

SOME BIOLOGICAL AND PHYSICAL CONSTRAINTS TO THE USE OF HEAT AND COLD FOR DISINFESTING AND PRESERVING STORED PRODUCTS

D.E. Evans

CSIRO Division of Entomology, Canberra, Australia

Abstract

Both heat and cold are valuable in disinfesting and preserving stored products but their use may be constrained by the tolerance of the product to be treated and that of the processes or organisms against which treatment is applied. Current knowledge on response to heat and cold is outlined.

Providing that moisture content is not high it appears that very low temperatures (-20°C) or lower can be used with impunity as a means of pest and quality control. Work with convective heating systems that provide good mixing, rapid heating and precise control of temperature permit grain temperatures of at least 60°C to be used to disinfest several major commodities.

Factors such as species, stage of development, acclimation, relative humidity, and rate and manner of temperature change all influence the efficacy of temperature manipulation as a means of pest control. Due to the long exposure periods needed, cold is generally more useful as a means of protecting grain from attack and deterioration than it is as a means of disinfestation, i.e. it is best as a preventative, often used in combination with drying. By contrast, heating can be very rapid and is well suited for disinfestation, i.e. as a curative process.

Although temperature is the more important of the two dosage variables, there is generally considerable flexibility in choosing a combination that will kill insects and yet not damage the product.

The need for further research to fill gaps in our knowledge of response to heat and cold is considered.

Introduction

Low and high temperatures have long been used to disinfest stored grains and like commodities, to protect them from damage by insects, mites and microflora, and to minimize deleterious chemical changes such as those associated with the respiration of the grain itself.

Except where specialised adaptations exist, the thermal limits of insects and other ectotherms usually fall between 0 and 45°C . The lower limit is that at water crystallizes causing cellular dehydration that

results in the collapse of cells, an increase in the concentration of solutes, and irreversible biochemical and physical damage. The upper limit is that at which the chemical components of cells become unstable and are irreparably damaged. Heat death is largely due to the denaturing of intracellular proteins and changes in membrane phospholipids (Bligh *et al.*, 1976). The thermal limits for microflora are considerably broader than those of insects. Lacey *et al.* (1980) indicate a range of at least -10 to 70°C. However, the causes of death are similar.

Within genotypically determined limits, the phenotypic response of a given species to unfavourable temperatures may be influenced, through the process of physiological acclimation, by its recent temperature history. Thus, insects held for a while at 15°C may survive longer when exposed to 0°C, for example, than equivalent insects held at 25°C before exposure to cold. Generally, the lower lethal temperature is changed more by acclimation to cold than is the upper lethal temperature by acclimation to heat. However, in spite of acclimation and, in some species, the occurrence of temperature-tolerant quiescent or diapause stages (Howe, 1962), insects and mites are highly amenable to control by manipulation of the temperature of their environment.

This paper considers some of the biological and physical factors that constrain the usefulness or applicability of cold or heat as means of pest and, to a lesser extent, quality control.

The Response of the Commodity

Storage temperature has a marked influence on the viability and keeping quality of stored seeds (Roberts, 1972; Pomeranz, 1982). Besides providing protection against pests and moulds (see below), cold slows down the respiration of stored grains, thereby minimizing dry matter loss, and prevents deleterious changes such as fat hydrolysis, as manifested by increased levels of free fatty acids. Provided that moisture content is not very high (> 20%), temperatures as low as -29 to -20°C appear to have little or no effect on most cereals (Pomeranz, 1982; Burrell, 1982; Obretenchev, 1983). However, chilling is generally less effective than drying in controlling the rate at which stored cereals deteriorate and, therefore, is best used as an adjunct to rather than a substitute for drying (Burrell, 1982; Pomeranz, 1982).

Sensitivity to high temperatures varies with commodity, cultivar, moisture content and time of exposure, sensitivity being measured in terms of decreased germination, deleterious chemical and biochemical changes and, particularly with large grains, physical damage, such as fissuring and shattering (Hutchinson, 1943; Bakker-Arkema *et al.*, 1977; Nellist, 1980; Pomeranz, 1982).

Much of the conventional wisdom concerning the temperatures to which grain can or cannot be safely heated stems from drying studies and, particularly, everyday drying practice where heating periods are long, mixing of the grain in the heating air is frequently poor, both heating air and grain temperatures typically range from as little as 20°C to 70°C (Nash, 1978; Nellist, 1980)), and moisture contents change by several percent. With convective heating in devices such as

pneumatic conveyors, fluid beds and spouted beds, on the other hand, mixing of the grain in the heating air is good, the difference between the heating air temperature and the grain temperature may be several hundred degrees Celsius, heating periods are short, and little drying occurs (Sutherland *et al.*, in press). Such factors permit grain to be heated to much higher temperatures than would be acceptable in conventional grain drying.

Working with a pneumatic conveyor using heating air temperatures as high as 600°C and having a particle residence time of 1-2 sec, Dzhorogyan (1957a and b) found that, in spite of a 1.3% decrease in moisture content, wheat of up to 18% m.c. could be heated to 60°C without either gluten content or loaf volume being significantly altered. Sutherland *et al.* (1986) also found that wheat of 10.6% m.c. could be heated to 70°C in a pneumatic conveyor without germination being influenced.

In laboratory studies with fluid beds, Ghaly and Taylor (1982) and Ghaly and van der Touw (1982) found that, depending on variety, wheat of 12 and 14% could be heated to at least 70°C for periods greater than those required for disinfestation before the onset of damage to germination and other functional properties. In subsequent field trials with a pilot plant, wheat, barley and oats (moisture contents ca. 11%) were heated to 65 to 70°C with air inlet temperatures of up to 250°C (Sutherland *et al.*, in press). Typical moisture losses were only 0.1 to 0.2% and no damage to germination and other functional properties was detected.

Ghaly and van der Touw (1985) have also shown that paddy of ca. 11% m.c. can be heated to 70-75°C for 5 min, i.e. for much longer than required for disinfestation, without germination and head yield being significantly affected. With paddy of ca. 21% m.c., germination was unaffected by heating to 60°C but head rice yield was greatly reduced. However, subsequent work has shown that intermittent tempering avoids reduction in head yield (Ghaly, unpublished) when paddy is dried from 21 to 14% m.c.

Clearly, much depends on the way the heat is delivered, the level of moisture loss experienced, and the fact that grain can tolerate much more extreme conditions than those required for disinfestation.

The Response of Insects, Mites and Moulds to Temperature

Data on response to temperature can be categorized as that dealing with the role of temperature in determining the limits for and rates of population growth, and that concerned with the acute influence of more extreme temperatures, i.e. temperatures that could be used to disinfest grain rather than to protect it from the consequences of population growth. Response to temperature is frequently modified by prevailing relative humidity or grain moisture content. Accordingly, the influence of moisture content as a limiting factor in the use of cold or heat will be considered concurrently with response to temperature rather than as a separate issue.

1) Population growth and decline

Burges and Burrell (1964) and Howe (1965) present data on minimal and optimal temperatures for population growth. These data are frequently quoted without it being realised the minimal values given represent either the temperatures at which development takes 100 days (Burges and Burrell, 1964) or those at which populations double annually (Howe, 1965). The actual thresholds of development and increase are respectively 3 to 5°C and 2 to 3°C lower than those listed by Howe (1965).

The 'minimal' temperature thresholds given by Howe (1965) range from 24°C for Trogoderma granarium Everts to 7°C for Acarus siro L. The temperature needed to modify population growth clearly depends on the range of species infesting the commodity to be protected, and the degree of modification required i.e. whether or not some increase in numbers is acceptable. A temperature of 10°C either prevents or strongly inhibits population growth in almost all of the insect species considered by Howe (1965) but 0 to 5°C may be needed for certain mites (Smith, 1975) and -7 to 0°C for moulds (Lacey et al., 1980). Because moulds grow quickly, temperatures of 0-5°C should be achieved within 24 hours of the grain being inloaded, the temperature required and subsequent safe storage period depending greatly on the moisture content of the grain (Burrell, 1982; Evans, in press c).

With properly dried commodities, however, such low temperatures may not be necessary, first, because mites and moulds cannot increase at equilibrium relative humidities below 60 to 65% (Howe, 1965; Lacey et al., 1980), and second, the influence of lowered relative humidity interacts synergistically with that of lowered temperature. By demonstrating a linear relationship between intrinsic rate of increase and wet-bulb temperature over much of the physiologically tolerable range, J.M. Desmarchelier (pers. comm.) has shown recently that, when cooling grain by aeration, the temperature required to prevent population growth can be conveniently expressed in terms of a single wet-bulb temperature rather than in several combinations of dry-bulb temperature and relative humidity. With Sitophilus oryzae (L.), for example, temperature:humidity combinations equivalent to a wet-bulb temperature of 9°C prevent increase.

The rate at which insect populations decline at temperatures below the threshold of development may be of practical importance where 'nil tolerance' standards prevail and non-breeding adults, for example, are likely to be found and considered unacceptable. Although oviposition may continue below the threshold of development (Evans, 1982), the rate of decline becomes largely a function of the survival of existing later immature stages and adults. Particularly where temperature falls gradually and acclimation occurs, both adults and immatures may survive long periods at temperatures as much as 10°C below developmental threshold. For example, depending on grain moisture content and species (Table I), adults and immature stages of Cryptolestes ferrugineus (Steph.), Oryzaephilus surinamensis (L.), Rhyzopertha dominica (F.) Sitophilus granarius (L.) S. oryzae and T. castaneum (Herbst) survived laboratory exposures to 9 or 13.5°C for 6 months or longer (Evans, 1983 and in press b). Once again, low relative humidities have a markedly

TABLE I. One percent survival periods (ET₁) for adult grain beetles exposed to 9°C in wheat with an e.r.h. of 70 or 45% (from Evans, 1983).

Temperature regime	% e.r.h.	ET ₁ (weeks)					
		<u>C. ferrugineus</u>	<u>O. surinamensis</u>	<u>R. dominica</u>	<u>S. granarius</u>	<u>S. oryzae</u>	<u>T. castaneum</u>
Constant 30 or 32°C	70	59.8	31.3	31.2	22.9	29.5	44.6
	45	41.5	29.1	29.9	16.1	18.5	41.2
Cooled gradually to 9°C	70	23.2	29.8	11.7	>55	15.8	10.5
	45	15.2	14.4	11.3	23.6	8.7	8.9
Transferred directly from 30 or 32°C to 9°C	70	4.7	10.3	3.9	>55	3.6	2.7
	45	3.4	6.8	3.6	27.8	1.8	2.0

deleterious influence on survival. Mathlein (1961), Stojanovic (1965) and Bahr (1978) provide further well supported data on the extended survival of several species at below threshold but non-freezing temperatures.

The upper values of optimal temperature ranges given by Howe (1965) range from 18°C for Tipnus unicolor (Pill. & Mitt.) (Ptinidae) to 37°C for Trogoderma granarium and Latheticus oryzae Waterh. Temperatures only a few degrees above the optimal range strongly depress population growth. For example, the finite rate of increase of R. dominica in wheat of 14% moisture content falls from 2.14 ♀♀/♀/wk at 34°C to 1.34 ♀♀/♀/wk at 38.2°C and 0 ♀♀/♀/wk at 38.6°C (Birch, 1953). The possibility of using moderately elevated temperatures as a means of modifying population growth has been studied by Kirkpatrick and Tilton (1973), who found that continuous exposure of immature S. oryzae and R. dominica to 30 or 43°C respectively yielded > 99% mortality.

ii) Lethal limits - low temperatures

There is much information on the response of insects and mites to temperatures close to or below 0°C, i.e. those having an acute influence on the survival of individuals rather than the growth of populations (see, for example, Ushatinskaya, 1950; Solomon and Adamson, 1955; Mathlein, 1961; Smith, 1975; Bahr, 1978; Mullen and Arbogast, 1979; Cotton et al., 1982; Obretenchev, 1983). The data stems both from 'overwintering' experiments in field, domestic and storage environments of varied climatic severity and from laboratory experiments. Regrettably, interpretation is difficult because the information is frequently fragmentary, often confounded by factors such as rate of cooling, grain moisture content and acclimation, and sometimes not supported by descriptions of experimental methods.

To illustrate the relationship between survival and temperature, data for some of the more cold tolerant species, i.e. O. surinamensis, S. granarius, Plodia interpunctella (Hb.) and Ephestia kuehniella (Zell.) (Solomon and Adamson, 1955) are given in Table II. They show that, although exposure to -18°C for < 1 day is fatal for these species, all but O. surinamensis can survive for some months at 0°C. Sinha (1964) has shown that the mites A. siro and Glycyphagus destructor (Schr.) may survive for more than 7 days at -18°C. Resistance to cold in both insects and mites is generally greatest with high equilibrium relative humidities (see, for example, Solomon and Adamson, 1955).

iii) Lethal limits - high temperatures

Information on susceptibility to temperatures of 45°C and above is again scattered and fragmentary. Data from the few studies that involve response to a wide range of constant temperatures are summarised in Table III.

Examples of the fragmentary data are: S. oryzae and S. granarius adults killed in 180 and 30 min at 49 and 54°C respectively (Back and Cotton, 1924); Tribolium confusum J. du V. adults killed in 60 and 15 min at 50 and 55°C respectively (Knipling and Sullivan, 1958); R. dominica adults killed in 3 min at 63°C and S. oryzae adults killed in

TABLE II. Periods required to kill several species of grain insect exposed to cold.

Species	Exposure period (days)			Source
	-18°C	-10°C	0°C	
<u>O. surinamensis</u>	<1	3	26	1
	1	3	21	3
	0.5	-	22	4
<u>S. granarius</u>	<1	12	73	1
	0.2	7.5	70	2
<u>P. interpunctella</u>	<1	6.5	>90	1
<u>E. kuehniella</u>	<1	5.5	>116	1

1. Cotton *et al.* (1950); all stages.
2. Solomon and Adamson (1955); adults only.
3. Obretchenchev (1983); all stages.
4. Solenov in 3; adults only.
- not reported.

3 min at ca. 52°C (Dendy and Elkington, 1920); *R. dominica* in sorghum killed in 15 min at 55°C (Pruthi, 1946). Sheppard (1984) provides further examples in the context of heat sterilization of mills and processing plants. Relative humidity has little or no influence at such temperatures (Kono, 1943).

Studies evaluating the efficacy of various forms of heating grains, such as infrared (e.g. Tilton and Schroeder, 1963), microwave (e.g. Kirkpatrick, 1975), conduction (e.g. Winterbottom, 1922) and convection (e.g. Sutherland, *et al.*, in press) seldom provide useful information on intrinsic heat tolerance. Heating period and exposure period are inevitably confounded in such investigations and the time for which a given 'lethal' temperature prevailed can seldom be determined. Nevertheless, evaluations of this type do show that first, modern heating techniques can give very quick kills of insects, e.g. 1-2 s in a pneumatic conveyor (Dzhorogyan, 1957a, b) and, second, insect and/or grain temperatures of at least 60°C must be achieved when heating periods are short, i.e. less than 60 s, say, and the grain is not held at such temperatures before cooling.

Information on the influence of high temperatures on moulds is scanty but Dzhorogyan (1955) reported a 3-8 fold reduction in "microorganisms" in wheat of 16% m.c. heated in a pneumatic conveyor. No reduction was observed with grain of 13% m.c. Jindal and Obaldo (1986) noted reduced mould levels in paddy heated to 69 and 88°C, for about 8 and 6 minutes respectively, in a rotary dryer.

TABLE III. Periods required to kill several species of grain insect exposed to constant high temperatures achieved in an oven or pneumatic conveyor.

Species	Exposure needed for 100% mortality (min)					Stages	Source	
	45°	48°	50°	55°	60°C			
<u>S. granarius</u>	300	60	55	10	2	All	1	
<u>S. granarius</u>)			50-52°	55°	60°C			
<u>S. oryzae</u>)			35-45	0	0	All	2	
		50°	60°	70°	80°	90°	100°C	
<u>S. oryzae</u>	70	3.5	1.75	0.83	0.58	0.5	Adult	3
	120	16.0	7.0	4.0	2.5	1.0	Larva in grain	4
		50°	55°	60°	65°	70°C		
<u>O. surinamensis</u>	3.08	1.58	0.63	0.37	0.17	Adult	5	

1. Dzhorogyan, 1965 (own data and those of several authors) : oven
2. Dzhorogyan, 1957 : pneumatic conveyor
3. Tsuchiya, 1943 : oven
4. Tsuchiya and Kosaka, 1943 : oven
5. Obretenchev, 1983 : oven

Differences Between and Within Species

As has been shown, differences in the way species respond to cold and heat may be manifested in many ways, e.g. rates of increase and survival at acutely unfavourable temperatures. Ability to overwinter in cold climates (see, for example, Solomon and Adamson, 1955; Mathlein, 1961) shows that C. ferrugineus, S. granarius, O. surinamensis, P. interpunctella and E. kuehniella are amongst the most cold hardy of insects and, by virtue of surviving brief exposures to > 60°C, R. dominica amongst the most heat tolerant (Tilton and Schroeder, 1963; Dermott and Evans, 1978). However, the 'observed' ranking of species in terms of their cold tolerance, for example, may sometimes differ from that 'expected'. For example, in laboratory studies on the survival of adults, Stojanovic (1965) found R. dominica exposed to -0.5 to 15°C consistently outlived S. oryzae, and Evans (1983) found that both O. surinamensis and S. granarius lived longer than C. ferrugineus when all were cooled gradually to 9°C (Table I).

Such results indicate the advisability of using more than one population, or strain, of a given species when determining its performance or comparing it with that of other species.

Populations of a given species can differ subtly in their response to temperature (Satomi, 1960; Nowosielski-Slepowron et al., 1968; Evans, 1977a, 1979, 1981a), but, apart from the finding of Bahr (1978) that O. surinamensis from East Germany were more cold-tolerant than those from Burma, there is little to suggest that such differences are more than random variations correlated with factors such as body weight.

Developmental Age

Tolerance to both cold and heat varies with the developmental age of the insect exposed.

Ushatinskaya (1950) found that the eggs of S. granarius were less cold tolerant than the pupae and larvae, the former being more tolerant than the latter. However, Howe and Hole (1968) reported that young eggs, prepupae and pupae of S. granarius were less tolerant of cold (15°C) than larvae. Smith (1970) and David et al. (1977) respectively demonstrated the same trend in C. ferrugineus and in S. granarius, S. oryzae and R. dominica. By contrast, Ushatinskaya (1950) showed that the cold tolerance of S. oryzae developmental stages differed with the temperature to which they were exposed, eggs being the most tolerant of -15°C. On balance (Ushatinskaya, 1950; Mathlein, 1966; Bahr, 1978; Evans, 1981 and in press), it appears that adults are more cold-tolerant than the immature stages (but see Ushatinskaya, 1950; Smith 1970; David et al., 1977).

The influence of temperatures close to the lower developmental threshold can also be important. For example, Howe and Hole (1968) showed that the longevity and fecundity of S. granarius exposed to cold (15°C) as prepupae and pupae are greatly reduced. This can greatly influence subsequent rates of increase (Evans, 1977a).

The studies of Tilton and Schroeder (1963) and Evans (1981a) demonstrate that the later developmental stages are more tolerant to heat than the early stages. Evans' experiments, for example, show that the LT_{99.9} for 0-35 day old R. dominica immatures exposed to 80°C is about 12% greater than that of 0-7 day immatures. In S. oryzae and O. surinamensis, at least, adults are more tolerant than larvae (Tsuchiya, 1943; Tsuchiya and Kosaka, 1943; Obretenchev, 1983).

Acclimation

Cold acclimation has been demonstrated in stored grain pests in terms of changed survival at low temperatures, chill-coma temperature, locomotor activity and dispersal, respiration rate, susceptibility to fumigants, enzyme kinetics and other biochemical changes (see Evans, 1981b). These manifestations embrace both 'resistance' and 'capacity' acclimation, i.e. changes to both the limits for and rates of processes (Prosser, 1973).

Perhaps the most striking demonstration of increased survival is that of Smith (1970), who found that cold-acclimated C. ferrugineus could survive exposure to -12°C for >4 weeks. Current views on the biochemical mechanisms that confer tolerance to such sub-zero temperatures are given by Baust and Rojas (1985) and Storey and Storey (1983). Increasingly, it appears that a given species may have two or more 'antifreezes' of both low and high molecular weights.

Even where sub-zero temperatures are not achieved, acclimation can considerably extend the period for which both adult and immature insects can survive (David et al., 1977; Evans, 1980, 1983, in press b). Increased survival is manifested even in species such as T. castaneum and R. dominica (Table 1), which are generally regarded as being cold-susceptible (Solomon and Adamson, 1955).

A practical implication of such findings is that rapid cooling that does not permit acclimation to occur is likely to be more effective than slow cooling.

Although Gonen (1977) showed that warm-acclimation increased the longevity of S. granarius exposed to 40°C , there is little evidence to suggest that acclimation has any practical significance when insects are raised to temperatures of 60°C or greater, i.e. those employed in rapid disinfestation. For example, the LT_{50} s of cold-acclimated R. dominica and S. oryzae differed by only 2% from those of warm acclimated individuals when both categories were exposed to air of 80°C in a fluid bed (Evans, 1981a).

Dispersal and Migration

Navarro and Calderon (1982), Armitage and Stables (1984), and Elder and Ghaly (1984) have noted that insects may alter their spatial dispersion within or even leave ventilated grain bulks. Rapid and even cooling would presumably counter such movements to some extent and guard against aggregation in warmer pockets of grain. Treatment with an insecticide could also be appropriate when insects aggregate at the warmest upper surface of an 'upwards' aerated grain mass.

Some Physical Factors

The rate at which an appropriate dosage of 'cold' or 'heat' is delivered can markedly influence both the perceived and biological efficacy of cooling and heating. Mullen and Arbogast (1979), for example, have shown that both the dimensions and consistency of packaged commodities have a marked influence on the time taken for the commodity to reach a desired temperature. On a larger scale, Bahr (1978) reports increased overwintering of Tribolium species, R. dominica and S. oryzae in East Germany since 'self-insulating' grain bulks of a thousand or more tonnes have come into use.

At the other end of the scale, studies with infrared (Tilton and Schroeder, 1963) microwave (Tilton and Vardell, 1984) and convective heating (Evans, in press a) have shown that rate of heating can influence

not only the time needed for disinfestation but the mortality achieved, in the latter case, even when a constant grain temperature results (Evans, in press a).

Grain moisture content can also be important in that it influences both rate of cooling and rate of heating (Evans, 1981a).

Discussion

i) The effective use of cold and heat

The effective use of cold and heat depends on a sound understanding of the tolerances of both the commodity to be protected and the agents that cause it to deteriorate during storage. This review has shown, first, that the response elicited depends on both the temperature experienced and the time for which it prevails and, second, that the response may vary with factors such as the process or species to be controlled, age-structure, acclimation, dispersal, moisture content or relative humidity, and rate and manner of cooling or heating.

With cereals, at least, it appears that even very low temperatures (-20°C or lower) can be used with impunity as a means of pest and quality control. Work with convective heating systems that provide good mixing, rapid heating and precise control of temperature permit grain temperatures of at least 60°C to be used to disinfest several major commodities.

Due to the relatively long exposure periods required, cold is generally more useful as a means of protecting grain from attack by pests and of arresting processes of deterioration than it is as a means of disinfestation, i.e. it is more effective as a preventative than as a curative measure. It is often best used subsequent to or in conjunction with drying or, even, an insecticide (Desmarchelier *et al.*, 1979). By contrast, heating can be very rapid and is well suited to use as a disinfestation or curative process. On the other hand, it has no residual effect and must be coupled with other processes, such as cooling or physical exclusion, where long-term protection is required.

Temperature manipulation is essentially a simple procedure. Once the 'tolerance envelope' of the commodity is known, it can be used in a variety of ways to suit prevailing technical and economic constraints. For example, heat disinfestation requires only that all particles of a given batch of infested grain are heated to an appropriate lethal temperature:time combination. Although temperature is the more important variable, there is considerable flexibility in choosing a combination that will kill insects and yet not damage the grain.

ii) The relationship between response and lethal temperatures

The relationship between the exposure needed to yield a certain level of mortality (LT₉₉ etc.) and temperature frequently resembles a hyperbola and can be described by equations such as $T(t - c) = k$ or $T \cdot t^k = C$ or, more easily, their linear equivalents, where T = exposure period, t = temperature and c , k and C are constants not presumed to

have biological meaning (Kono, 1943; Tsuchiya and Kosaka, 1943; Dermott and Evans, 1978; Mullen and Arbogast, 1979). Where a wide range of temperatures is employed, a series of such relationships may prevail, each having different values for the various constants (Tsuchiya and Kosaka, 1943; Evans, in press a). Hence, although such equations provide useful, empirical tools in describing results and planning experiments, they must be used with caution in extrapolating likely responses or likely lethal temperatures.

The tolerance of cold and heat within populations appears to be normally distributed in that plots of probit response x exposure period, for example, provide best fit when exposure period is not transformed to logarithms (Kono, 1943; Wadley, 1949; Evans, 1977b, 1981). Although often needing to be based on data for many insects, probit analysis is valuable in that it allows the distribution of tolerances within a population to be measured as well as permitting estimation of the exposures or temperatures corresponding to specific levels of mortality. Such information can be useful in considering whether tolerance distributions change with time.

Where serial observations are used to determine the survival of a given cohort of insects over time, the methods of Bliss (1937) and Sampford (1952) may be used to estimate mean survival time and its confidence limits.

iii) The need for further research

From the research view point, this review shows that our knowledge of response to temperature is often fragmentary and that the methods used to study this response are sometimes far from rigorous. There is need, for example, to consider experimental protocols such as numbers and/or types of organisms to be exposed, rates of cooling and heating, and methods of and periods of assessment, besides the mathematical procedures employed to analyse data and to describe relationships. The use of broader experimental domains than is required for immediate practical purposes would contribute greatly to our understanding of the processes and relationships involved.

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