THE CONTROL OF STORED-PRODUCT INSECTS AND MITES WITH EXTREME TEMPERATURES*

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Abstract—Heating or cooling is used extensively to control stored-product insect and mite pests. For most stored-product insects 25–33°C is optimal for growth and reproduction, at 13–25 or at 33–35°C insects are able to complete their development and produce offspring, but <13 or >35°C insects eventually die. The more extreme the temperature the more quickly insects die, with death occurring in a few minutes at −20 or 55°C. Lethal temperatures vary considerably and depend on species, stage of development, acclimation, and relative humidity. Extensive tables listing the survival of the major stored-product insects and mites at extreme temperatures from over 50 papers is presented. There are many ways to cool the commodity: turning, aeration or refrigerated aeration, or to heat the commodity: infrared, microwaves, high frequency irradiation, or hot air in fluidized-bed. Some of these processes are available commercially, while others have been tested only in the laboratory.

The proposed behavioral, physiological, and biochemical mechanisms that enable stored-product insects to survive extreme temperatures are reviewed. Possible synergists that might make stored-product insects more susceptible to extreme temperatures are suggested. One example is the use of ice-nucleating active bacteria to increase the supercooling points of insects, thereby making them less cold-hardy. The supercooling points of four beetles has been measured and compared to published data for other stored-product insects. A standard protocol for examining the survival of stored-product insects at extreme temperatures is outlined.

INTRODUCTION

In the last 50 yr the story of insect control has been written predominantly by chemists and toxicologists. The stunning successes of the organochlorines and organophosphates in the 1950s led to a dramatic increase in the number and quantity of insecticides used in agriculture (Ware, 1983). There has been a movement away from chemical control of insects in the last 15 yr because of two basic problems (Huffaker, 1980). One, insecticides are usually toxic to more species than those they are intended to control. Insecticides often kill predators and parasites that reduce insect pest populations. Also, insecticides can be toxic to fish, birds, or mammals. The deregistration in 1984 of the liquid fumigants for controlling stored-product insects in Canada and the U.S.A. is a recent example of society's concerns about toxic residues on food. Secondly, the continued use of a single insecticide or class of insecticides often leads to resistance within insect populations. In extreme cases the insecticide can no longer be used because it does not control the insect pest. This is the case for malathion and stored-product insects in Australia where widespread resistance to malathion required the replacement of this insecticide 16 yr after it was first introduced as a grain protectant (Collins and Wilson, 1986).

The challenge of controlling insect pests with a minimum of chemical insecticides has led to the development of integrated pest management strategies. There are several methods to reduce the amount of insecticide applied; baited insecticides, treatments synchronized with pest populations, resistant plants, biological control, mass trapping, insect growth regulators, cultural control or physical control, and many are currently being used against field crop pests (Huffaker, 1980). Several of these techniques have been used effectively to control stored-product pests (Evans, 1987a) and their implementation has been facilitated because the storage environment is largely determined by man.

One technique that is not readily applicable to field insect pests, but has been used successfully for many years against stored-product pests, is the use of extreme temperatures. As early as the 16th century high temperature was used as a means to control the moth *Sitotroga cerealella*

Table 1. The response of stored-product insects to temperature*

Zone	Temp. (°C)	Effect
Lethal	50–60	death in minutes
	45	death in hours
Suboptimum	35	development stops
	33–35	development slows
Optimum	25–33	maximum rate of development
Suboptimum	13–25	development slows
	13–20	development stops
Lethal	5	death in days (unacclimated), movement stops
	−10–5	death in weeks to months (acclimated)
	−25 to −15	death in minutes, insects freeze

*Species, stage of development and moisture content of food will influence the response to temperature.

(Oliver) in France (Oosthuizen, 1935). There are three temperature zones for any organism: optimum, where the species' fitness is greatest rate of development, number of offspring; suboptimum, where temperatures are above or below the optimum zone but where species can still complete their life cycle; lethal, where temperatures are above or below the suboptimum zone and kill the organism over time. Table 1 describes these zones for stored-product insects.

To describe situations that have fluctuating temperatures, Turnock *et al.* (1983) have further divided the cold lethal zone into three zones: cold-injury, where cold-injury occurs and cannot be repaired; neutral, where cold-injury does not occur and cannot be repaired; active, where cold-injury does not occur but can be repaired. This hypothesis has not been tested using stored-product insects, as most work with stored-product insects has used single temperature exposures rather than fluctuating temperatures.

The purpose of this paper is to (1) review the research on the use of extreme temperatures to control stored-product insects, (2) review the mechanisms by which insects survive extreme temperatures and suggest ways that insects could be made more susceptible to extreme temperatures, and (3) suggest standard protocols for examining the effects of extreme temperature on insects.

Low Temperature: Suboptimum

Lowering the grain temperature below the optimum will reduce damage caused by insects, mites, and molds (Longstaff, 1981; Flinn and Hagstrum, 1990). Howe (1965) did an extensive review of the minimum temperatures and humidities that insects needed to double their numbers annually. Grain held at 20°C will stop the development of most stored-product insects, the most important exception being *Sitophilus granarius* (Linnaeus) which can complete its development at 15°C. To prevent mites from developing on damp grain, temperatures must be lowered to 2°C. However, on grain at moisture contents of 13%, the minimum temperature is 6°C (Burges and Burrell, 1964). Low temperature can help to prevent grain from becoming moldy before it can be dried (Burrell and Laundon, 1967). However, temperatures as low as −23°C did not reduce mold populations in feed (Brown and Hill, 1984).

Low Temperature: Lethal

There are over 30 papers examining the survival of stored-product insects and mites at temperatures below their developmental thresholds (Tables 2–5). There are basically two types of studies, those that report laboratory experiments on low temperature survival (Tables 2–4), and those that report survival at low temperatures in the field (Table 5). The laboratory studies are easier to replicate and they can be used to examine single factors in isolation, but they can only approximate field conditions. Field experiments are a much better estimate of what is happening in the field, but they take much longer and require considerable resources. Since conditions vary from year to year and place to place, comparisons are often difficult.

Temperature, duration of exposure, species, stage of development, acclimation, relative humidity, and gender determine the survival of insects at low temperature. It is useful to know the general relationship between time and temperature to design experiments, to develop computer models and to suggest possible cold-injury mechanisms. The relationship between the time necessary to kill a given percentage of the population (y-axis) and temperature (x-axis) is usually a concave (j-shaped)

curve (Solomon and Adamson, 1955; Mullen and Arbogast, 1979; Evans, 1987c; Fig. 1). Occasionally, straight-line relationships are reported. In some cases this is probably due to the narrow range of temperatures used (e.g. Nowosielski-Slepowron et al., 1968), and a wider range of temperatures would probably yield a concave curve. In other cases, data taken from a number of studies may produce a straight line because of significant differences in protocols [Fig. 1, *Cryptolestes ferrugineus* (Stephens), unacclimated]. Finally, there are a few species that the temperature–mortality relationships is neither a concave nor straight curve (Stratil and Reichmuth, 1984; data in Table 3).

The relationship between mortality (y-axis) and time (x-axis) at a given temperature is usually sigmoidal (Nagel and Shepard, 1934; Sømme, 1968a; Evans, 1983; Turnock et al., 1983; Evans, 1987c). Probit analysis is often used to determine the lethal time for 50, 95, or 99% of the population, and produces variance estimates (fiducial limits) that can be used to compare tests. Unfortunately, these are rarely reported, perhaps because they often have wide ranges. Caution should be used when using probit analysis because all mortality vs time data are not sigmoidal (Robinson, 1926; Evans, 1983, 1987b). Also, extrapolating beyond the range of values that are actually covered by the experiment is tenuous.

Different species have different capacities to survive low temperatures (Tables 2–4). It is difficult to make comparisons between studies because of the differences in acclimation, temperatures, and durations used to test cold-survival. To avoid these problems several studies have examined the cold-tolerance of many species under the same conditions (Table 5). There is a general concurrence between these studies. The most cold-susceptible species are *Tribolium castaneum* (Herbst), *Tribolium confusum* Jacquelin du Val, and *Oryzaephilus mercator* (Fauvel). The most cold-tolerant insects are *Trogoderma granarium* (Everts), *S. granarius*, and the stored-product Lepidoptera, *Ephestia elutella* (Hübner), *E. kuehniella* (Zeller), and *Plodia interpunctella* (Hübner), with the rest of the species falling in between these extremes. With the correct tests and enough insects one could probably list all the species from most to least cold-susceptible with each species being significantly different from the other. However, that is not possible using data from Tables 2–4 because different studies rarely have used the same conditions, and often do not use probit analysis with fiducial limits.

These results also pose a dilemma for explaining the abundance of stored-product pests in the Canadian Prairies, the world's grain-growing area with the coldest winters. If cold plays a major role in the population dynamics in the Canadian Prairies, one would expect a preponderance of cold-hardy species. This is not the case. *Tribolium castaneum*, one of the most cold-susceptible stored-product insects, is the second most common species in grain stored on Canadian Prairie farms (Madrid et al., 1990). The most common stored-product insect pest is *C. ferrugineus*, a relatively cold-hardy insect. Yet the other cold-hardy insects, such as *Trogoderma granarium*, *S. granarius*, *P. interpunctella*, *E. elutella*, and *E. kuehniella*, are generally absent. Although this is predictable for the Lepidoptera exposed to extremely low temperatures at the top surface of the grain (Bell, 1983), it does not explain the absence of the other cold-hardy species. Therefore, cold-tolerance alone is not a good predictor of stored-product species occurrence or abundance in cold temperate climates.

The stage of development is also an important factor in determining an individual insect's cold-tolerance (Nagel and Shepard, 1934; Howe and Hole, 1968; Smith, 1970; David et al., 1977; Evans, 1983, 1987b; data in Tables 2 and 3). Temperate insects usually overwinter in diapause in one particular stage (Tauber et al., 1985) that is more cold-hardy than the other stages (Danks, 1978). Since few stored-product insect pests have a diapausing stage that would be considered *a priori* the most cold-tolerant stage, all developmental stages must be tested to determine the most cold-hardy one. An exception is the Pyralidae which diapause as prepupae and diapause increases their cold-tolerance (Cox, 1987; data in Table 3). Eggs are usually the most cold-susceptible stage. Susceptibility varies greatly with the age of the egg, with young and old eggs being the least cold-hardy (Watters, 1966; Cline, 1970; Daumal et al., 1974; Jacob and Flemming, 1986; Johnson and Wofford, 1991; data in Tables 2 and 3). The larva is the most cold-tolerant stage for *Rhyzopertha dominica* (Fabricius) and *Sitophilus oryzae* (Linnaeus) (David et al., 1977). The adult is the most cold-tolerant stage for *C. ferrugineus* (Smith, 1970) and *Tribolium confusum* (Nagel and Sheppard, 1934). For *S. granarius*, certain larval stages are as cold-hardy as the adults (Howe and

Table 2. A review of the survival of stored-product beetles at low temperatures under laboratory conditions

Reference	Stage[1]	Strain[2]	Acclimation[3]	r.h.[4]	Temp.[5] (°C)	Percent survival (duration of exposure in days)[6]
Callosobruchus maculatus (F.)						
Mullen and Arbogast (1979)[7]	e (12 h)	L	27°	?	5	50 (4.2), 5 (7.2)
					0	50 (1.5), 5 (5.0)
					−5	50 (0.6), 5 (1.7)
					−10	5 (1.3)
					−15	5 (0.2)
Cryptolestes ferrugineus (Steph.)						
Mathlein (1961)	a	?	"room", 6°/7 d	?	0	3 (45), 0 (60)
					−2	27 (25)
					−4	26 (20), 10 (26)
					−5	1 (28), 0 (30)
Smith (1970)[7]	e	L	30°	70	2	50 (5.3)
					−6	50 (0.6)
					−12	50 (0.5)
	l (1–2 d)	L	30°	70	2	50 (5.0)
					−6	50 (1.4)
					−12	50 (0.1)
	l (10–17 d)	L	30°	70	2	50 (8.6)
					−6	50 (2.7)
					−12	50 (0.8)
	p	L	30°	70	2	50 (8.8)
					−6	50 (1.4)
					−12	50 (0.3)
	a (7–21 d)	L	30°	70	2	50 (15.3)
					−6	50 (3.5)
					−12	50 (0.6)
			30°	70	−6	52 (3)
			30°, 15°/1 d	70	−6	98 (3), 21 (5)
			30°, 15°/3 d	70	−6	100 (3), 24 (5)
			30°, 15°/7 d	70	−6	99 (3), 25 (5), 3 (9)
			30°, 15°/14 d	70	−6	98 (3), 83 (5), 46 (9), 35 (14)
			30°, 15°/21 d	70	−6	100 (3), 98 (5), 98 (9), 91 (14), 79 (21), 56 (28), 13 (35)
			30°	70	−12	0 (5), 0 (9)
			30°, 15°/17 d	70	−12	33 (5), 31 (9), 19 (14)
			30°, 15°/14 d	70	−12	80 (5), 41 (9), 41 (14)
			30°, 15°/20 d	70	−12	76 (14), 77 (22), 51 (28)
			30°, 15°/28 d	70	−12	75 (14), 74 (22), 61 (28)
Evans (1983)[7]	a	?	32°	70	9	50 (7), 1 (33)
			32°	45	9	50 (11), 1 (24)
			32° to 13.5°/28 d, (4.5°/7 d)	70	13.5	50 (265), 1 (>364)
			32° to 13.5°/28 d, (4.5°/7 d)	45	13.5	50 (144), 1 (294)
			32° to 9°/35 d, (4.5°/7 d)	70	9	50 (75), 1 (162)
			32° to 9°/35 d, (4.5°/7 d)	45	9	50 (52), 1 (106)
Barker (1990)[7]	l, p	L	30°	75	15	50 (18), 1 (245)
					10	50 (12), 1 (335)
					5	50 (12), 1 (43)
					0	50 (10), 1 (30)
					−5	5 (7), 0 (14)

Reference	Stage	Dev.	Temperature	RH (%) / m.c.	(35, 75 and 88)	Test temp (°C)	Mortality % (exposure, d)
Kawamoto et al. (1990)	a (0–7 d)	L	30°[8]	70		15	100 (7), 100 (35), 100 (70), 99 (175), 97 (224), 91 (175), 87 (224)
			30°[8]	70		10	100 (7), 99 (35), 98 (70), 97 (105), 95 (140), 83 (49), 56 (77)
			30°, 15°/21 d	70		0	100 (7), 100 (14), 100 (21), 98 (28), 94 (42), 13 (49)
			30°, 15°/21 d	70		−9	100 (7), 94 (14), 71 (21), 60 (28), 34 (42), 99 (42)
			30°	70		15	100 (7), 99 (14), 99 (21), 99 (28), 6 (35), 4 (42)
Khan (1990)[8]	a (28 d)	?				10	67 (7), 28 (14), 13 (21), 16 (28), 7 (35), 5 (42)
						5	84 (7), 59 (14), 28 (21), 8 (28), 1 (35), 1 (42)
						0	56 (7), 20 (14), 16 (21)
				70		0	95 (7), 94 (14), 91 (21), 50 (28), 38 (35), 31 (42), 28 (49), 26 (56)
				70		0	94 (7), 86 (21), 85 (28), 84 (35), 79 (42), 44 (49), 42 (56), 42 (63)
							36 (70), 28 (77)
Fields (1990)[7]	a (7–28 d)	L	30°/7 d, 15°/7 d	70		0	96 (7), 95 (14), 94 (21), 53 (28), 44 (35), 39 (42), 34 (49), 0 (56)
			30°/7 d, 15°/14 d	70		0	90 (7), 90 (14), 86 (21), 74 (28), 0 (35), 0 (42), 0 (49), 0 (56)
			30°/7 d, 15°/21 d	70		0	94 (7), 94 (14), 92 (21), 54 (28), 0 (35), 0 (42), 0 (49)
			field 20 to 15°/Oct.–Nov.	16 m		−10	50 (5), 5 (10)
			field 20 to 15°/Oct.–Nov.	14 m		−10	50 (6), 5 (11)
			field 20 to 15°/Oct.–Nov.	12 m		−10	50 (5), 5 (11)
			field 20 to −2°/Oct.–Feb.	16 m		−10	50 (40), 5 (73)
			field 20 to −2°/Oct.–Feb.	14 m		−10	50 (30), 5 (76)
			field 20 to −2°/Oct.–Feb.	12 m		−10	50 (24), 5 (38)
Cryptolestes pusillus (Sch.) Williams (1954)	e	?	25°		35, 75 and 88	2	62 (1), 26 (2), 15 (3), 7 (4)
	l (1)	?	25°			2	61 (2.5)
	l (2)	?	25°			2	83 (2.5)
	l (3)	?	25°			2	80 (2.5)
	l (4)	?	25°			2	93 (2.5)
	p	?	25°			2	98 (2.5)
	a		25°			2	95 (1), 80 (2), 67 (2.5), 39 (3), 13 (4)
Lasioderma serricorne (F.) Childs et al. (1970)	1 (3)	?	21.1°/1 d, 15.6°/4 d	75		4.4	100 (0), 60 (7), 20 (14), 0 (21), 40 (42)
						7.2	90 (9), 90 (7), 20 (14), 0 (21), 30 (56)
						10	100 (0), 70 (14), 60 (28), 20 (35), 70 (49), 70 (63)
							70 (70)
	1 (4)	?	21.1°/1 d, 15.6°/4 d	75		4.4	100 (0), 100 (7), 50 (14), 0 (21), 0 (35), 0 (35)
						7.2	100 (0), 100 (7), 90 (14), 20 (21), 90 (42)
						10	100 (0), 100 (14), 100 (28), 100 (35), 100 (49), 80 (63), 80 (70)
Mullen and Arbogast (1979)[7]	e (12 h)	L	27°	?	35, 75 and 88	5	50 (3.8), 5 (12.1)
						0	50 (2.5), 5 (9.2)
						−5	50 (1.0), 5 (4.4)
						−10	50 (0.2)
Oryzaephilus surinamensis (L.) Mathlein (1961)	a	?	room°, 6°/7 d	?		−2	5 (21), 0 (25)
						−5	0 (20)
						−5.5	3 (10), 0 (15)
Mullen and Arbogast (1979)[7]	e (12 h)	L	27°	?		5	50 (1.0), 5 (2.9)
						0	50 (0.3), 5 (0.6)
						−5	50 (0.3), 5 (0.6)
						−10	5 (0.6)
Evans (1983)[7]	a (0–7)	?	32°	70		9	50 (19), 1 (72)
				45		9	50 (11), 1 (48)
			32° to 13.5°/28 d, (4.5°/7 d)	70		13.5	50 (221), 1 (>350)
				45		13.5	50 (117), 1 (278)
			32° to 9°/35 d, (4.5°/7 d)	70		9	50 (99), 1 (209)
				45		9	50 (55), 1 (101)

Table 2—continued

Reference	Stage[1]	Strain[2]	Acclimation[3]	r.h.[4]	Temp.[5] (°C)	Percent survival (duration of exposure in days)[6]
Jacob and Fleming (1986)	e (0–1 d)	L	25°	70	5	25 (1) 25 (2) 5 (3) 0 (4) 40 (5) 50 (6) 30 (7) 15 (8) 10 (9)
					10	92 (1) 67 (2) 57 (3) 67 (4) 88 (5) 48 (6) 67 (7) 52 (8) 46 (9)
					15	2 (10) 2 (11) 2 (12) 0 (13) 7 (14) 2 (15) 0 (16)
	e (1–2 d)	L	25°	70	5	80 (1) 36 (2) 0 (3) 90 (4) 92 (5) 75 (6) 87 (7) 30 (8) 37 (9)
					10	95 (1) 100 (2) 92 (3) 77 (4) 83 (5) 60 (6) 52 (7) 26 (8) 12 (9)
					15	23 (10) 23 (11) 5 (12) 0 (13) 17 (14) 27 (15) 10 (16)
	e (0–1 d)	L	25°	20	5	71 (1) 29 (2) 0 (3) 37 (4) 26 (5) 19 (6) 4 (7) 0 (8)
					10	89 (1) 52 (2) 33 (3) 13 (4) 17 (5) 27 (6) 10 (7) 3 (8) 3 (9)
					15	57 (1) 40 (2) 50 (3) 0 (10)
	e (1–2 d)	L	25°	20	5	35 (1) 81 (2) 89 (3) 70 (4) 56 (5) 44 (6) 19 (7) 12 (8) 0 (9)
					10	100 (1) 100 (2) 100 (3) 93 (4) 47 (5) 3 (6) 7 (7) 0 (8)
					15	100 (1)
Evans (1987b)	e, l, p	L	32° to 13.5°/28 d, (4.5°/7 d)	11m	13.5	1 (91) 0 (182) 1 (273) 1 (364)
			32° to 9°/35 d, (4.5°/7 d)		9	0 (91) 0 (182) 0 (273) 0 (364)
Rhyzopertha dominica (F.) Mathlein (1961)	a	F	room°, 13°/7 d	70	5	21 (21)
			room°, 13°/7 d	70	1.2	0 (18)
			room°, 13°/25 d	70	1.7	60 (5)
			room°, 13°/35 d	70	−1.5	28 (10)
Stojanovic (1965)	a	?	25°, 20 to 18°/20 d	12m	11	50 (47) 10 (68)
				14m	11	50 (47) 10 (68)
				17m	11	50 (47) 10 (68)
				12m	0.5	50 (20) 10 (27)
				14m	4.5	50 (20) 10 (27)
				17m	4.5	50 (20) 10 (30)
				12m	0.5	50 (6) 10 (8)
				14m	0.5	50 (6) 10 (8)
				17m	0.5	50 (7) 10 (8)
				17m	0.5	10 (11)
Swain (1975)	a	?	?	?	−5	50 (0.03) 0 (0.40)
					−10	0 (0.16)
					−12	0 (0.13)
					−18	0 (0.04)
			?, starved for 48 h	?	−5	50 (0.00) 0 (0.11)
					−10	0 (0.06)
					−12	0 (0.04)
					−18	0 (0.02)
David et al. (1977)	e	F	27°	13.2m	4.4	1 (14) 0 (28) 0 (42)
		L	27°	13.2m	4.4	1 (14) 0 (28) 0 (42)
	l (7–10 d)	F	27°	13.2m	4.4	26 (14) 0 (28) 0 (42)
		L	27°	13.2m	4.4	8 (14) 0 (28) 0 (42)
	l (14–17 d)	F	27°	13.2m	4.4	3 (14) 0 (28) 0 (42)
		L	27°	13.2m	4.4	1 (14) 0 (28) 0 (42)
	l (21–24 d)	F	27°	13.2m	4.4	16 (14) 0 (28) 0 (42)
		L	27°	13.2m	4.4	16 (14) 0 (28) 0 (42)

Reference	Stage	F/L	Temperature regime	RH	Value	Data columns (% (d))						
	a (7–14 d)	F	27°	13.2m	4.4	1 (14)	0 (28)	0 (42)				
		L	27°	13.2m	4.4	2 (14)	0 (28)	0 (42)				
	e	F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	0 (14)	0 (28)	0 (42)				
		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	1 (14)	0 (28)	0 (42)				
	l (7–10 d)	F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	38 (14)	7 (28)	0 (42)				
		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	42 (14)	1 (28)	0 (42)				
	l (14–17 d)	F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	15 (14)	2 (28)	0 (42)				
		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	37 (14)	1 (28)	0 (42)				
	l (21–24 d)	F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	56 (14)	9 (28)	0 (42)				
		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	77 (14)	18 (28)	0 (42)				
	a (7–14 d)	F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	54 (14)	6 (28)	0 (42)				
		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	39 (14)	8 (28)	0 (42)				
Evans (1983)[7]	a	?	32°	70	9	50 (13)	1 (27)					
			32° to 13.5°/28 d, (4.5°/7 d)	70	9	50 (12)	1 (25)					
				45	13.5	50 (158)	1 (337)					
Jay (1984)	e, l, p	?	32° to 9°/35 d, (4.5°/7 d)	70	13.5	50 (90)	1 (165)					
				45	9	50 (57)	1 (82)					
			26.7°	60	15.4	50 (54)	1 (79)					
Evans (1987b)	e, l, p	L	32° to 13.5°/28 d, (4.5°/7 d)	11m	10	75 (7)	46 (14)	24 (28)				
			32° to 9°/35 d, (4.5°/7 d)		4.4	83 (7)	26 (14)	11 (28)				
					1.7	36 (7)	5 (14)	0 (28)	0 (364)			
					13.5	27 (7)	1 (14)	0 (28)	0 (364)			
Khan (1990)[8]	a (28 d)	?	30°	70	9	100 (7)	100 (14)	99 (21)	98 (28)	98 (35)	98 (42)	
					15	93 (7)	65 (14)	25 (21)	10 (28)	1 (35)	0 (42)	
					10	98 (7)	78 (14)	45 (21)	18 (28)	8 (35)	2 (42)	
					5	68 (7)	32 (14)	1 (21)	0 (28)	0 (35)	0 (42)	
			30°/7 d, 20°/7 d, 10°/7 d	70	0	98 (7)	98 (14)	98 (21)	90 (28)	28 (35)	0 (42)	
			30° to 5°/42 d, (5°/7 d)		0	99 (7)	97 (14)	97 (21)	97 (28)	97 (35)	97 (42)	70 (49)
			30°/7 d, 15°/7 d		0	90 (7)	80 (14)	70 (21)	53 (28)	0 (35)	32 (42)	54 (49)
			30°/7 d, 15°/14 d		0	96 (7)	96 (14)	96 (12)	96 (28)	74 (35)	86 (42)	41 (56)
			30°/7 d, 15°/21 d		0	100 (7)	100 (14)	100 (21)	100 (28)	96 (35)		13 (63)
Sitophilus granarius (L.)												
Back and Cotton (1924)	a	?	?	?	12.8	0 (873)						
					5.8	0 (105)						
					3	0 (111)						
					0	0 (73)						
					−2.5	0 (46)						
					−5	0 (33)						
					−8	0 (14)						
					−15	0 (0.3)						
					−17.8	0 (0.2)						
Robinson (1926)[7]	a	?	27 to 18°	13.5m	1.6	50 (16)	0 (37)					
				13.5m	−1.1	50 (11)	0 (23)					
				13.5m	−6.6	50 (2)	0 (4)					
				17.2m	−12.2	50 (0.8)	0 (3)					
				13.5m	−12.2	50 (5)						
Mathlein (1961)	e	F	room°, 9°/2 d, 5°/2 d	13.5m	5	0 (60)						
					0	0 (40)						

Table 2—continued

Reference	Stage[1]	Strain[2]	Acclimation[3]	r.h.[4]	Temp.[5] (°C)	Percent survival (duration of exposure in days)[6]
	e, l, p.	F	room[c], 9°/2 d, 5°/2 d	13.5m	−2.5	0 (15) 3 (100)
					−5.5	0 (10) 0 (50)
					5	11 (59) 0 (30)
					−2.5	1 (40)
					−5.5	2 (20)
					5	0 (15)
	a (7–42 d)	F	room[c], 13°/7 d	13.5m	5	92 (18)
			room[c], 13°/7 d	13.5m	1.2	82 (10)
			room[c], 13°/25 d	13.5m	1.7	99 (5)
			room[c], 13°/35 d	13.5m	−1.5	99 (10)
	a (7–42 d)	F	room[c], 9°/2 d, 5°/2 d	13.5m	0	0 (85) 2 (80) 2 (90)
					−2.5	17 (70) 10 (35) 3 (40)
					−5	25 (30) 0 (30) 1 (45)
					−6.5	1 (28)
Stojanovic (1965)	a	?	25°, 20 to 18°/20 d	12m	11	50 (32) 10 (60)
				14m	11	50 (42) 35 (70)
				17m	11	50 (52) 35 (70)
				12m	4.5	50 (16) 10 (32)
				14m	4.5	50 (34) 10 (50)
				17m	4.5	50 (41) 10 (56)
				12m	0.5	50 (18) 10 (26)
				14m	0.5	50 (20) 10 (37)
				17m	0.5	50 (29) 10 (40)
Howe and Hole (1968)	e	L	25°	70	15	59 (42) 42 (56)
	1 (1)				15	90 (56)
	1 (2)				15	95 (56)
	1 (3)				15	72 (56)
	1 (4)				15	32 (56)
	p				15	78 (56)
	a				15	92 (56)
	1 (7–14 d)				15	86 (35) 95 (42) 92 (49) 96 (56)
	1 (14–21 d)				15	88 (35) 90 (42) 75 (49) 65 (56)
	1 (21–28 d)				15	60 (35) 42 (42) 26 (49) 29 (56)
	p (28–35 d)				15	77 (35) 77 (49) 87 (56)
David et al. (1977)	c	F	27°	13.2m	4.4	16 (14) 1 (28) 0 (42)
	1 (7–10 d)	L	27°	13.2m	4.4	5 (14) 0 (28) 0 (42)
		F	27°	13.2m	4.4	4 (14) 0 (28) 0 (42)
	1 (14–17 d)	L	27°	13.2m	4.4	0 (14) 4 (28) 1 (42)
		F	27°	13.2m	4.4	38 (14) 3 (28) 0 (42)
	1 (21–24 d)	L	27°	13.2m	4.4	37 (14) 25 (28) 10 (42)
		F	27°	13.2m	4.4	64 (14) 11 (28) 5 (42)
	a (7–14 d)	L	27°	13.2m	4.4	53 (14) 78 (28) 2 (42)
		F	27°	13.2m	4.4	93 (14) 4 (28) 0 (42)
	c	F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	34 (14) 0 (28) 0 (42)
		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	24 (14) 6 (28)
	1 (7–10 d)	F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	80 (14) 45 (28) 46 (42)
		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	68 (14) 33 (28) 28 (42)

Reference	Stage		Temperature	RH / m.c.	°C				
Evans (1983)	l (14–17 d)	F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	82 (14)	54 (28)	75 (42)	
	l (21–24 d)	L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	97 (14)	76 (28)	83 (42)	
		F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	38 (14)	16 (28)	14 (42)	
	a (7–14 d)	F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	100 (14)	17 (28)	12 (42)	
		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	86 (14)	91 (28)	91 (42)	
	a	?	30°	70	9	50 (263)	26 (28)	16 (42)	
Evans (1987b)	e, l, p	L	30° to 13.5°/28 d, (4.5°/7 d)	45	9	50 (36)	1 (195)		
			30° to 9°/28 d, (4.5°/7 d)	70	13.5	50 (281)	1 (>385)		
			30° to 13.5°/28 d, (4.5°/7 d)	45	13.5	50 (155)	1 (329)		
			30° to 9°/35 d, (4.5°/7 d)	70	9	50 (200)	1 (>385)		
				45	9	50 (52)	1 (165)		
				11m	13.5	19 (91)	5 (182)	3 (273)	0 (364)
				11m	9	24 (91)	3 (182)	0 (273)	0 (364)
Sitophilus oryzae (L.)									
Back and Cotton (1924)	a	?	?						
Robinson (1926)[7]	a	?	27 to 18°	13.5m	12.8	0 (558)	50 (19)	0 (15)	
				13.5m	5.8	0 (80)	50 (4)	0 (7)	
				8.4m	3	0 (18)	50 (2.5)	0 (8.4)	
				13.5m	0	0 (8)	50 (4)	0 (14)	
				16.0m	−2.5	0 (8)	50 (5)	0 (16)	
				19.6m	−5	0 (3)	50 (6)	0 (20)	
				13.5m	−8	0 (3)	50 (0.4)	0 (0.6)	
				13.5m	−15	0 (0.2)	50 (0.1)	0 (0.1)	
					−17.8	0 (0.2)			
Stojanovic (1965)	a	?	25°, 20 to 18°/20 d	12m	11	50 (29)	10 (35)		
				14m	11	50 (35)	10 (42)		
				17m	11	50 (37)	10 (42)		
				12m	4.5	50 (10)	10 (14)		
				14m	4.5	50 (11)	10 (21)		
				17m	4.5	50 (16)	10 (28)		
				12m	0.5	50 (3)	10 (4)		
				14m	0.5	50 (3)	10 (5)		
				17m	0.5	50 (4)	10 (6)		
David et al. (1977)	e	F	27°	13.2m	4.4	0 (14)	0 (28)	0 (42)	
		L	27°	13.2m	4.4	0 (14)	0 (28)	0 (42)	
	l (7–10 d)	F	27°	13.2m	4.4	0 (14)	0 (28)	0 (42)	
		L	27°	13.2m	4.4	2 (14)	0 (28)	0 (42)	
	l (14–17 d)	F	27°	13.2m	4.4	1 (14)	0 (28)	0 (42)	
		L	27°	13.2m	4.4	20 (14)	2 (28)	0 (42)	
	l (21–24 d)	F	27°	13.2m	4.4	26 (14)	1 (28)	0 (42)	
		L	27°	13.2m	4.4	1 (14)	0 (28)	0 (42)	
	a (7–10 d)	F	27°	13.2m	4.4	0 (14)	0 (28)	0 (42)	
		L	27°	13.2m	4.4	0 (14)	0 (28)	0 (42)	

Table 2—continued

Reference	Stage[1]	Strain[2]	Acclimation[3]	r.h.[4]	Temp.[5] (°C)	Percent survival (duration of exposure in days)[6]			
	e	F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	5 (14)	0 (28)	0 (42)	
1 (7–10 d)		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	1 (14)	0 (28)	0 (42)	
		F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	56 (14)	6 (28)	3 (42)	
1 (14–17 d)		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	35 (14)	2 (28)	1 (42)	
		F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	84 (14)	53 (28)	26 (42)	
1 (21–24 d)		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	83 (14)	48 (28)	37 (42)	
		F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	30 (14)	3 (28)	1 (42)	
a (7–14 d)		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	27 (14)	2 (28)	1 (42)	
		F	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	4 (14)	0 (28)	0 (42)	
		L	21°/3 d, 15°/7 d, 10°/7 d	13.2m	4.4	6 (14)	0 (28)	0 (42)	
Evans (1983)[7]	a	?	30°	70	9	50 (9)	1 (25)		
				45	9	50 (6)	1 (13)		
			30° to 13.5°/28 d, (4.5°/7 d)	70	13.5	50 (274)	1 (>364)		
				45	13.5	50 (74)	1 (371)		
			30° to 9°/35 d, (4.5°/7 d)	70	9	50 (62)	1 (111)		
				45	9	50 (39)	1 (61)		
Evans (1987b)	e, l, p	L	30° to 13.5°/28 d, (4.5°/7 d)	11m	13.5	22 (91)	5 (182)	0 (273)	0 (364)
			30° to 9°/35 d, (4.5°/7 d)	11m	9	8 (91)	3 (182)	0 (273)	0 (364)
Tribolium castaneum (Hbst.) Nowosielski *et al.* (1968)	a (14–21 d)	L	27°	70	−3.5	50 (0.5)	0 (28)		
					−5	50 (0.1)	0 (28)		
					−6.5	50 (0.1)	0 (28)		
Smith (1974)	1 (late)	?	21°/7 d, 15.6°/7 d, 10°/7	?	3	34 (7)	2 (14)	0 (21)	
	a	?	21°/7 d, 15.6°/7 d, 10°/7 d	?	3	86 (7)	25 (14)	5 (21)	
Mullen and Arbogast (1979)[7]	e (12 h)	L	27°		5	50 (1.3)	5 (2.4)	0 (28)	
					0	50 (0.3)	5 (0.8)		
					−5	50 (0.3)	5 (0.8)		
Evans (1983)	a	?	32°	70	9	50 (6)	1 (7)		
				45	9	50 (5)	1 (14)		
			32° to 13.5°/28 d, (4.5°/7 d)	70	13.5	50 (115)	1 (194)		
				45	13.5	50 (8)	1 (140)		
			32° to 9°/35 d, (4.5°/7 d)	70	9	50 (49)	1 (74)		
				45	9	50 (43)	1 (62)		
Evans (1987)	e, l, p	L	32° to 13.5°/28 d, (4.5°/7 d)	11m	13.5	1 (91)	0 (182)	0 (273)	0 (364)
			32° to 9°/35 d, (4.5°/7 d)		9	0 (91)	0 (182)	0 (273)	0 (364)
Tribolium confusum Duv. Nagel and Shepard (1934)[7]	e (1 d)	?	27°	6 or 50 or 74	12	50 (5)	0 (12)		
					7	50 (2)	0 (9)		
					0	50 (0.2)	0 (0.5)		
					−4	50 (0.1)	0 (0.4)		
					−6		0 (0.3)		
					−12		0 (0.4)		
	e (3 d)	?	27°	6 or 50 or 74	12	50 (11)	0 (22)		
					7	50 (9)	0 (18)		
					−4	50 (0.1)	0 (0.3)		
					−6	50 (0.1)	0 (0.3)		
					−12	50 (0.1)	0 (0.5)		

Reference	Stage[1]	Strain[2]	Temp. before exposure[3]	RH (6 or 50 or 74)[4]	Low temp.[5]	Survival (%) (period, d)[6]			
	e (5.5 d)	?	27	74	12	50 (7)	0 (13)		
					7	50 (5)	0 (12)		
					−6	50 (0.2)	0 (0.5)		
					−12	50 (0.1)	0 (0.3)		
	l (1)	?	27	74	7	50 (6)	0 (12)		
					−6	50 (0.4)	0 (0.7)		
	l (3)	?	27	74	7	50 (6)	0 (10)		
					−6	50 (0.4)	0 (0.7)		
	l (6)	?	27	74	7	50 (8)	0 (22)		
					−6	50 (0.5)	0 (0.7)		
	p	?	27	74	7	50 (11)	0 (18)		
	a (30–150 d)	?	27	74	7	50 (14)	0 (22)		
					−6	50 (0.3)	0 (1)		
					−12		0 (0.1)		
Edwards (1958)[7]	a (male)	L	38	75	−3	50 (2)	58 (1)		
	a (female)	L	38	75	−3	50 (1)	88 (1)		
	a (male)	L	30	75	−3	50 (2)	79 (1)		
	a (female)	L	30	75	−3	50 (1)	100 (1)		
	a (male)	L	18	75	−3	50 (4)	92 (1)		
	a (female)	L	18	75	−3	50 (4)	88 (1)		
Nowosielski et al. (1968)	a (14–21 d)	L	27	70	−3.5	50 (1.7)			
					−5	50 (0.3)			
Watters (1966)	e (1–2 h)	L	28	70	10	58 (1)	0 (5)	0 (10)	0 (15)
					5	88 (1)	0 (5)	0 (10)	0 (15)
	e (1 d)	L	28	70	10	79 (1)	58 (5)	0 (10)	0 (15)
					5	100 (1)	67 (5)	0 (10)	0 (15)
	e (3 d)	L	28	70	10	92 (1)	79 (5)	88 (10)	79 (15)
					5	88 (1)	63 (5)	25 (10)	0 (15)
Somme (1968a)	a	L	27	?	0	85 (2)	49 (3)	18 (4)	5 (5)
	a	L	27, 12°/4 d	?	0	91 (3)	82 (4)	40 (6)	8 (8)
Trogoderma granarium (Everts)									
Mathlein (1961)	l	?	room, 10°/4 d, 4°/2 d	?	−2	99 (120)	55 (180)		
	l	?	room, 10°/4 d, 4°/2 d	?	−5	77 (90)			
	1	?	room, 4°/2 d, −5°/2 d	?	−10	2 (30)	0 (10)		
	1	?	room, 4°/2 d, −5°/2 d	?	−19	33 (5)	0 (15)		

[1] e = egg, l = larva with the instar given in parentheses, pp = prepupa, p = pupa, a = adult, age for a given stage in parentheses.
[2] L = strain that has been in the laboratory for > 2 yr, F = field strain.
[3] Temperature conditions before exposure to low temperature.
[4] Relative humidity in percent or if followed by an "m" the moisture content in percent.
[5] Low temperature that insects were exposed to.
[6] Usually, survival was estimated by hatching for eggs, movement for larvae or adults and emergence of adults for late instars or pupae, duration given in days except when followed by an "m" for minutes, or "h" for hours.
[7] Probit analysis.
[8] Same set of individuals used throughout the exposure period.

Table 3. A review of the survival of stored-product moths at low temperature, under laboratory conditions

Reference	Stage[1]	Strain[2]	Acclimation[3]	r.h.[4]	Temp.[5] (°C)	Percent survival (duration of exposure in days)[6]
Ephestia cautella (Wlk.) Mullen and Arbogast (1979)[7]	e (12 h)	L	27	?	5	50 (4.6) 5 (8.0)
					0	50 (0.2) 5 (0.8)
					−5	50 (0.2) 5 (0.7)
					−10	5 (0.6)
					−15	5 (0.4)
Stratil and Reichmuth (1984)	e (1 d)	L	20	75	2	50 (0.2) 10 (3)
					5	50 (1.5) 10 (6)
					8	50 (4.5) 10 (8)
					11	50 (6.0) 10 (12)
					14	50 (8.0) 10 (15)
	e (2 d)	L	20	75	2	50 (0.5) 10 (5)
					5	50 (2.5) 10 (6)
					8	50 (4.0) 10 (8)
					11	50 (6.0) 10 (11)
					14	50 (8.0) 10 (15)
	e (3 d)	L	20	75	2	50 (0.5) 10 (6)
					5	50 (4.0) 10 (11)
					8	50 (5.0) 10 (11)
					11	50 (6.0) 10 (11)
					14	50 (7.0) 10 (12)
	e (4 d)	L	20	75	2	50 (0.5) 10 (4)
					5	50 (4.0) 10 (12)
					8	50 (5.0) 10 (8)
					11	50 (6.0) 10 (9)
	e (5 d)	L	20	75	2	50 (0.5) 10 (4)
					5	50 (3.0) 10 (7)
					8	50 (3.0) 10 (7)
					11	50 (3.0) 10 (6)
	e (6 d)	L	20	75	2	50 (0.5) 10 (3)
					5	50 (3.5) 10 (8)
					8	50 (5.0) 10 (12)
Ephestia elutella (Hüb.) Stratil and Reichmuth (1984)	e (1 d)	L	20	75	2	50 (3) 10 (11)
					5	50 (7) 10 (12)
					8	50 (12) 10 (28)
					11	50 (18) 10 (41)
	e (2 d)	L	20	75	2	50 (7) 10 (14)
					5	50 (11) 10 (18)
					8	50 (13) 10 (25)
					11	50 (17) 10 (36)
	e (3 d)	L	20	75	2	50 (2) 10 (8)
					5	50 (10) 10 (21)
					8	50 (14) 10 (25)
					11	50 (12) 10 (28)
	e (4 d)	L	20	75	2	50 (3) 10 (15)
					5	50 (12) 10 (28)
					8	50 (13) 10 (22)
					11	50 (11) 10 (24)

Species / Reference	Stage	Dev.	Temp	RH	Conditioning	Exp. (°C)	Survival % (n)
Ephestia kuehniella Zell. Mathlein (1961)	e (5 d)	L	20°	75		2	50 (7); 10 (20)
						5	50 (12); 10 (27)
						8	50 (8); 10 (17)
						11	50 (13); 10 (24)
	e (6 d)	L	20°	75		2	50 (7); 10 (15)
						5	50 (11); 10 (20)
						8	50 (7); 10 (14)
						11	50 (7); 10 (24)
	e	?	18°, 4 to 0°/3 d			11.5	10 (43); 85 (5); 65 (7)
						10	0 (43); 1 (10); 0 (7)
	l	?				−6	4 (5); 100 (2)
						−7.5	25 (5)
						−9.5	18 (2)
						−18	0 (1)
	1	?	18°, 4 to 0°/3 d			−7	48 (10); 30 (12); 1 (15); 0 (17)
						−9.5	68 (5); 0 (6)
	p	?	18°, 4 to 0°/3 d			−19	0 (1); 32 (12)
						−7	43 (10); 0 (6)
Sømme (1968b)	l (last)		20°/4 d (no food)			−6	86 (4); 94 (2); 71 (6); 39 (8); 17 (16)
						−10	78 (2); 83 (1); 24 (3); 0 (4); 13 (6)
	l (last)	L	20°/4 d (no food), 6°/7 d			−6	78 (8); 82 (0); 80 (10); 70 (12)
						−10	88 (2); 94 (0); 88 (3); 72 (4)
Daumal *et al.* (1974)	e (0.1 d)	L	20°			4.5	50 (2); 90 (2); 10 (22)
						−1	50 (1); 90 (4); 10 (22)
	e (1 d)	L	20°			4.5	50 (16); 90 (8); 10 (28)
						−1	50 (17); 90 (10); 10 (31)
	e (4 d)	L	20°			4.5	50 (24); 90 (17); 10 (11)
						−1	50 (22); 90 (10); 10 (12)
	e (7 d)	L	20°			4.5	50 (8); 90 (5)
						−1	50 (9); 90 (4)
Le Torc'h (1977)	l (5, female)	L	25°	80		2	22 (20); 88 (0); 28 (30); 32 (40); 2 (50); 0 (60)
	l (5, male)	L	25°	80		2	16 (20); 86 (0); 6 (30); 6 (40); 0 (50); 0 (60)
	l (5, female)	L	25°	60		2	12 (30); 18 (20); 4 (40); 2 (50); 0 (60)
	l (5, male)	L	25°	60		2	14 (30); 22 (20); 4 (40); 0 (50); 0 (60)
Cox (1987)	l (pp) diapause	L	25° to −2.5, (5°/d)			2.5	95 (0); 95 (28); 80 (56)
						−2.5	95 (0); 80 (28); 0 (56)
	l (pp) nondiapause	L	25° to −2.5, (5°/d)			2.5	100 (0); 40 (28); 20 (56)
						−2.5	100 (0); 10 (28); 0 (56)
Plodia interpunctella (Hüb.) Cline (1970)	e (0–1.5 h)	L	27°	85		2.4	69 (1 h); 39 (2 h); 12 (1); 15 (2); 5 (3); 0 (4)
	e (3–3.5 h)	L	27°	85		2.4	48 (2 h); 13 (1); 0 (2); 0 (3); 1 (4)
	c (4–4.5 h)	L	27°	85		2.4	67 (1 h); 45 (2 h); 29 (1); 11 (2); 8 (4); 1 (5)
	e (5–5.5 h)	L	27°	85		2.4	96 (2 h); 68 (1); 35 (2); 12 (4); 0 (7)
	e (6–6.5 h)	L	27°	85		2.4	99 (1); 84 (2); 48 (3); 23 (5)
	e (17.5–18 h)	L	27°	85		2.4	100 (1 h); 95 (2); 93 (2); 54 (4)
	e (23–25 h)	L	27°	85		2.4	97 (1 h); 94 (1); 89 (2); 54 (4)
	e (71–72 h)	L	27°	85		2.4	94 (1 h); 90 (1); 86 (2); 74 (3); 55 (4); 28 (5)
Le Torc'h (1977)	l (5, female)	L	25°	80		2	90 (0); 14 (30); 6 (40); 0 (8)
	l (5, male)	L	25°	80		2	31 (20); 18 (30); 6 (40); 11 (6)
	l (5, female)	L	25°	80		2	53 (20); 14 (30); 2 (40); 23 (6)
	l (5, male)	L	25°	80		2	11 (20); 32 (30); 8 (40); 10 (6); 0 (8)
							40 (20)

Table 3—continued

Reference	Stage[1]	Strain[2]	Acclimation[3]	r.h.[4]	Temp.[5] (°C)	Percent survival (duration of exposure in days)[6]
Johnson and Wofford (1991)	e (33 h)	L	28	60	-12	90 (10 m) 95 (20 m) 95 (30 m) 95 (40 m) 95 (50 m) 85 (60 m)
					-15	85 (10 m) 90 (20 m) 90 (30 m) 90 (40 m) 75 (50 m) 60 (60 m)
					-19	80 (10 m) 90 (20 m) 90 (30 m) 25 (40 m) 3 (50 m) 0 (60 m)
	e (55 h)	L	28	60	-12	100 (10 m) 95 (20 m) 80 (30 m) 80 (40 m) 65 (50 m) 60 (60 m)
					-15	98 (10 m) 95 (20 m) 30 (30 m) 0 (40 m) 0 (60 m)
					-19	98 (10 m) 0 (20 m) 0 (40 m) 0 (60 m)
Sitotroga cerealella (Oliver) Vincent et al. (1980)	e	?	26.7	60	16	100 (4 h) 100 (8 h) 97 (12 h)
					10	100 (4 h) 89 (8 h) 100 (12 h)
					4	85 (4 h) 90 (8 h) 94 (12 h)
					-1	80 (4 h) 75 (8 h) 67 (12 h)
					-7	12 (4 h) 18 (8 h) 9 (12 h)
	e	?	26.7	60	16	57 (4 h) 67 (8 h) 56 (12 h)
					10	26 (4 h) 23 (8 h) 34 (12 h)
					4	62 (4 h) 67 (8 h) 59 (12 h)
					-1	23 (4 h) 30 (8 h) 31 (12 h)
					-7	48 (4 h) 69 (8 h) 45 (12 h)
	p	?	26.7	60	16	71 (4 h) 65 (8 h) 60 (12 h)
					10	27 (4 h) 8 (8 h) 37 (12 h)
					4	73 (4 h) 64 (8 h) 61 (12 h)
					-1	10 (4 h) 26 (8 h) 16 (12 h)
					-7	48 (4 h) 62 (8 h) 24 (12 h)
	a	?	26.7	60	16	69 (4 h) 83 (8 h) 83 (12 h)
					10	66 (4 h) 79 (8 h) 74 (12 h)
					4	77 (4 h) 81 (8 h) 94 (12 h)
					-1	88 (4 h) 88 (8 h) 79 (12 h)
					-7	91 (4 h) 87 (8 h) 83 (12 h)

[1] e = egg, l = larva with the instar given in parentheses, pp = prepupa, p = pupa, a = adult, age for a given stage in parentheses.
[2] L = strain that has been in the laboratory for > 2 yr, F = field strain.
[3] Temperature conditions before exposure to low temperature.
[4] Relative humidity in percent or if followed by a "m" the moisture content in percent.
[5] Low temperature that insects were exposed to.
[6] Usually, survival was estimated by hatching for eggs, movement for larvae or adults and emergence of adults for late instars or pupae, duration given in days except when followed by an "m" for minutes, or "h" for hours.
[7] Probit analysis.
[8] Same set of individuals used throughout the exposure period.

Table 4. A review of the survival of stored-product mites at low temperatures under laboratory conditions

Reference	Stage[1]	Strain[2]	Acclimation[3]	r.h.[4]	Temp.[5] (°C)	Percent survival (duration of exposure in days)[6]
Acarus siro L. Sinha (1964)	a, n, l	F	6°/730 d, 10°/1 d, 2°/1 h	50 to 85	−18	88 (0.04), 38 (1), 2 (3.5), 1 (7)
Sinha (1964)	a, n, l	F	21°/365 d, 10°/1 d, 2°/1 h	50 to 85	−18	45 (0.04), 15 (1), 0 (3)
Cunnington (1984)	e (1 d)	?	10°	20	0	80 (10), 60 (20), 75 (30), 20 (40), 5 (50), 1 (60), 1 (70), 0 (80)
				90	0	78 (10), 80 (20), 55 (30), 45 (40), 80 (50), 60 (60), 50 (70), 70 (80), 50 (100), 25 (120), 10 (140), 5 (150)
				20 or 90	−5	90 (1), 80 (2), 60 (4), 53 (6), 50 (7), 35 (8), 50 (10), 15 (12), 10 (14), 20 (16), 15 (18), 10 (20)
				20 or 90	−10	70 (1), 55 (2), 30 (4), 35 (5), 28 (6), 10 (7), 9 (8), 10 (9), 5 (10), 0 (11), 0 (12)
	e (0.2 d)	?	10°	90	−10	68 (2)
	e (1.8 d)	?	10°	90	−10	60 (2)
	e (3.8 d)	?	10°	90	−10	20 (2)
	e (5.8 d)	?	10°	90	−10	5 (2)
	e (7.8 d)	?	10°	90	−10	1 (2)
	e (9.5 d)	?	10°	90	−10	0 (2)
	l (active)	?	10°	90	−10	28 (1)
	l (resting)	?	10°	90	−10	7 (1)
	n (active)	?	10°	90	−10	31 (1)
	n (resting)	?	10°	90	−10	10 (1)
	a	?	10°	90	−10	17 (1)
Catoglyphus berlexei (Mich.) Sinha (1964)	a, n, l	F	21°/2 d, 10°/1 d, 2°/1 h	50 to 85	−18	0 (0.04)
Cheyletus eruditus (Schr.) Sinha (1964)	a, n, l	F	10°/7 d, 10°/1 d, 2°/1 h	50 to 85	−18	65 (0.04), 0 (1)
Glycyphagus destructor (Schr.) Sinha (1964)	a, n, l	F	10°/14 d, 10°/1 d, 2°/1 h	50 to 85	−18	20 (0.04), 18 (1), 3 (3), 3 (7)
Haemogamasus pontiger (Berl.) Sinha (1964)	a, n, l	F	21°/6 d, 10°/1 d, 2°/1 h	50 to 85	−18	30 (0.04), 0 (1)
Haemolaelaps casalis (Berl.) Sinha (1964)	a, n, l	F	10°/30 d, 10°/1 d, 2°/1 h	50 to 85	−18	55 (0.04), 50 (1), 15 (3), 0 (7)
Haemolaelaps glasgowi (Ew.) Sinha (1964)	a, n, l	F	10°/3 d, 10°/1 d, 2°/1 h	50 to 85	−18	100 (0.04), 7 (1), 0 (3)
Kleemania plumosus Oud. Sinha (1964)	a, n, l	F	21°/60 d, 10°/1 d, 2°/1 h	50 to 85	−18	0 (0.04)
Leiodinychus krameri (Can.) Sinha (1964)	a, n, l	F	21°/7 d, 10°/1 d, 2°/1 h	50 to 85	−18	85 (0.04), 80 (1), 20 (3), 1 (7)
Tydeus interruptus (Thor.) Sinha (1964)	a, n, l	F	10°/2 d, 10°/1 d, 2°/1 h	50 to 85	−18	98 (0.04), 98 (1), 15 (3), 20 (7)

[1] e = egg, l = larva with the instar given in parentheses, pp = prepupa, p = pupa, a = adult, age for a given stage in parentheses.
[2] L = strain that has been in the laboratory for > 2 yr, F = field strain.
[3] Temperature conditions before exposure to low temperature.
[4] Relative humidity in percent or if followed by a "m" the moisture content in percent.
[5] Low temperature that insects were exposed to.
[6] Usually, survival was estimated by hatching for eggs, movement for larvae or adults and emergence of adults for late instars or pupae, duration given in days except when followed by an "m" for minutes, or "h" for hours.
[7] Probit analysis.
[8] Same set of individuals used throughout the exposure period.

Table 5. The relative cold-hardiness of some stored-product insects

Reference	Site	Stage[2]	Most susceptible			Most tolerant
Mansbridge[1] (1936)	Field	l or a	*T. castaneum* *T. confusum*	*C. turcicus* *E. cautella* *L. serricorne* *R. dominica* *S. oryzae*	*O. surinamensis* *S. granarius*	*E. elutella* *E. keuhniella* *P. interpunctella* *T. granarium* *T. molitor*
Solomon and Adamson[1] (1955)	Field	e, l, p, a,	*O. mercator*	*E. cautella* *S. oryzae* *S. granarius* *T. castaneum* *T. confusum*	*S. cerealella*	*C. ferrugineus* *C. turcicus* *E. elutella* *E. kuehniella* *S. surinamensis* *P. interpunctella* *T. granarium* *T. molitor*
Mathlein (1961)	Field and Lab	l or a	*E. cautella* *O. surinamensis* *R. dominica* *S. oryzae*	*C. ferrugineus* *E. elutella* *E. kuehniella* *T. granarium* *S. granarius*		
David *et al.* (1977)	Lab	e, l, p, a	*R. dominica*	*S. oryzae*	*S. granarius*	
Bahr (1978)	Field	l, a	*C. pusillus* *O. mercator* *R. dominica* *T. castaneum* *T. confusum*	*S. cerealella* *S. oryzae* *S. zeamais*	*C. turcicus* *C. ferrugineus* *O. surinamensis* *S. granarius*	
Mullen and Agrobast (1979)	Lab	e	*E. cautella* *O. surinamensis* *T. castaneum*	*C. maculatus*	*L. serricorne*	
Evans (1983)	Lab	a	*T. castaneum*	*O. surinamensis* *C. ferrugineus* *S. oryzae* *R. dominica*	*S. granarius*	
Evans (1987)	Lab	l, p	*O. surinamensis* *T. castaneum*	*S. oryzae*	*S. granarius*	*R. dominica*
Wohlgemuth (1989)	Field	l, a	*T. confusum*	*C. turcicus* *O. surinamensis*	*T. granarium*	*S. granarius*

[1]Only a partial list of species studied.
[2]e = egg, l = larva, p = pupa, a = adult.
[3]Within a given study, species not separated by a space had similar cold-hardiness.

Hole, 1968; David *et al.*, 1977). Most studies do not incude the pupal stage as it is difficult to manipulate.

The criterion for cold-survival is different for the various stages and it is difficult to make direct comparisons of cold-tolerance within a species. For eggs and pupae, the criterion is usually transition to the next stage, for adults and larvae it is co-ordinated movement. The ultimate test
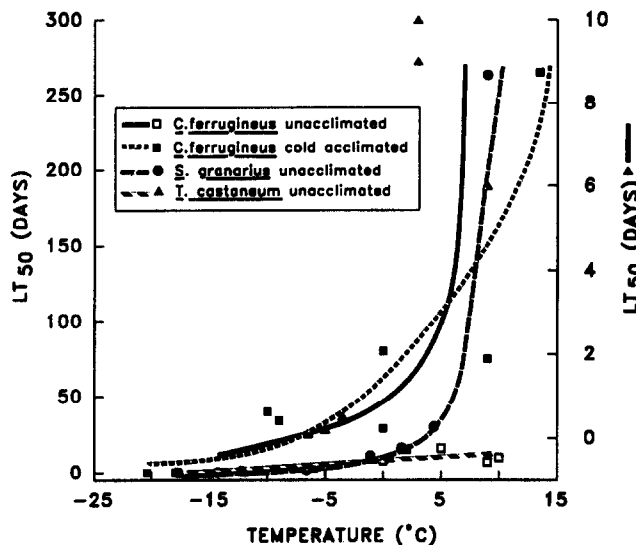

Fig. 1. The lethal time for 50% of the population for some stored-product insects at temperatures below their developmental thresholds. Data are from papers cited in Table 2.

for the effects of cold-stress would be to measure the effects of low temperature on fitness under field conditions. A few studies suggest that cold-stress, in addition to increasing mortality, reduces the fitness of surviving individuals (Howe and Hole, 1968; Kawamoto et al., 1989).

Of all the factors that affect cold-survival, acclimation is the one most often ignored. Generally, exposing insects to cool temperatures (20–10°C) increases their survival by 2 to 10 times at lower temperatures (Tables 2–4). There are only two studies, both with *S. granarius*, in which acclimation did not increase cold-tolerance (Robinson, 1926; Evans, 1983). The practical application of results from studies that do not use cold-acclimated individuals is limited to situations where refrigeration is used to rapidly cool commodities. In all other field situations the temperature declines are gradual enough for the insects to cold-acclimate.

What is the best method to acclimate insects to cold? As a guide for his step-wise acclimation regime, Evans (1983) took the temperature declines that could be attained by refrigerated aeration in Australia. Smith (1970) chose 15°C because it was just below the development threshold for *C. ferrugineus*. Fields (1990) tried to approximate field acclimation by placing caged insects into 100-tonne grain bulks and removing them during the winter. Smith (1970) and Khan (1990) tested several different acclimation regimes and found that the longest and slowest temperature declines give the greatest cold-tolerance, suggesting that slower temperature declines would give even greater cold-tolerance. These studies also indicate that most of the acclimation regimes used in other studies are too brief for the insects to attain their maximum cold-tolerance. For the purpose of insect control, acclimation regimes that approximate those in the field are probably the best to use in cold-hardiness studies. A limitation of this approach is that these temperature declines are slow and vary according to storage facilities and climate.

Relative humidity affects many aspects of stored-product insect biology (Birch, 1953; Howe, 1965) and low relative humidity can shorten by half the time to kill 50% of the population at low temperature (Stojanovic, 1965; Le Torc'h, 1977; Evans, 1983, 1987b; Fields, 1990; data in Table 2). The cold-tolerance of eggs is not usually affected by relative humidity (Nagel and Shepard, 1934; Jacobs and Flemming, 1986; data in Table 2).

A few studies have examined the possibility that there could be differential mortality between the sexes, since this could greatly affect population dynamics. However, gender has only a minor, although significant, effect on survival at low temperatures. Edwards (1958; data in Table 2), working with *Tribolium castaneum* adults, showed that unacclimated males were twice as cold-hardy as females, but acclimated insects showed no differences. Williams (1954) reported that *Cryptolestes pusillus* (Schönherr) males died slightly sooner than females. Kawamoto et al. (1989) showed that *C. ferrugineus* females survived slightly better than males did on four of the seven sampling dates. Finally, Le Torc'h (1977; data in Table 3) working with fifth-instar larvae found no difference between the sexes for *E. kuehniella*, but did for *P. interpunctella*.

Low Temperature: Mechanisms

The differences in cold-tolerance outlined in Tables 2–5 are dependent on behavioral, physiological, or biochemical mechanisms used to avoid cold-injury. A better understanding of how insects survive the cold should make it easier to control them with low temperature.

Most temperate field insects overwinter in sheltered micro-habitats, such as under the bark on the southern exposure of the tree (Danks, 1978). Grain bulks are usually much warmer than ambient winter air temperatures. Considerable seasonal variation in temperature and moisture content exists within the grain bulk (Hagstrum, 1987; Fields, 1990). Intuitively, one would assume that stored-product insects would migrate to the warmest grain in the bin as the bulk slowly cooled during the winter. A few laboratory studies have shown that *Oryzaephilus surinamensis* (Linnaeus) (Amos, 1968), and *Tribolium castaneum* (Graham, 1958) aggregate where it is between 25 and 32°C. However, *Tribolium confusum* aggregates at 15°C, the lowest temperature available (Graham, 1958). These behaviors have not been rigorously tested in commercial-sized grain silos. Hagstrum (1987) showed that *C. ferrugineus* populations were more numerous in the warmer grain during the winter, but could not show that this was due to movement alone, rather than differences in mortality or emergence from the various locations within the grain bulk. Ability to move in grain varies between species (Surtees, 1965) and this may affect their ability to respond to a temperature

gradient. Finally, some species such as stored-product Lepidoptera larvae cannot move more than a few centimeters below the grain surface (Bell, 1983), and therefore would be exposed to the highest and lowest temperatures in the grain bulk. It is interesting to note that stored-product Lepidoptera are among the most cold-tolerant insects that attack grain (Table 5).

Although behavior may enable some insects to avoid cold temperatures and thereby minimize cold-injury, physiological and biological mechanisms determine if an insect can survive when low temperatures cannot be avoided. There are many theories; "frozen" lipids, rate imbalances, changes in ionic activity, and ice formation (Hochachka and Somero, 1984; Hazel, 1989; Storey and Storey, 1989) have been proposed to explain why organisms live or die at cold temperatures. These theories often have not been rigorously supported with experimental data nor are they mutually exclusive.

A convincing mechanism of cold-injury is the "frozen" lipid hypothesis. The phospholipid membrane is essential for the normal function of cells, organelles, and membrane-bound enzymes. These membranes must remain homeoviscous (maintain a stable viscosity) to carry out their various functions (Bretscher, 1985). As temperatures drop, membranes become less viscous or "freeze" (Hochachka and Somero, 1984; Hazel, 1989; Storey and Storey, 1989). There is some evidence that cold-acclimated plants (Lynch, 1990) and animals (Hazel, 1989) have less viscous membranes due to an increase in the proportion of unsaturated fatty acids. This hypothesis has not yet been tested on stored-product insects.

Imbalances in the rate of biochemical reactions have also been cited as a cause of cold-injury (Hochachka and Somero, 1984; Hazel, 1989; Storey and Storey, 1989). Like any chemical reaction, enzyme-catalyzed reactions are slower at lower temperatures. If reduced enzyme activity at low temperature was the only factor, poikilotherms would slow down but not die. However, the activity of some enzymes is reduced more than others, causing biochemical reactions to be uncoupled and physiological balances to be upset. One way that organisms acclimate to cold is to increase the quantity of enzyme present. The other option is to change the type of enzyme (isoenzyme) present under cold conditions. Isoenzymes occur in closely related species from different thermal habitats, but are not seen within species as a response to cold temperatures (Hochachka and Somero, 1984).

Another mechanism of cold-injury concerns the ionic activity of molecules as a function of temperature. For example, a temperature shift from 35 to 0°C increases the solubility of oxygen in water by two-fold, increases the concentration of hydrogen ions by 2.5-fold, but does not change the solubility of NaCl. Minor shifts in pH can radically change the activity of enzymes: digestive enzymes would be reduced by 20% solely due to pH changes occurring when the temperature drops by 20°C (equivalent to a 0.34 unit increase in pH) (Houseman and Downe, 1981).

Freezing is lethal for many insects (freeze-intolerant or freeze-susceptible), although some insects can tolerate extracellular freezing (freeze-tolerant). Freeze-susceptible species generally have lower supercooling points (temperature at which water in the insect begins to freeze) in the winter than in the summer. This reduction is thought to be adaptive because freezing is lethal. However, the supercooling point is not an absolute measure of cold-hardiness. Because one species freezes at −15°C does not mean it is less cold-hardy than one that freezes at −25°C. Temperatures above the supercooling point are often lethal, as observed for stored-product insects (Tables 2 and 6), and for other insects (Turnock et al., 1983). The supercooling point is useful because it represents a temperature that causes death in a matter of minutes.

It is believed that freezing is lethal because ice crystals physically destroy cell structure, cause severe osmotic shocks as salt concentrations increase in the unfrozen cytoplasm during freezing and rapidly decrease during thawing, or prevent the movement of molecules within and between cells (Storey and Storey, 1989). Freeze-susceptible insects avoid freezing by many different mechanisms. One is to eliminate or mask ice nucleators. Small volumes of water cooled rapidly can attain −40°C before freezing, even larger bulks of water can remain supercooled at −5°C for long periods of time (Franks, 1985). However, if an ice crystal is placed in the water, no supercooling occurs and the water will freeze at 0°C. The ice crystal acts as a nucleator or template that enables the formation of ice. Ice causes nucleation at the highest temperatures, but many other compounds, such as dust, silver iodide, food, proteins, amino acids, or alcohols can act as ice nucleators (Lindow, 1983). Before the onset of winter, insects commonly empty their guts which often contain potent nucleators (Sømme, 1982). They also may eliminate nucleators within the cells (Baust and Zachariassen, 1983; Neven et al., 1986). Another mechanism to lower the supercooling point is to

Table 6. The supercooling points of some stored-product insects

Reference	Stage[1]	Acclimation	Supercooling	Standard error of the mean	n
Cryptolestes ferrugineus					
Smith (1977)	a	30°	−17.9		20
		30°, 15°C/28 d	−20.2		20
Fields (1990)	a	30°	−17.0	1.0	34
		30°, nucleators[2]	−8.1	0.5	36
Cryptolestes pusillus					
This study[3]	a	30°	−14.0	1.0	38
		30°, nucleators[2]	−12.0	1.5	33
Ephestia kuehniella					
Sømme (1966)[4]	l	26°, 20°/2 d	−16.9	0.5	10–25
		26°, 0°/7 d	−20.3	0.3	10–25
		26°, 6°/14–42 d	−18.3	0.7	10–25
			−21.7	0.4	10–25
Gibbium psylloides					
Lee et al. (1992)	a	23°	−10.7	0.9	11
		23°, nucleators	−6.0	0.5	11
Oryzaephilus surinamensis					
This study[3]	a	30°	−13.7	1.9	32
		30°, nucleators[2]	−11.0	1.3	33
Plodia interpunctella					
Lee et al. (1992)	l	23°	−10.3	0.4	54
		23°, nucleators	−5.4	0.5	33
Rhyzopertha dominica					
Lee et al. (1992)	a	23°	−15.2	0.8	23
		23°, nucleators	−3.3	0.1	7
Sitophilus granarius					
This study[3]	a	30°	−14.3	0.8	41
		30°, nucleators[2]	−7.8	0.5	72
Lee et al. (1992)	a	23°	−15.7	1.0	16
		23°, nucleators	−8.0	0.6	18
Tenebrio molitor					
Patterson and Duman (1978)	l	20°, long day, 90% r.h.	−7.7	1.0	7
		20°, short day, 90% r.h.	−13.6	0.9	10
		20°, short day, 15% r.h.	−12.8	1.5	8
		20°, 5°C/1 d, 90% r.h.	−14.9	0.7	8
Constantinou and	l	23°	−10.3	0.4	39
Cloudsley-Thompson (1986)		23°, 6°/5 d	−11.1	0.5	17
	p	23°	−13.3	0.2	79
		23°, 6°/15 d	−13.7	0.3	42
	a	23°	−7.1	0.4	28
Tribolium castaneum					
This study[3]	a	30°	−12.3	1.0	41
		30°, nucleators[2]	−5.8	0.3	77
Lee et al. (1992)	a	23°	−13.9	0.8	23
		23°, nucleators	−4.7	0.4	11

[1] a = adult, l = larva, p = pupa.
[2] Ice-nucleating active bacteria on grain at 1000 ppm.
[3] Same methods as Fields (1992).
[4] Standard deviation given instead of the standard error of the mean.

produce solutes, such as glycerol, mannitol, sorbitol, trehalose, fructose, or glucose, that lower the freezing point because of their colligative properties, the same way antifreeze in an automobile's radiator prevents freezing. These solutes may have other roles, such as stabilizing proteins (Storey and Storey, 1989). Finally, some insects produce thermal hysteresis proteins which lower the melting point of the insect by as much as 5°C (Duman, 1982). These proteins are thought to bind to ice nuclei to prevent them from causing freezing throughout the insect.

Most of the work on low temperature physiology has used arctic or temperate field insects, although there has been some work using stored-product insects. Smith (1970) found that supercooling points for *C. ferrugineus* adults decrease by only 2°C when they are held at 15°C for 4 weeks. In the same period, the lethal time for 50% of the population at −12°C went from 2 to 30 days, hence the supercooling point is a poor indicator of changes in cold-tolerance. Constantinou and Cloudsley-Thompson (1986) measured the supercooling points for *Tenebrio molitor* Linnaeus) adult (−7.1°C), pupae (−14.1°C) and larvae (−10.3°C), and concluded that the low supercooling point of the pupae was a pre-adaptation to survive low temperatures. They did not support this hypothesis with low temperature survival data. It is not unusual for pupae to have lower supercooling points than adults and larvae (Sømme, 1982), but it is probably a reflection of nucleators (food) rather than a measure of their cold-tolerance. Sømme (1968a) showed that glycerol injected into unacclimated *E. kuehniella* larvae increased their survival at −10°C beyond

that of cold-acclimated insects. He did not determine if cold-acclimation increased the levels of low molecular solutes as observed in other insects. Additional work suggested that cold acclimation or the injection of glycerol enables larvae to maintain a better balance of enzymes during cold exposure (Sømme, 1972). Insect thermal hysteresis proteins were first discovered in *Tenebrio molitor* (Ramsay, 1964) and have been shown to increase during cold-acclimation (Duman, 1982). They are present in unacclimated insects and may serve to reabsorb water in the hind gut.

Knowledge of cryobiology has been used to develop a new control method for stored-product insects by using ice-nucleating active bacteria to increase the supercooling point of insect pests (Fields, 1990; Lee *et al.*, 1992). After ice crystals, ice-nucleating active bacteria are the most potent nucleators. Many bacteria that live on the surface of leaves act as ice nucleators. The presence of these bacteria raises the freezing point of plants by several degrees. This is thought to be adaptive for the bacteria, since plant tissue damaged by freezing is better for their growth than unfrozen plant tissue (Lindow, 1983). Strong-Gunderson *et al.* (1990) suggested that the ingestion of ice-nucleating active bacteria could reduce the cold-hardiness of insects, because when adults of the Coccinellid beetle *Hippodamia convergens* Guérin were fed on ice-nucleating active bacteria their supercooling point rose by 11°C.

Ice-nucleating active bacteria have been reared commercially and used in snowmakers to increase the production of artificial snow. Fields (1990) found that the supercooling points of *C. ferrugineus* adults increase from −17 to −8°C when they are exposed to wheat that had been treated with commercial ice-nucleating active bacteria (Snomax Technologies Division of Genencor International, Rochester, N.Y., U.S.A.). Also, the mortality of insects held at −10°C for 1 day increased from 8 to 81% with the application of the nucleators. Other stored-product insects react in a similar way with their supercooling point and their mortality increasing at sub-zero temperatures and their supercooling point increasing when they are exposed to ice-nucleating active bacteria (Lee *et al.*, 1992; data in Table 6). Additional work is needed to determine if this technique works under field conditions.

High Temperature: Suboptimum

Temperatures for maximum rate of multiplication and development are only about 5°C below temperatures that stop development. For example, *S. oryzae* has a maximum multiplication rate at 29.1°C, but this drops to zero at 35°C. For *R. dominica* the maximum multiplication rate occurs at 34°C, and drops to zero at 38.6°C (Birch, 1953). High temperatures (37–42°C), in addition to causing some mortality, cause reduced fecundity (number of eggs laid) and fertility (percent hatch) (Oosthuizen, 1935; Kirkpatrick and Tilton, 1973; Vardell and Tilton, 1980; Arbogast, 1981). Diapausing larvae of *E. elutella* are more resistant to high temperatures than non-diapausing larvae in that they produced fertile adults, whereas the non-diapausing larvae did not (Bell, 1983).

High Temperature: Lethal

As with low temperature mortality, temperature, duration of exposure, species, stage of development, acclimation, and relative humidity can determine the survival of insects at high temperatures. The research on high temperature control has focused on using hot air in fluidized-beds, high frequency waves (10–100 MHz), microwaves (300–3000 MHz), or infrared (100–100,000 GHz) to heat (50–80°C) briefly the grain or flour before rapidly cooling the commodity. The temperatures are in constant flux and the rates of heating and cooling depend on the instruments used for heating, the product being treated, its moisture content, and packaging. All these factors make comparisons difficult. Most species will not survive more than 24 hr at 40°C, 12 hr at 45°C, 5 min at 50°C, 1 min at 55°C, and 30 sec at 60°C (Table 7). Different species have different susceptibilities to heat treatment. Kirkpatrick and Tilton (1972) tested the heat-tolerance of several species, and found that the survival at 49°C of adult *Lasioderma serricorne* (Fabricius) > *C. pusillus* = *R. dominica* > *S. oryzae* = *Tribolium castaneum* = *Trogoderma variable* Ballion > *S. granarius* = *Gibbium psylloides* (Czenpinski) > *Cathartus quadricollis* (Guérin-Méneville) = *O. mercator* > *Tribolium confusum* = *O. surinamensis*. Oosthuizen (1935) summarized the early literature on heat-tolerance ranking from highest to lowest; *R. dominica, Tribolium ferrugineum* (Fabricius), *Tribolium confusum, Tenebrio obscurus* (Fabricius), *Tenebrio molitor, S. granarius, S. oryzae*. Tests with high

frequency heating revealed two groups of insects, those that were killed at temperatures between 41 and 47°C (*S. granarius*, *S. oryzae*, and *O. surinamensis*) and those that were killed at temperatures between 48 and 57°C [*Tenebroides mauritanicus* (Linnaeus), *L. serricorne*, *Trogoderma glabrum* (Herbst), and *Trogoderma parabile* Beal] (Nelson and Kantack, 1966). *Rhyzopertha dominica* and *S. oryzae* have often been used to test the effectiveness of heat treatment because they tolerate heat better than other stored-product insects (Table 7). Temperatures used to control immature *R. dominica* will control virtually all other species (Evans and Dermott, 1981).

There have been few thorough tests of heat-tolerance of the different developmental stages of various species. Immature stages of the boring insects are believed to be more difficult to control with heat treatment because they are inside the seed, and experience lower temperatures than adults, which are often outside the seed (Dermott and Evans, 1978; Fleurat-Lessard, 1985). Working at lower temperatures than those used in fluidized-beds, Oosthuizen (1935) ranked pupae > eggs > larvae > adults of *Tribolium confusum* in order of heat-tolerance at 44°C. However, there were no significant differences at 50°C.

The lower the relative humidity or moisture content of the grain, the more susceptible insects are to heat treatment (Mellanby, 1932; Kirkpatrick and Tilton, 1973; Evans, 1981; Vardell and Tilton, 1981; data in Table 7). These differences are greatest between 40 and 45°C. At the higher temperatures used in fluidized-bed treatments, it takes less time to kill insects in dry grain than in wet grain, but this can be explained by the longer times needed to heat wet grain, as the grain temperature needed to kill 99.9% of the population is the same in both wet and dry grain (Evans, 1981).

Acclimation to high temperature has been examined in few stored-product insects. Gonen (1977; data in Table 7) found that acclimated *S. granarius* were three times more tolerant to 40°C than non-acclimated insects. However, *S. oryzae* had only marginal increases in heat-tolerance with acclimation. Using much higher temperatures (55°C), Evans (1981; data in Table 7) showed that acclimation did not increase tolerance of *R. dominica* or *S. oryzae*.

High Temperature: Mechanisms

Many of the mechanisms proposed to explain why insects die at high temperatures are the same as those proposed for low temperature mortality. Changes in lipids, rate imbalances, perturbation of ionic activities, as well as desiccation have been proposed as possible mechanisms of death due to high temperatures.

Phospholipid membranes become more fluid at higher temperatures. The nervous system, because it is so dependent upon membrane integrity, is thought to be especially sensitive to high temperatures. Warm-acclimated goldfish have higher heat coma temperatures than non-acclimated goldfish. This increased heat-tolerance is believed to be due to the higher melting temperatures of the lipids in synaptic membranes, which contain fewer saturated fats (Cossins and Prosser, 1978). Insects reared at high temperatures also have lipids with higher melting points (Fraenkel and Hopf, 1940; Cherry, 1959), which supports the hypothesis that high temperatures destabilize phospholipid membranes and are responsible for the death of animals.

The structure of proteins is affected adversely by high temperatures. There is a positive correlation between the temperature at which pyruvate kinase, a key enzyme in glycolysis, is inactivated and body temperature (Hochachka and Somero, 1984). This enzyme is inactivated by a 3 min exposure to temperatures from 56 to 60°C, the same conditions that kill most stored-product insects (Table 7). Enzymes will be affected adversely at temperatures below which there is gross denaturation, and this causes rate imbalances as discussed in the section on low temperature.

Ionic activity changes with temperature as previously mentioned. This hypothesis for mortality is supported by work on desert insects showing that insects that died because of heat-stress had a more acidic hemolymph than live insects (Cloudsley-Thompson, 1962).

Water-stress may also cause insects to die at high temperatures. In many cases low relative humidity makes insects more susceptible to heat (Table 7). Cloudsley-Thompson (1962), working with desert arthropods, found that the mean percent desiccation was greater in insects that died after 24 hr at high temperature and low relative humidity than those that survived. Dead insects do lose water at a faster rate than live insects, but not enough to account for the differences between

Table 7. A review of the survival of stored-product insects at high temperatures, under laboratory or field conditions

Reference	Stage[1]	Strain[2]	Acclimation[3]	r.h.[4]	Temp.[5] (°C)	Percent survival (duration of exposure)[6]
Ephestia cautella						
Arbogast (1981)	p	L	27°, incubator	60	40	100 (2 h) 100 (4 h)
					45	94 (2 h) 18 (4 h)
					50	0 (2 h)
Ephestia elutella						
Bell (1983)[7]	l, diapause	L	25°, incubator	60	40	50 (63 h) 0 (96 h)
					43	50 (13 h) 0 (24 h)
					45	50 (8 h) 0 (16 h)
Lasioderma serricorne						
Kirkpatrick and Tilton (1972)	a	?	26°, infrared	13.5m	49	65 (20 s)
					57	1 (32 s)
					66	0 (40 s)
Oryzaephilus surinamensis						
Nelson and Kantack (1966)	a	L	27°, high frequency	13m	35	50 (2.2 s)
					44	10 (4.4 s)
Kirkpatrick and Tilton (1972)	a	?	26°, infrared	13.5m	49	3 (20 s)
					57	2 (32 s)
					66	0 (40 s)
Locatelli and Traversa (1989)	e	?	27°, microwaves and oven	?	81	1 (2 m)
	l, p				80	1 (2 m)
Plodia interpunctella						
Arbogast (1981)	p	L	27°, incubator	60	40	97 (2 h) 8 (4 h)
					45	0 (2 h)
					50	0 (2 h)
Rhyzopertha dominica						
Tilton and Schroeder (1963)	e, l, p	?	27°, infrared	14m	55	50 (10 s)
					63	10 (15 s)
Kirkpatrick and Tilton (1972)	a	?	26°, infrared	13.5m	49	55 (20 s)
					57	3 (32 s)
					66	0 (40 s)
Kirkpatrick and Tilton (1973)	e	L	27°, incubator	60	39	9 (31 d)
	l			60	39	1 (17 d)
	p			60	39	35 (7 d)
	a			60	39	92 (4 d)
	a			50	43	0.3 (4 d)
Evans (1981)[7]	e, l, p	L	22°, fluidized-bed	11.3m	55	50 (2.4 m) 0.1 (3.3 m)
			32°, fluidized-bed	11.3m	55	50 (2.4 m) 0.1 (3.3 m)
			32°, fluidized-bed	14m	55	50 (3.1 m) 0.1 (4.0 m)
Evans and Dermott (1981)	e, l, p	L	30°, fluidized-bed	11.3m	56	47 (2.4 m) 5 (6.4 m) 1 (10.4 m)
Vardell and Tilton (1981)	e, l, p, a	L	27°, fluidized-bed	12.3m	55	58 (?) 0.6 (18.4)
					57	52 (?)
					59	29 (?)
					61	15 (?)
					63	10 (?)
					65	1 (?)
					67	0 (4.8 m)
Vardell and Tilton (1981)	a	L	27° incubator	40	40	76 (7 d)
				40	42	2 (7 d)

Reference	Stage		Conditions	Size	Temp	Mortality (time)	
Tilton et al. (1983)	e, l, p, a	L	?, infrared	50	42	56 (7 d)	
				60	42	41 (7 d)	
				?	52	71 (30 s)	
			?, infrared and vacuum		54	45 (38 s)	
					56	33 (45 s)	
				?	52	38 (60 s)	
					54	24 (75 s)	
					56	22 (90 s)	
Sitophilus granarius							
Baker et al. (1956)	a	?	?, microwaves	?	32	60 (3 s)	
					42	45 (6 s)	
					57	2 (9 s)	
					72	0 (12 s)	
Nelson and Kantack (1966)	a	L	27°, high frequency	12.2m	39	50 (2.5 s)	
					52	10 (5 s)	
Kirkpatrick and Tilton (1972)	a	?	26°, infrared	13.5m	49	30 (20 s)	
					57	6 (32 s)	
					66	0 (40 s)	
Gonen (1977)[7]	a	?	27°, incubator.	65	40	50 (9 h)	5 (15 h)
			27°, 32/14 d, incubator	65	40	50 (26 h)	5 (34 h)
Locatelli and Traversa (1989)	e	?	27°, microwaves and oven	?	83	1 (2 m)	
	l, p				80	0 (2 m)	
Sitophilus oryzae							
Tilton and Schroeder (1963)	e, l, p	?	27°, infrared	14m	45	50 (10 s)	
					58	5 (15 s)	
Nelson and Kantack (1966)	a	L	27°, high frequency	11.8m	38	50 (2.4 s)	
					47	10 (4 s)	
Kirkpatrick and Tilton (1972)	a	?	26°, infrared	13.5m	49	40 (20 s)	
					57	2 (32 s)	
					66	0 (40 s)	
Kirkpatrick and Tilton (1973)	e	L	27°, incubator	60	39	0 (31 d)	
	l			60	39	0 (17 d)	
	p			60	39	1 (7 d)	
	a			60	39	0 (4 d)	
	a			65	39	88 (4 d)	
	a			75	40	98 (2 d)	
Gonen (1977)	a	?	27°, incubator	65	40	50 (9 h)	5 (11 h)
			27°, 32/14 d, incubator	65	55	50 (11 h)	5 (15 h)
Evans (1981)[7]	e, l, p	L	15°/14 d, fluidized-bed	11.3 m	55	50 (1.9 m)	0.1 (2.9 m)
			30°/35 d, fluidized-bed	11.3m	50	50 (1.6 m)	0.1 (2.8 m)
Vardell and Tilton (1981b)	e, l, p, a	L	27°, fluidized-bed	12.3m	50	62 (1.8 m)	
					52	32 (?)	
					54	17 (?)	
					56	11 (?)	
					58	1 (?)	
					60	0 (?)	
Tilton et al. (1983)	e, l, p, a	L	?, infrared	?	52	33 (30 s)	
					54	20 (38 s)	
					56	21 (45 s)	
			?, infrared and vacuum	?	52	14 (60 s)	
					54	11 (75 s)	
					56	5 (90 s)	

Table 7—continued

Reference	Stage[1]	Strain[2]	Acclimation[3]	r.h.[4]	Temp.[5] (°C)	Percent survival (duration of exposure)[6]	
Fleurat-Lessard (1985)	e, l, p	?	?, fluidized-bed	13m	54	0.1 (66 s)	
					64	0.1 (16 s)	
					72	0.1 (12 s)	
					80	0.1 (10 s)	
Locatelli and Traversa (1989)	e	?	27°, microwaves and oven	?	82	0 (2 m)	
	l, p				80	1 (2 m)	
Tribolium castaneum							
Kirkpatrick and Tilton (1972)	a	?	26°, infrared	13.5m	38	38 (20 s)	
					57	2 (32 s)	
					66	0 (40 s)	
Tribolium confusum							
Oosthuizen (1935)	e	?	?, incubator	75	44	50 (14 h)	5 (19 h)
					46	50 (1.2 h)	5 (2 h)
	l				44	50 (10 h)	5 (19 h)
					46	50 (1 h)	5 (1.5 h)
					48	50 (8 m)	
					50	50 (4.7 m)	
	p				44	50 (20 h)	5 (29 h)
					46	50 (1.5 h)	5 (2.7 h)
					48	50 (12 m)	
					50	50 (4.5 m)	
	a				44	50 (7 h)	5 (11 h)
					46	50 (1.2 h)	5 (2.2 h)
					48	50 (26 m)	
					50	50 (4.9 m)	
Edwards (1958)[7]	a	L	18°, incubator	75	40	50 (5.2 d)	
			30°, incubator	75	40	50 (4.0 d)	
			38°, incubator	75	40	50 (1.2 d)	
Kirkpatrick and Tilton (1972)	a	?	26°, infrared	13.5m	49	5 (20 s)	
					57	2 (32 s)	
					66	0 (40 s)	
Trogoderma granarium							
Fleurat-Lessard (1985)	l	?	?, fluidized-bed	14m	73	0.1 (14 s)	
					77	0.1 (9 s)	
					78	0.1 (5 s)	

[1] e = egg, l = larva with the instar given given parentheses, pp = prepupa, p = pupa, a = adult, age for a given stage in parentheses.
[2] L = strain that has been in the laboratory for >2 yr, F = field strain.
[3] Temperature conditions before exposure to low temperature.
[4] Relative humidity in percent or if followed by an "m" the moisture content in percent.
[5] Highest temperature insects were exposed to.
[6] Duration of exposures; s = seconds, m = minutes, d = days.
[7] Probit analysis.

the two groups. At temperatures above 50°C, water-stress is unlikely to be the prime cause of death because the durations of exposure are too short to cause significant desiccation. Mellanby (1932) showed that there was no relationship between relative humidity and lethal temperature for 1 hr exposures, but there was a direct relationship for insects exposed to test temperatures for 24 hr.

Heat-shock proteins are found in insects, bacteria, mammals, and plants (Petersen and Mitchell, 1985). Most of the work has focused on the heat-shock proteins produced by *Drosophila*. These proteins are produced between 30 and 40°C, and are associated with increased survival at 40°C. Heat-shock proteins aggregate around mRNA, and may help to repair heat-damaged proteins and lipids (Nagao *et al.*, 1990). However, experimental data are not available to support this theory. The role that heat-shock proteins play in the ability of stored-product insects to survive high temperatures is unknown.

Engineering Solutions: Low Temperature

Once the duration and temperature needed to control an insect are determined, there are three ways to lower grain temperature. Turning or mixing the grain is a recommended practice to avoid grain spoilage. As there is little heat exchange when the grain is moved, the overall temperature of the grain bulk remains about the same, but "hot spots" are dispersed and cooled by coming in contact with cooler grain (Watters, 1963). Turning the grain causes breakage of kernels, particularly in maize, and grain temperature cannot be quickly reduced, factors which limit the usefulness of this method.

Ambient air ventilation is the most widely used means for cooling bulk grain. There are many types of ventilation systems, and care must be taken to insure that adequate and even air flow is maintained. To maximize cooling, systems have been designed to ventilate only when the ambient air temperatures are below the grain temperature (Metzger and Muir, 1983; Armitage and Llewellin, 1987; Epperly *et al.*, 1987; Lasseran and Fleurat-Lessard, 1990). Studies on full-sized commercial silos have shown that aeration reduces or even eliminates insect populations (Thorpe *et al.*, 1982; Cuperus *et al.*, 1986; Armitage and Llewellin, 1987), although this is not always the case (Armitage and Stables, 1984). Under certain conditions, ambient air ventilation will also cool grain through evaporative cooling and will dry grain to a limited extent (Desmarchelier, 1988; Sanderson *et al.*, 1988).

Ambient air cooling can be assisted by refrigerating air used to ventilate the grain. Tests have been conducted in Britain (Burrell, 1967; Burrell and Laundon, 1967), Israel (Donahaye *et al.*, 1974), and Australia (Hunter and Taylor, 1980; Thorpe and Elder, 1980). The primary goal is to cool grain enough to slow or even stop the development of molds (Burrell and Laundon, 1967) and insects (Evans, 1987a). Commercial units are available in Europe (Sulzer-Escher Wyss) and Australia (McBea Services), and over 60 million tonnes of grain are cooled via refrigeration in some 50 countries around the world. These units can be mobile, making it easy for one unit to service many granaries. Large permanent units are also used, and can cool up to 300,000-tonne grain bulks. The energy required to cool the grain varies from 3 kWh/tonne in insulated silos (Hunter and Taylor, 1980) to 12.0 kWh/tonne for uninsulated bins in tropical conditions. Condensation on the grain can be a problem if warm wet air comes in contact with cool dry grain (Navarro *et al.*, 1973), although this was not a problem encountered in other studies using refrigerated air (Donahaye *et al.*, 1974; Hunter and Taylor, 1980).

Engineering Solutions: High Temperature

There are two ways that grain can be heated to temperatures high enough to kill insects. Fluidized-beds use hot air (60–120°C) blown at rates high enough to lift and mix the grain. This raises the temperature of the grain to between 56 and 72°C in < 1 min. Small-scaled batch (Dermott and Evans, 1978) and continuous flow (Evans *et al.*, 1983; Fleurat-Lessard, 1985) fluidized-beds that can treat 150 tonnes/hr have been built and tested. Grain is rapidly cooled by spraying water on the grain (Evans *et al.*, 1983) or a fluidized-bed with ambient air (Fleurat-Lessard, 1985). Costs to operate fluidized-beds are similar to the cost of fumigation if large-scale treatment of grain is required (Fleurat-Lessard, 1987).

Non-ionizing electromagnetic energy has also been used to heat grain and other stored products to temperatures high enough to kill insects. High frequency or radio frequencies have been studied

over the last 50 yr as a means to disinfest grain (Ark and Parry, 1940; Nelson and Kantack, 1966; Fleurat-Lessard, 1987). Microwaves tend to remove the water from the product during heating which may be undesirable, but this has been used in conjunction with a vacuum to dry grain (Tilton et al., 1983). Infrared irradiation has been used effectively in the laboratory (Tilton and Schroeder, 1963) but this work has not been followed by pilot-scale studies. One advantage of these methods is that they can easily be incorporated onto conveyor belts and in some instances can even be used on packaged products. Commercial units using high frequencies and microwaves are now available.

Heat sterilization of food processing plants has been used in the U.S.A. as early as 1901. Today a few plants use this method on a regular basis, heating the facility to 54°C for 30 hr. Some precautions, such as insuring the fire sprinklers will not be activated and removing material that will be adversely affected by these high temperatures, must be taken before the heat treatment (Sheppard, 1984).

FUTURE RESEARCH

There has been an immense amount of research on the ability of stored-product insects to survive extreme temperatures. The diversity of experimental protocols makes it difficult to compare studies. Also, many of the studies are inadequate to predict survival in field situations. To avoid these problems I suggest the following standard protocols for testing the effects of extremes of temperature on insects. (1) Populations that have been reared in the laboratory for <2 yr should be used. (2) The most temperature-resistant stage of development should be used. For insects with diapause, diapausing individuals should be used (Howe, 1962). (3) Insects should be acclimated before exposing them to the extreme temperatures. For low temperature studies, acclimation at 15°C for 3 weeks should give a moderate level of cold-hardiness for most species. However, this probably will not give the maximum level of cold-hardiness. An additional acclimation schedule that reflects temperature declines that are observed in the field should also be incorporated into a complete study of cold-hardiness. Acclimation to high temperatures does not seem to affect survival at the very high temperatures (55–80°C) used in fluidized-beds and irradiation heating. However, at lower temperatures (40–50°C) acclimation can affect survival. (4) A range of extreme temperatures should be used to facilitate the development of predictive models. (5) Probit analysis should be used to analyze the data. The lethal time for 50% (best for comparisons), and 99% (best for designing control programs) of the population should be given with the fiducial limits. Fiducial limits are often not reported, perhaps because the ranges are large. Not reporting the fiducial limits with the survival data is like not giving the standard deviation with the means, making comparisons very difficult. The survival of insects at extreme temperature is highly variable. Large fiducial limits are a reflection of this fact and should be accepted as part of the biological system. (6) The final phase of any study should be a validation of laboratory results under field conditions.

The use of synergists is common with chemical control systems, an example being the use of food baits to increase consumption of the pesticide, or the addition of chemicals that inhibit the enzymes that degrade the pesticide such as piperonyl butoxide (Ware, 1983). This concept has considerable potential to increase the effectiveness of extreme temperature controls. However, a thorough knowledge of the mechanisms that enable insects to deal with extremes in temperature is needed before procedures to synergize extreme temperature control can be implemented. There are several promising avenues of research that could disclose low temperature control synergists. Information on the physiological and biochemical control of cold-acclimation and methods to block this process would make insects 3–10 times more susceptible to cold treatments. It is possible that there is no unified control of cold-acclimation and the best way to make insects more susceptible is to block the biochemical changes that enable them to survive low temperature. Lipids and enzymes have been suggested as key molecules in the temperature adaptions of other organisms, but this has yet to be investigated in any depth with stored-product insects. Preliminary work on ice nucleators indicate that insects could be controlled at −5°C in a few hours (Fields, 1990; Lee et al., 1992). The use of a synergist is also possible with high temperature control, but we know less about how organisms deal with high temperature than how they deal with low temperature. Lipids and enzymes have been suggested as the key molecules that break down at high temperatures, and the blocking of the mechanisms that protect these molecules (perhaps heat-shock proteins) would be the first step to uncover heat synergists.

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