Temperature Coefficients in Plant Pathology

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ABSTRACT

Temperature coefficient (Q_{10}) for growth of plant pathogens and other organisms is about 3 below the optimum temperature and 9 above the optimum temperature. Q_{10} is useful or essential in studies of heat inactivation and heat therapy, averages about 100 for these purposes, but differs greatly for different situations, and decreases with increasing temperature. Q_{10} for heat injury to higher plants is usually lower than for inactivation of microorganisms including plant pathogens. Q_{10}'s for heat inactivation of fungi, bacteria, and viruses are not clearly different. The highest Q_{10} observed in this study was about 150 for inactivation of tobacco mosaic virus, and the lowest was 7 for tobacco necrosis virus.

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The effect of temperature on growth of plant pathogens and the development of infections is one of the most studied aspects of plant disease. Togashi (27) brought together the results of 1,767 reports up to 1936, and there have been more since then. A large, but lesser amount of information is available on heat inactivation of pathogens (2, 21) and heat therapy of diseases (19). Most reports of temperature responses fail to consider the Q_{10}. While raw data on temperature responses is essential, the data are often more useful when reduced to constants and generalizations. Temperature coefficient (Q_{10}) is a good example, with wide application in biology (2, 21) but it is rarely used in plant pathology. Q_{10} is the ratio of activity at any temperature to the activity at a temperature 10 C lower. Since the time required for inactivation of pathogens and disease therapy decreases with increasing temperature, the Q_{10} for inactivation and therapy is the ratio of time at any temperature to the time for the same inactivation at a temperature 10 C *higher*. The 10 C interval is arbitrary and standard, and intervals of 5 C (1) and 1 C (17) may be used.

Q_{10} was first applied to chemical and physical reactions and one of the most useful generalizations is Van't Hoff's rule that the Q_{10} is usually 2-3 for chemical reactions. This rule also applies to many biological processes. Some treatments of Q_{10} and related phenomena in biology and methods of calculation are given by Buchanan and Fulmer (3), Belehradek (2) and Precht et al. (21), and in plant pathology by Fawcett (12) and Price (23). Heat of activation (Belehradek, 1935) is another expression of differences in rates due to temperature, but this does not appear to have any advantage over Q_{10} in plant pathology.

This report is confined to growth and inactivation of pathogens and disease as influenced by temperature. Other aspects of plant pathology, such as enzyme activity (28) and fungicidal activity (32) are influenced by temperature and may be expressed by the Q_{10}. I will discuss the calculation, applicability, and significance of Q_{10}, and present representative data, my own as well as those of others, though the coverage of the literature must be only a small fraction of that available. In most cases, the work of others was originally presented as raw data, and the calculations of Q_{10} here are mine.

When plant pathogens, as well as other fungi, bacteria, and viruses are placed at a range of temperatures (e. g., 5 to 35 C) the growth, whether calculated from linear dimensions or as fresh or dry weight, typically increases from about 0 at 5 C to a maximum at about 25 C and then decreases to 0 at about 35 C. In this case, 5, 25, and 35 are the cardinal temperatures. When plotted on arithmetic scales, the data give an approximately straight line ascending from the minimum to the optimum temperature and an approximately straight descending line from the optimum to the maximum temperature for growth (Fig. 1). The straightness of these lines is not established, but is strongly suggested when more temperature values are used [(24), but also (12) and others].

Q_{10} for growth as conventionally calculated (32) for progressive 10 C (or smaller or greater) intervals ranges from infinity to 0 (12), and therefore seems to me of little significance. The weakness of Q_{10} values for such data has also been pointed out by Higarty (16) and Farrell and Rose (11). One expression of the slope of such a response line would be the numerical difference in response divided by the numerical difference in temperature, but this would not be Q_{10} even if the temperature interval was 10 C. Also, it seems improper to calculate Q_{10} values for intervals which include ascending and descending parts of the responsive curve. Furthermore, the use of an exponential equation for data which give a straight line on arithmetic scale may be mathematically incorrect. It can be argued that Q_{10} should not be used for this type of data, but it can be useful if its determination is standardized in a logical manner.

RESULTS.—*Growth*.—I hereby propose that Q_{10} for growth responses be determined from the slope of the growth curve using growth values at 25% and 75% of the maximum growth. These values will be equidistant from the 50% point but still well distant from the 0 and 100% points. For example, in the ascending part of the curve (below the optimum temperature) in Fig. 1, 25% of the maximum growth is at 11 C and 75% is at 21.5 C. Q_{10} for these data is therefore:

$$Q_{10} = \left(\frac{75}{25}\right)^{\frac{10}{21.5-11}} = 2.84.$$

Q_{10} values above the optimum temperature for growth could be expressed as a decimal or fractional value on the logic that Q_{10} is the rate at T (any given temperature) divided by the rate at T − 10 C, or could be considered a negative value on the logic that the slope of the curve is negative, or could be given as a positive value and the position on the curve specified, as is done here. In Fig. 1, the Q_{10} for the values above the optimum then is:

$$Q_{10} = \left(\frac{75}{25}\right)^{\frac{10}{33.5-29}} = 11.51.$$

For this growth curve with an optimum at 26.7 and a range of 29.8, the other useful characters are: the minimum at 5.9 C, the maximum at 35.7 C, Q_{10} (below optimum) 2.84, Q_{10} (above optimum) of 11.5, temperature range below optimum of 19.8, temperature range above optimum of 9, and a ratio of 2.2 for range below and above the optimum temperature. Which of these values or combination of values will be most useful in plant pathology is not easily decided.

On the basis of the data in Table 1, the Q_{10} for microbial growth below the optimum temperature ranges from 2.3 to 4.7 and for growth above the optimum the Q_{10}'s range from 4.8 to 20,000. For reasons given below, Q_{10} values differing greatly from 3 for below the optimum, or from 9 above the optimum are suspect. Errors may be due to difficulty of measurement, inadequate control of temperature, inadequate temperature ranges tested, and inadequate replication.

Growth curves of the response of plant pathogens to temperature show a remarkable similarity in shape, though differing considerably in the position of the optimum temperature. On this basis, Q_{10}'s should also be similar. For a range of 20 C (about the average for most plant pathogens) between the minimum and optimum temperatures for growth, the Q_{10} would be about 3, regardless of the actual values of the minimum and optimum. Similarly, for a range of 10 C (about the average for most pathogens) between the optimum and the maximum temperature for growth, the Q_{10} would be 9. Cochrane (7) gives examples where the temperature range above the optimum is about equal to the temperature range below the optimum, but I regard these as unusual, and they could be due to faulty data.

Inactivation and therapy.—None of the objections to the use of Q_{10} values for growth, apply to inactivation and therapy, but even here Q_{10} is little used by plant pathologists, though much data from which Q_{10} can be calculated has been published.

To determine Q_{10} for therapy, recently inoculated attached leaves were heated at a range of temperatures (40-55 C) and times in a water bath. The rust or mildew was allowed to develop and the incidence of infection counted or rated. From this the ED_{50} (dosage for 50% therapy) in seconds was determined by inspection or interpolation. From ED_{50} values, Q_{10} was calculated as:

$$Q_{10} = \left(\frac{ED_{50} \text{ at } T_1}{ED_{50} \text{ at } T_2}\right)^{\frac{10}{T_2 - T_1}}$$

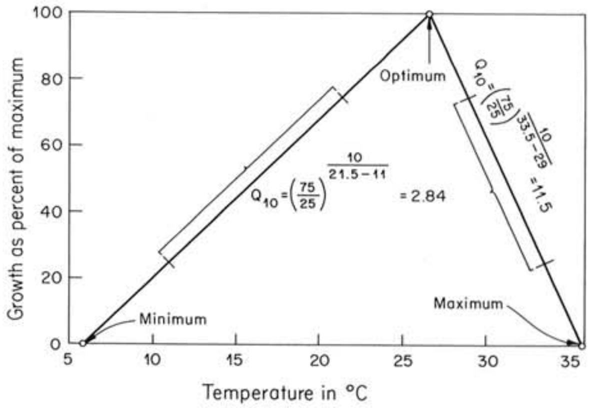

Fig. 1. Temperature response curve as the average of: *Alternaria solani, Botrytis cinerea, Corticium vagum, Gibberella saubinetii, Pythium debaryanum, Rhizopus nigricans, Schizophyllum commune*, and *Verticillium albo-atrum*, as previously presented by Cohen and Yarwood (8).

where T_1 and T_2 are the lower and higher temperatures respectively. For inactivation of virus, pieces of infected leaves were similarly heated, then the tissue was used as inoculum, and ED_{50} and Q_{10} values were calculated as above from the numbers of lesions resulting on indicator hosts.

My results are compared with those of others in Table 2. Q_{10} values for therapy were usually much greater than those for growth (see Table 1). It is not clear that Q_{10}'s for virus inactivation were different from those for fungi, but there were significant differences within each group. Tobacco mosaic inactivation had a much higher Q_{10} than tobacco necrosis virus, as previously noted by Price (22). Q_{10} for bean, cowpea, and cucumber leaves was apparently less than for rust or mildew fungi in these leaves. Many investigators have reported that Q_{10} values decrease with increasing temperature, though usually not as much as indicated by the data from Smith (25) in Table 2. On the other hand, Price (23) reports that for tobacco mosaic virus and tobacco necrosis virus Q_{10} values increase with temperature. I find that Q_{10} decreases with increasing temperature.

DISCUSSION.—With increasing necessity of brevity in publication, Q_{10} values will likely be increasingly used in expressing certain temperature relations. For the growth of pathogens, it seems likely that in most cases the essential facts are the optimum temperature, and the Q_{10}'s below and above the optimum. Since these Q_{10}'s appear to be relatively constant at about 3 and 9 respectively, this leaves the optimum temperature as the major necessary characteristic of growth of mesophiles. Not enough information is available to guess if this also applied to psychrophiles and thermophiles.

Knowledge of Q_{10} values is a clear necessity in studies of heat inactivation or heat therapy over a series of temperatures. For example, if 100 seconds at 40 C is necessary for therapy, then the dosage necessary for therapy at 50 C would be 50 seconds if the Q_{10} was 2, 10 seconds if the Q_{10} was 10, and 1 second if the Q_{10} was 100.

Therapeutic index (TI) is the dose for injury to the host divided by the dosage for therapy of the pathogen. The

TABLE 1. Temperature coefficients (Q_{10}) for growth of representative organisms

Organism	Source of data	Optimum temperature (C)	Temperature coefficient Below optimum	Above optimum
Bacillus ramosus	Ward, 1895 (29)	37	2.8	400
Diplodia natalensis	Fawcett, 1921 (12)	28	2.4	118
Echinodontium tinctorum	Paine, et al., 1962 (20)	22	4.2	54
Humicola stillata	Cooney and Emerson, 1964 (9)	40	3.0	9.0
Neurospora crassa	Ryan, et al., 1943 (24)	35	2.3	21
Phytophthora citrophthora	Fawcett, 1921 (12)	27	3.4	20,000
Phytophthora parasitica	Engelhard, 1974 (10)	32	3.0	38
Rhizopus chinensis	Weimer, et al., 1923 (30)	35	3.0	17
Sclerotium bataticola	Norton, 1953 (18)	35	4.7	20
Septoria apii	Cochran, 1932 (6)	24	3.4	15
Lycopersicum roots	White, 1937 (31)	30	3.5	180
Lepidium roots	Talma, 1918 (26)	27	3.0	39
Erysiphe polygoni on pea	Yarwood, et al., 1954 (33)	25	4.1	79
Sphaerotheca fuliginea on melon	Yarwood, et al., 1954 (33)	28	2.5	40
Average of five thermophilic fungi	Chapman, 1974 (4)	40	4.4	4.8
Average of eight plant pathogenic fungi	Cohen and Yarwood, 1952 (8)	27	2.8	11.5

TABLE 2. Temperature coefficients (Q_{10}) for thermal inactivation and therapy

Organism	Source of data	Representative LD_{50}	Q_{10} average for given temperature range
Six species of bacterial spores	Belehradek, 1935 (2)		5.7 (90-140 C)
Three species of vegetative bacteria	Belehradek, 1935 (2)		59 (48-59 C)
14 spp. of thermophylic fungi	Fergus, 1971 (13)		1500 (59-68 C)
Tobacco mosaic virus	Price, 1939 (22)		750
Tobacco mosaic virus	This study, seven trials	125 sec at 90 C	150 (60-90 C)
Tobacco necrosis virus	Price, 1939 (22)		4
Tobacco necrosis virus	This study, three trials	(50 sec at 75 C)	7.3 (60-90 C)
Alfalfa mosaic virus	Price, 1940 (23)		50 (50-62 C)
Alfalfa mosaic virus	This study, one trial	18 sec at 55 C	22 (55-60 C)
Cucumber mosaic virus	This study, nine trials	20 sec at 55 C	58 (55-60 C)
Citrus tatter leaf virus	This study, eight trials	45 sec at 60 C	56 (55-65 C)
Erysiphe graminis	This study, seven trials	15 sec at 45 C	183 (40-50 C)
Erysiphe polygoni	This study, 12 trials	50 sec at 45 C	56 (40-45 C)
Sphaerotheca fuliginea	This study, 14 trials	78 sec at 45 C	227 (40-55 C)
Puccinia pelargoni zonalis	Grouet, 1965 (14)		3.1 (34-38 C)
Uromyces phaseoli	This study, 30 trials	42 sec at 45 C	110 (35-50 C)
Botrytis cinerea	Smith, 1923 (25)	240 min at 37 C	690 (31-37 C)
Botrytis cinerea	Smith, 1923 (25)	50 sec at 50 C	29 (47-50 C)
Aphelenchoides fragariae	Christie et al., 1935 (5)		110 (38-44 C)
Triticum vulgare, seeds	Groves, 1917 (15)	100 min at 70 C	9 (56-91 C)
Phaseolus vulgaris leaves	This study, 30 trials	14 sec at 55 C	30 (50-60 C)
Vigna sinensis leaves	This study, eight trials	14 sec at 55 C	69 (50-55 C)
Cucumis sativus, cotyledons	This study, 21 trials	16 sec at 55 C	16 (50-55 C)

higher the TI, the greater the margin of safety. Here I take the dosage for 50% inactivation or 50% therapy from Table 2. This 50% point (LD_{50}) is too low for practical therapy and too high for practical tolerance to injury, but is is the most accurately determined value, and it will illustrate the application of Q_{10} to TI. According to data in Table 2, 50% injury to bean and 50% therapy of bean rust would be attained with 2,250 and 450 seconds respectively at 40 C, with 410 and 42 seconds at 45 C, with 75 and 4.1 seconds at 50 C, and with 14 and 0.4 seconds at 55 C. Therefore, the TI would be 5 at 40 C, 9.8 at 45 C, 18 at 50 C, and 35 at 55 C. This greater relative (TI), but smaller absolute (seconds), margin of safety at 55 C than at lower temperatures, would be an advantage to the use of higher temperature for therapeutic treatments, but the short periods at high temperature require a precision of timing which might be difficult to attain in practical agriculture. Also the relatively low TI for heat therapy, in contrast to the high TI with most chemical fungicides, is a major limitation to the use of heat therapy.

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