observed dry weight and carbon loss.

INTRODUCTION

In very general terms, the rates at which the metabolic processes of organisms, other than homeotherms, proceed are predictably related to the temperature of the environment. Van't Hoff's Law and Arrhenius' equation are commonly quoted in this context. Van't Hoff's Law was originally applied to chemical reactions and states that the logarithm of the reaction rate is proportional to the temperature (^{o}C). Arrhenius (1889) derived the following equation to describe the effects of temperature on rates of chemical reactions:

$$\frac{d \ln k}{dT} = \frac{A}{RT^2}$$

where k is the reaction velocity constant, R is the gas constant, T is the absolute temperature, and A is a constant which can be calculated from the plot of log k against 1/T where the slope is equal to A/2.303R (e.g. see Fruton and Simmonds, 1953, pp. 254-260). Arrhenius (1908) extended his formula to include biological processes and A was replaced by μ, the temperature characteristic of the process. Arrhenius' equation assumed theoretical importance when it was realised that the reaction rate might be the product of the number of activated molecules and their frequency of collison (Lewis, 1918). A (or μ) is related to the probability that molecules that collide will have enough energy to react, and Arrhenius' equation may be given in the form:

$$k = Ze^{-A/RT}$$

where k is the number of molecules reacting per second per unit volume, Z is an integration constant modified to include the collision number and a probability factor and represents the number of molecules colliding per second per unit volume. The exponential term is a measure of the fraction of the molecules having excess energy A or more, and A is a constant which is considered to be the minimum energy that reacting molecules must possess before they react.

Although this relationship has been shown to hold for a wide range of chemical reactions, several types of reactions and processes are known not to give a straight line with such a plot. Such cases include microbial growth and enzyme reactions studied in vivo or in vitro, and attempts have been made to explain their deviatons (Farrell and Rose, 1967; Brandts, 1967). It is thus scarcely surprising that larger organisms should fail to conform strictly to either Van't Hoff's Law or Arrhenius' equation (e.g. see Krogh, 1916).

For some time, biologists have been using a simple method for comparing rates of processes or activities at different temperatures. This involves the Q_{10} value, $Q_{10} = \frac{\text{rate at } t + 10^{o}C}{\text{rate at } t^{o}C}$. The Q_{10} value for microbial respiration approaches 2.0. This Q_{10} value was also obtained by Macfadyen (1967) for carbon dioxide evolution of intact soil cores in temperature ranges between 10°C and 25°C. However, Newell (1966) and Newell and Northcroft (1967) have shown that for some animals the Q_{10} is frequently nearer 1.0 between 7° and 22°C. On the other hand, Berthet (1964) obtained Q_{10} values around 4.0 for oribatid mites.

The Q_{10} value is derived from Van't Hoff's Law (Krogh, 1916, p.97) and from the exceptions quoted above one would expect it to have limitations. It is well established that the Q_{10} value for the total respiration of organisms varies with the temperature range over which it is calculated. Krogh (1916, p.98) found that temperature-metabolism (carbon dioxide evolution) curves for a variety of animals showed this variation of Q_{10} with temperature. Therefore, when Q_{10} values are given it is essential to specify the temperature range. Even so, a mathematician would question the value of the Q_{10} ratio and would suggest other, mathematically better, ways of handling data of this type.

The two basic requirements from temperature/metabolism data are (a) a simple way of comparing the change in rate of a process or activity with temperature for such purposes as experiments in temperature adaptation, and (b) a method for predicting values for the rates at various temperatures from limited sets of data, for such purposes as extrapolation to the field from laboratory experiments. I shall consider how these requirements might be met.

The Q_{10} value is a mathematically unsatisfactory way of expressing variations of activity or reaction rate with temperature. Its main use appears to be in providing a simple number for comparing the responses of organisms, as in (a) above. Even for this limited purpose it is not really satisfactory. Figure 1 shows plots of rate against temperature obtained by taking arbitrary origins

and slopes. The lines have the same slope and therefore the same change of rate per degree change in temperature. However, it can be seen that, for each line, the Q_{10} value varies with temperature. Furthermore, because the lines have different intercepts on the y axis at 0°C, the Q_{10} values for the two plots over a given temperature range are different. Figure 2 shows plots obtained similarly in which the Q_{10} values are all equal to 2.0 over the temperature range of the plots. Again this illustrates the effect of the intercept on the y axis at 0°C on the shape of the curve. It also shows that, although the Q_{10} value is constant over the temperature range of the plots, the change in rate per degree change in temperature varies with the temperature.

Although the use of the Q_{10} value is cumbersome and mathematically dubious, it is so firmly entrenched in certain types of biological work that one hesitates to suggest that it should be dropped entirely. The Q_{10} figure can still be of some value as long as its limitations are recognised. However, I wish to focus attention on another way of handling temperature/metabolism data which deserves the attention of biologists, especially those having access to an electronic computer. This method is illustrated by results from a study of leaf litter decomposing under the influence of mixed microbial populations in the field in the absence of animals. This work is part of a series of experiments on litter decomposition which are being carried out at Meathop Wood I.B.P. site in North Lancashire, England (Nat. Grid Ref. SD 436795). Full details of these experiments will be published later. This paper presents some of the preliminary findings which are relevant to the above discussion on temperature/metabolism relationships.

EXPERIMENTAL METHODS

The method used for studying litter decomposition is similar to that described by Howard (1967), where weighed litter is placed on the surface of soil in glass tubes 2.5 cm diameter and 15 cm long with a plug of glass wool at the bottom. Before use, the air-dry litter was subjected to a total of 20 kR of X-rays in three separate doses. This treatment kills litter animals and their eggs with minimum effect on micro-organisms and leaf chemical composition (Howard and Frankland, in prep.). The soil was heated moist to 50°C for two periods of 24 hours with 24 hours at room temperature between. This treatment kills soil animals and their eggs. The soil was left to stand in the tubes for a week after this treatment. The litter was then added and the tubes were watered with a general inoculum of micro-organisms prepared by incubating water with soil and litter from the field. Tubes of litter and soil treated in this way can be kept free of animals for up to two years in the field if they are placed in a large plastic container which must be freely drained and is itself supported in a box having terylene or nylon fine netting (0.5 x 1 mm mesh) top and bottom. The boxes

used in our experiments are 90 cm long, 55 cm wide, and 33 cm deep, and are supported on legs 42 cm long which is sufficiently high to avoid the carrying up of small animals into the boxes in rain splash. Sticky bands on the legs of the boxes and a coat of grease on the outside of the plastic container complete the protection against small animals. Each box also contained two thermistor temperature probes lying on the lower terylene netting and connected to a Grant temperature recorder which recorded hourly.

Three tubes of each litter species were collected at each sampling and the litter was removed, weighed fresh and, after respiration measurement, weighed oven-dry (105°C). Respiration was measured as oxygen uptake in a Gilson respirometer at as many different temperatures as time allowed, using successive runs. Oxygen uptake was corrected to NTP. Mean, maximum and minimum values for weight loss against time are shown in Figure 3 for hazel (Corylus avellana L.) during the first year of decomposition by mixed microbial populations in the absence of animals.

The Gilson differential respirometer (Umbreit et al, 1964, pp. 104-105) is one of several recent modifications of the Dixon respirometer (Dixon, 1952, p.6). We have used both types of respirometer during the past six years for measuring the oxygen uptake of soils and decomposing plant material. These respirometers have a number of advantages in this type of work.

MATHEMATICAL TREATMENT OF RESULTS

At the start of the experiment, each tube contained approximately 0.25 g of leaves. Because we have not yet explored the statistical consequences of expressing these results on a "per gram" basis, our initial calculations are on a "per 0.25 g" or "per sample" basis. Temperature/respiration plots like those in Figure 4 were obtained for each of the points in Figure 3. It was evident that most of the relationships were linear, although a few were quadratic. A computer program was written which tested the data for goodness-of-fit of linear and quadratic regressions and also gave the regression constants and coefficients so that the appropriate curve could be fitted. The results for hazel have been used to illustrate the computations, but results for ash (Fraxinus excelsior L.) and hawthorn (Crataegus monogyna Jacq.) are similar. Having obtained the curve equation and fitted the curve, it is a simple matter to take the respiration at any temperature and calculate the probable change in respiration for any change in temperature within the limits of the plot. If curves were fitted for the maximum and minimum points, they would give a good estimate of the limits within which the expected result might fall.

In Figure 4, the different graphs represent samples having different moisture contents which will affect the absolute values for oxygen uptake but will not have much effect on the shape of the plot. The data are being examined for possible temperature/moisture/respiration relationships by multiple regression analysis. In this paper, I will examine the temperature/respiration relationships using a different approach.

A problem often encountered in studies on decomposer organisms is the calculation of total metabolism of soil or litter in the field for a defined period from relatively few field observations and with the aid of laboratory data. As we have a number of plots like those in Figure 4 for the first year of decomposition of litter by microbial populations and we also have almost a year of hourly temperature readings, we calculated the total respiration of the litter during this period. To do this, we took the values for oxygen uptake/sample/hour at the different temperatures and fitted the appropriate regression. We subdivided the long period into shorter periods of a few weeks each, each period being centered on one of the respiration/temperature curves. For each period we calculated the mean temperature. Using this mean temperature, the regression equation, and the number of hours in the period, we calculated the total oxygen uptake for each period. For present purposes we assumed that the RQ = 1.0 and calculated the expected carbon dioxide evolution during the period. From this we obtained the weight of carbon lost by respiration. This we compared with the actual loss of carbon obtained from measurements of dry weight loss. The results of these calculations for hazel and ash litter are given in Table 1. The overall agreement between calculated loss of carbon as carbon dioxide and the actual loss of carbon from weight loss measurements is good over the long period and is generally quite good over the shorter periods. The poor agreement for hazel litter in the period January 4th to March 28th clearly needs further investigation.

Finally, it must be emphasized that these are preliminary findings. More detailed statistical calculations are being done and full details will be published later.

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TABLE 1

Comparison of respiration of litter decomposed by mixed microbial populations in the absence of animals with carbon loss over the period 28th to 372nd day of decomposition

A. hazel (*Corylus avellana* L.) litter

period	total oxygen uptake in period (ml)	calculated weight of carbon in evolved CO_2 if RQ = 1 (mg)	actual carbon loss from litter (mg)
Nov 21 - Jan 3	8.67	4.7	6.1
Jan 4 - Mar 28	9.53	5.1	0.5
Mar 29 - May 2	4.18	2.3	2.3
May 3 - June 13	5.17	2.8	4.9
June 14 - Aug 8	7.40	4.0	3.6
Aug 9 - Oct 31	10.71	5.8	7.2
Nov 21 - Oct 31	45.67	24.6	24.4

B. ash (*Fraxinus excelsior* L.) litter

Nov 21 - Jan 3	9.83	5.3	7.5
Jan 4 - Mar 28	13.29	7.2	10.2
Mar 29 - May 2	7.61	4.1	4.6
May 3 - June 13	9.29	5.0	2.4
June 14 - Aug 8	13.22	7.1	7.4
Aug 9 - Oct 31	12.87	6.9	6.3
Nov 21 - Oct 31	66.11	35.6	38.3

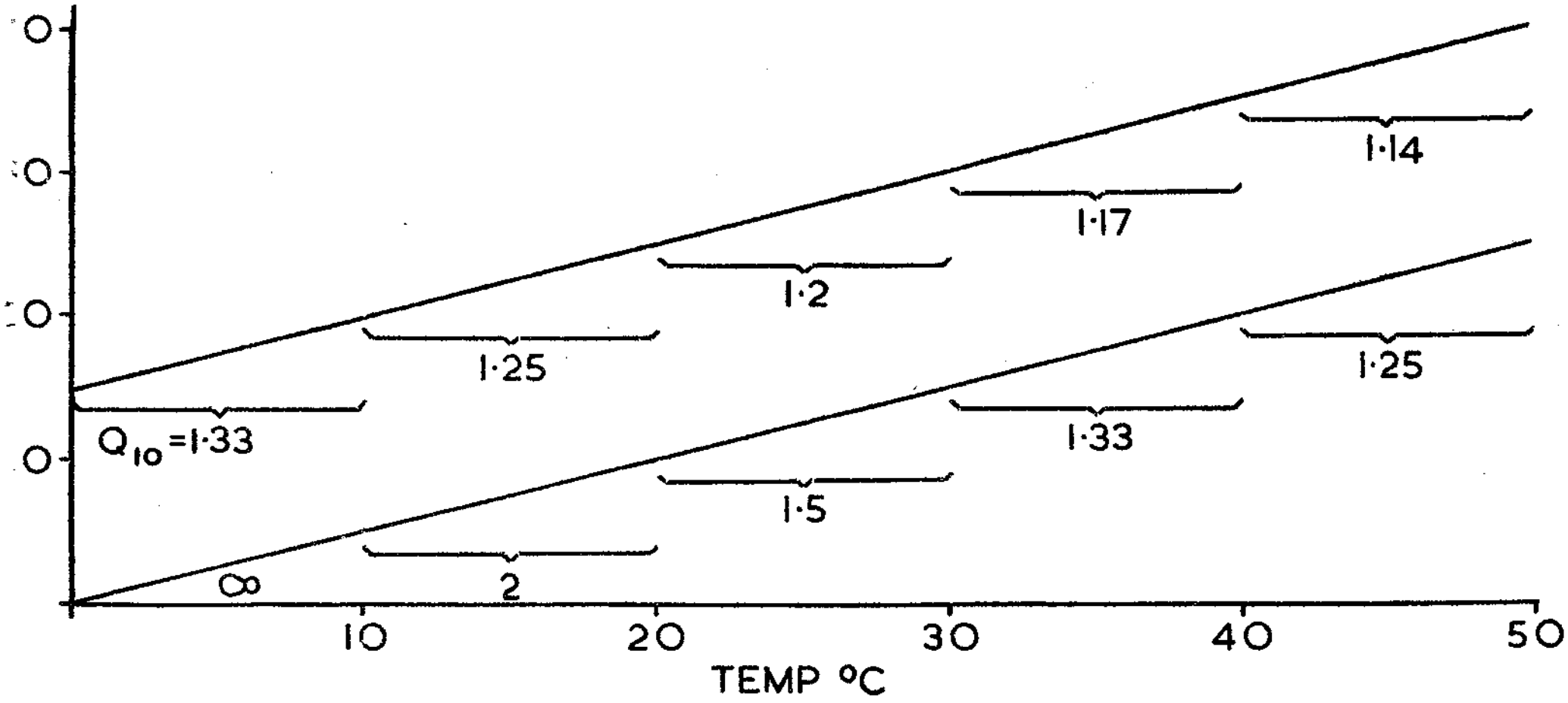

Figure 1. Plots of activity rate against temperature for two sets of arbitrary data having the same change of rate per degree change in temperature over the given temperature range.

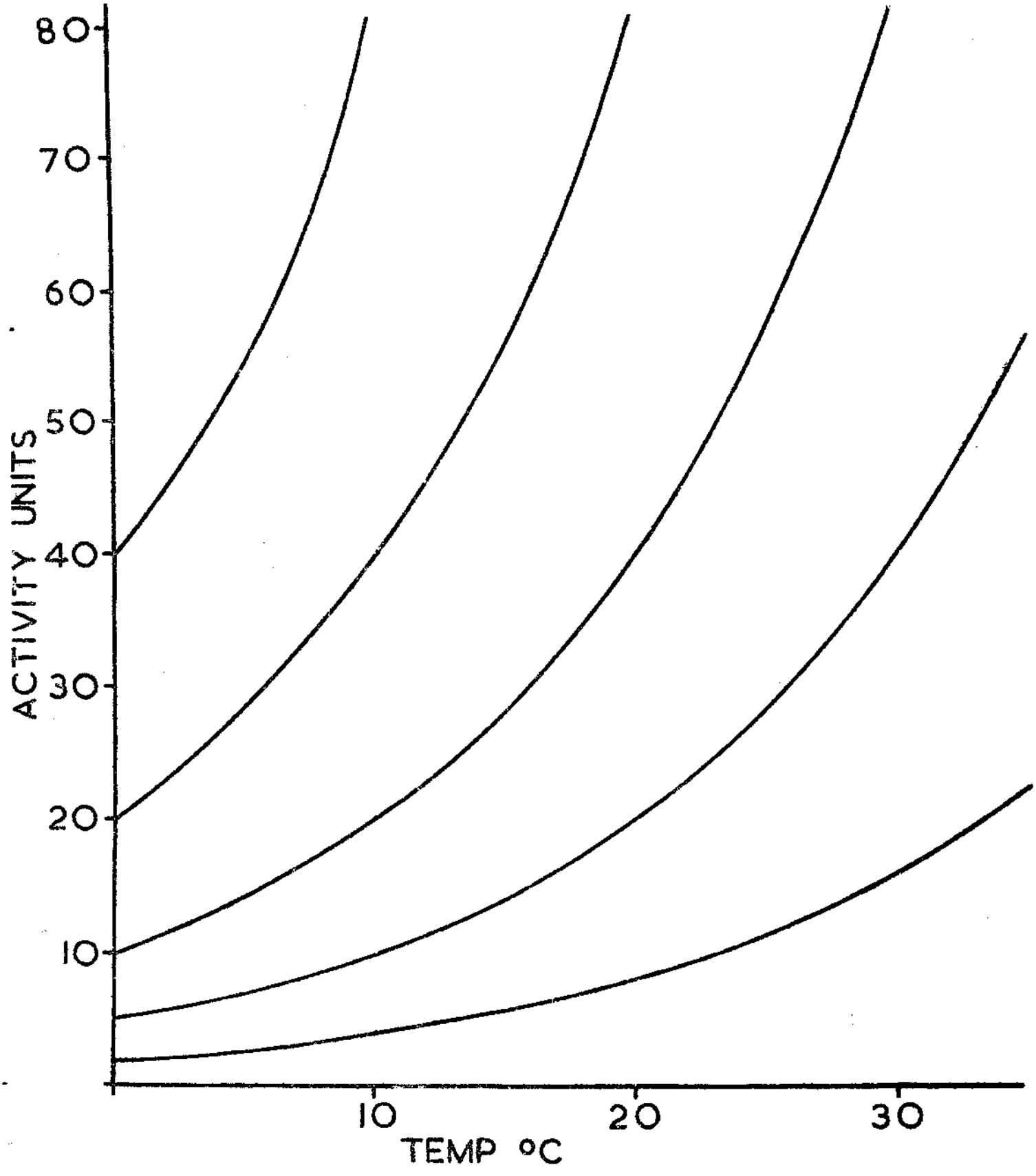

Figure 2. Plots of activity rate against temperature for sets of arbitrary data of Q_{10} = 2.0 over the given temperature range.

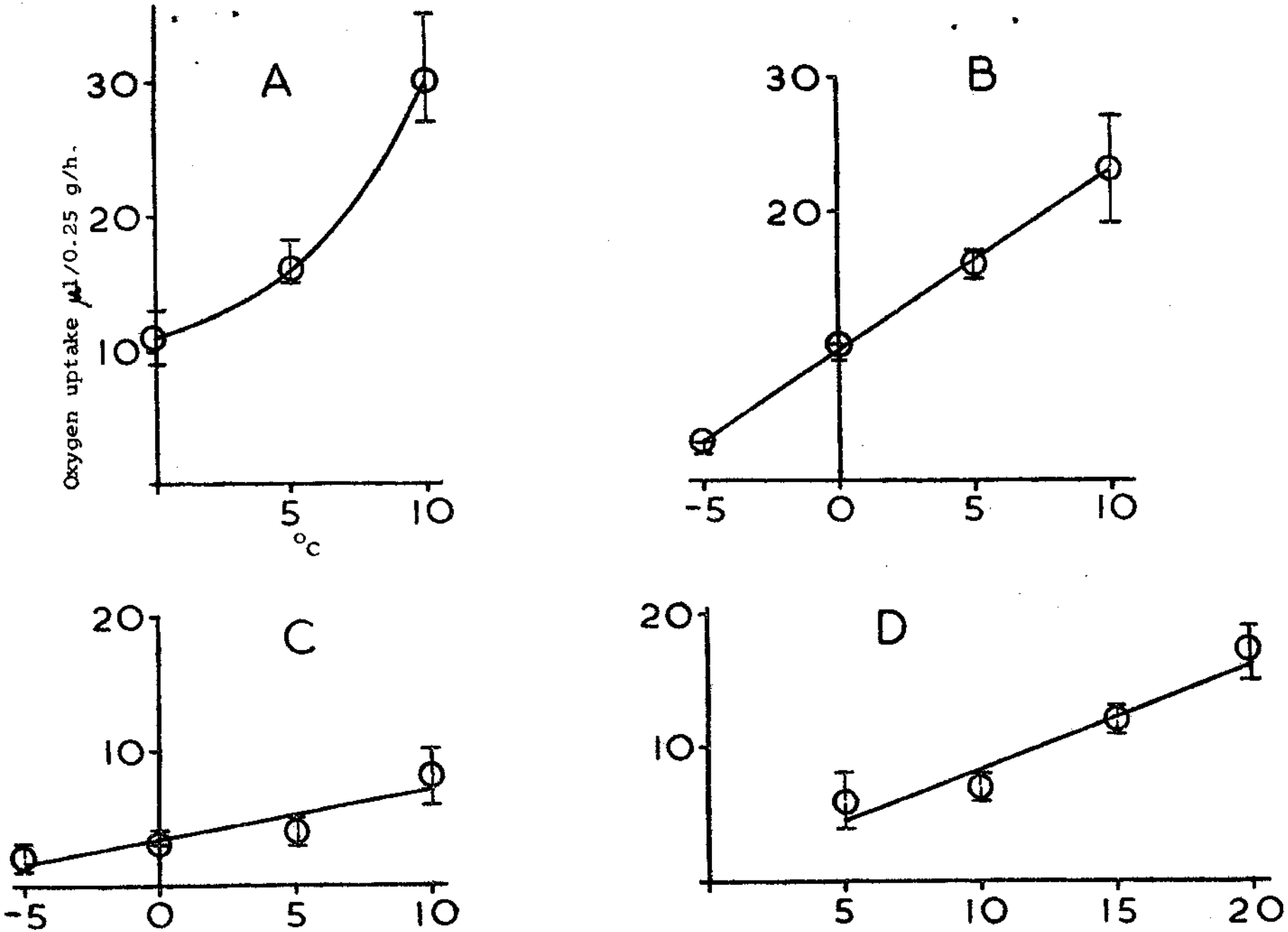

Fig. 4. Plots of mean oxygen uptake against temperature for hazel leaves decomposed by mixed microbial populations in the absence of animals. Maximum and minimum values shown. A = day 14, B = day 71, C = day 155, D = day 372.