ENVIRONMENTAL MANIPULATION AS A PHYSIOLOGICAL CONTROL MEASURE

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Abstract

Grain storage systems provide environments that are generally homogeneous and self-contained and, as such, amenable to manipulation in various ways. Components of the environment that have been manipulated with success include grain temperature, relative humidity/grain moisture-content, and atmospheric composition. This paper concentrates upon the first of these. The effects of temperature upon various demographic parameters are illustrated and a computer model is used to assess the efficiency of various cooling strategies upon population growth. The integration of cooling with fumigation or treatment with a residual insecticide is also investigated. By itself, cooling to 15°C is shown to be unable to stop population growth in certain species, although it does slow down the growth rate. When used after fumigation, rapid cooling is shown to provide a measure of long-term protection to an otherwise vulnerable grain bulk. The efficacy of combining grain cooling and treatment with a residual insecticide is shown to vary with the type of insecticide used. With pyrethroids, which have negative temperature-toxicity relationships, cooling is shown to be very beneficial and considerable savings in treatment costs could result. With organophosphorus insecticides, however, the positive temperature-toxicity relationship means that the benefits of cooling are less obvious. The use of grain cooling is shown to be beneficial for the management of insecticide resistance, because of the effect upon generation time.

Introduction

The grain handling industry is under increasing pressure to reduce its dependence upon residual insecticides to provide long-term protection to stored grains. The pressures are two-fold: first, an increasingly expensive fight against insecticide resistance and, second, a growing reluctance of customers to accept chemicals in the purchased commodities.

One way in which the dependence upon residual insecticide may be reduced is the modification of the environment so as to adversely affect the physiology of the pest insects. The stored grain environment, particularly in a bulk storage structure, is relatively homogeneous and self-contained and, therefore, amenable to manipulation. Components of the environment that have been modified with success include grain

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temperature, relative humidity/grain moisture content, and atmospheric composition. A number of control strategies employing some form of environmental manipulation are listed in Table I. The physical and engineering aspects of some of these will be dealt with elsewhere, but this paper will concentrate upon the effects of temperature upon the biology of insects and how temperature manipulation affects population growth.

The integration of temperature manipulation with the use of a residual insecticide is conventionally considered to be beneficial because population growth rate is reduced and the insecticide breaks down more slowly and therefore less insecticide needs to be applied to achieve control. This paper will show that physiological response of the insect to temperature and to the interaction between temperature and insecticide toxicity are much more important than temperature-dependent rates of insecticide decay.

TABLE I. Alternative strategies for the control of insect pests, involving environmental manipulation.

1. MODIFIED ATMOSPHERES

   (a) Nitrogen
   (b) Carbon Dioxide
   (c) Fumigation (Phosphine or Methyl Bromide)

2. TEMPERATURE MANIPULATION

   (a) Cooling by means of aeration with ambient air
   (b) Refrigerated Aeration
   (c) Thermal Disinfestation
   (d) Fumigation followed by rapid cooling
   (e) Cooling by aeration and admixture of insecticide or insect growth regulator at reduced levels.

Temperature and Insect Demography

Temperature has marked effects upon all the aspects of insect biology important to population growth. These include:

(a) Rate of development of all life-history stages.

(b) Immature survival.

(c) Adult survival.

(d) Age-specific fecundity.

There is no need to consider these in detail here, but they may be summarised in terms of a net population growth rate (Fig. 1).

Where the population growth rate (conventionally known as the finite rate of increase (λ)) is less than 1, the population is unable to maintain itself. Thus one can see that there is an optimum temperature at which population growth rate is highest, and upper and lower thresholds beyond which the population declines. It is also apparent that the range of temperature between these thresholds contracts as relative humidity declines; thus, manipulating the grain temperature towards one of these thresholds will bring about a reduction in population growth rate. In order to assess the impact of such a strategy, a mathematical model was developed from a very large data set describing the demographic performance of the rice weevil, Sitophilus oryzae (L.) (Longstaff and Evans, 1983). The details of this model are unimportant in the present context, and may be found elsewhere (Longstaff and Cuff, 1984), but in essence, it described various age-specific demographic parameters as functions of grain temperature and moisture-content. An earlier version of this model has been used in conjunction with a model of the effects of cooling by aeration, to determine optimal aeration strategies for specific conditions (Longstaff et al., 1982; Thorpe et al., 1982). The present model provides a vehicle to assess the effect of a range of grain-cooling strategies and, whilst developed for S. oryzae, has the potential to be used with any species.

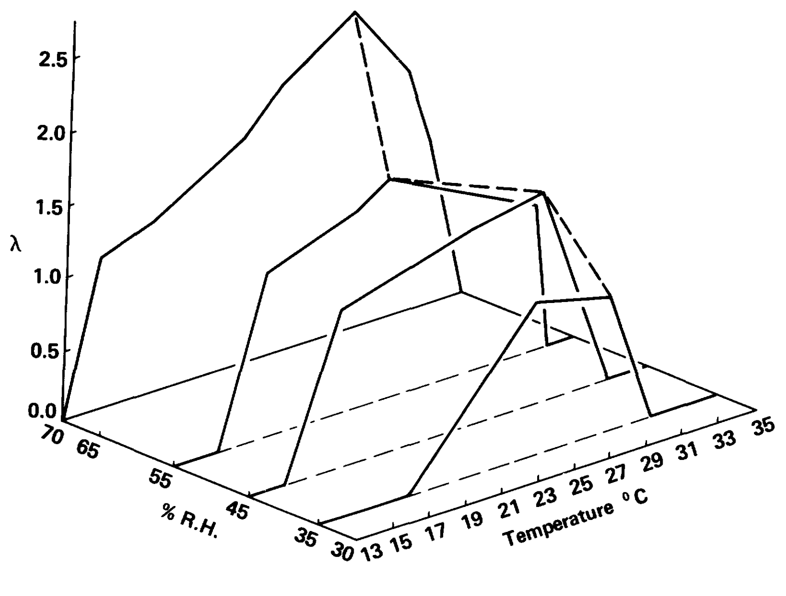

Fig. 1. The relationship between population growth rate (λ), temperature, and relative humidity for Sitophilus oryzae.

Four temperature regimes were used in the simulations:

(a) No cooling, a constant 32°C ("Uncooled").

(b) A cooling regime similar to that commonly used in Australia (and used by Thorpe *et al.* (1982) in a simulation study). Here the grain is cooled from 32°C to about 25°C after two weeks, to 23°C after 17 weeks, to 17°c after 23 weeks, and 15°C after 38 weeks ("Slow").

(c) Cooling to 25°C after one week and 0.5°C per week thereafter, until 15°C is achieved ("Medium").

(d) Cooling to 20°C after one week and 0.5°C per week thereafter, until 15°C is achieved ("Fast").

These regimes are illustrated in Fig. 2. A minimum temperature of 15°C was chosen because it was felt that temperatures below this would be difficult to achieve under Australian conditions with the use of

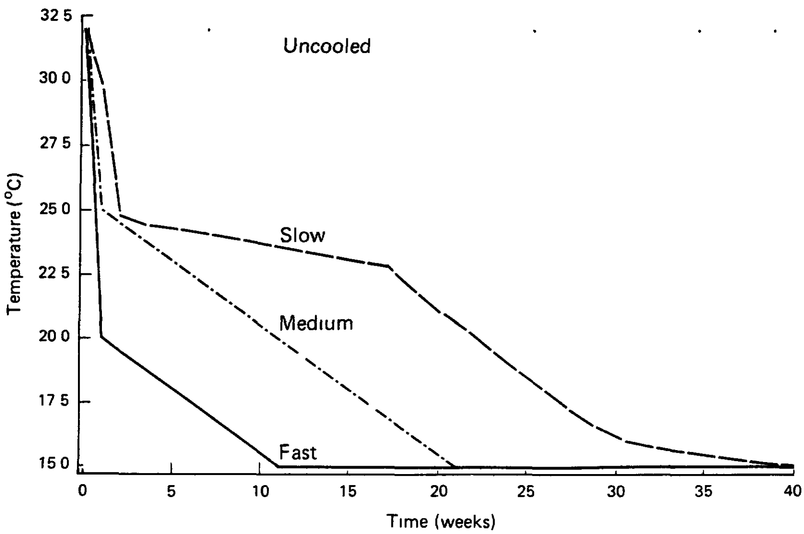

Fig. 2. The four temperature regimes used in simulations to assess the efficacy of various control strategies.

refrigeration. However, the model structure could accommodate such conditions without major modification.

The results of the simulations are shown in Fig. 3, and as one might expect the four regimes differed considerably in the population sizes produced. Regime (a) where no cooling occurred produced a population 25 times as large as that of regime (b) after 40 weeks, 500 times as large as that of regime (c) and 5000 times as large as that of regime (d). Not surprisingly, therefore, rate of cooling is of paramount importance in restricted population growth. It must be noted that none of these regimes were able to control the pest populations and so some other additional controlling factor is required to achieve this.

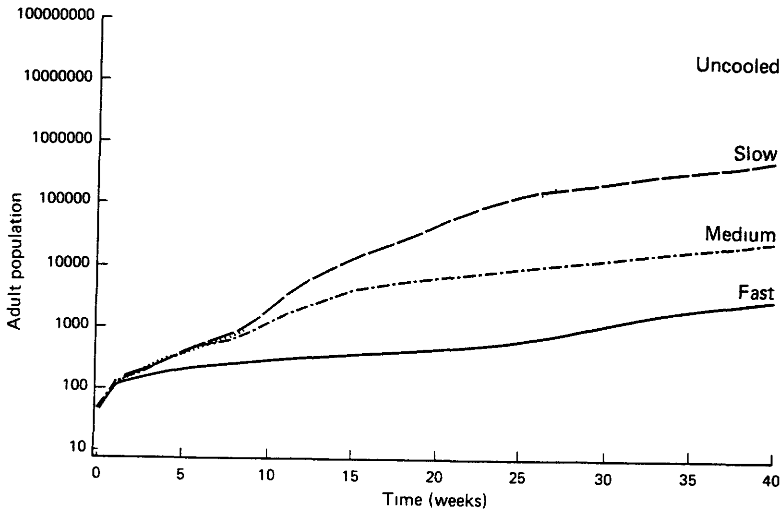

Fig. 3. The effect of grain cooling upon the population growth of *S. oryzae*.

Of the other strategies involving grain cooling, cited in Table 1, refrigerated aeration is not dealt with here because of the high capital and running costs and lack of detailed biological data on the performance of insects under such conditions. The use of grain cooling to follow fumigation and the combination of admixture of insecticide with grain cooling will now be considered.

Integrated Control - Fumigation and Cooling

This strategy was foreshadowed by Desmarchelier et al (1979). In the current simulations it was assumed here that fumigation was not completely successful and that, after a week of exposure to the fumigant, 99% of adult, 90% of pupae, and all eggs and larvae were killed. After this period of a week, one of the four temperature regimes described earlier was applied and the subsequent population growth determined (Fig. 4).

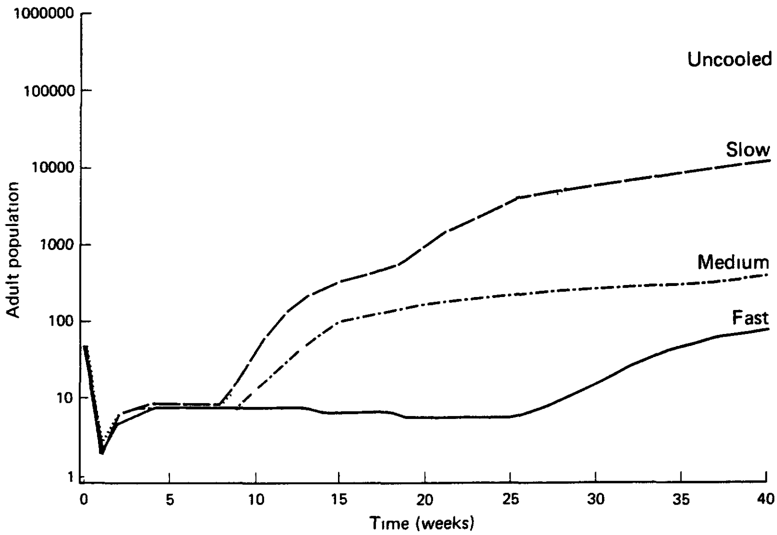

Fig. 4. The effect upon population growth of combining fumigation and grain cooling.

The populations experiencing no cooling recovered to the arbitrary detection level after about 10 weeks. Those experiencing regimes (b) and (c) were only slightly slower. However, the survivors subjected to regime (d) did not achieve this level until 34 weeks. Thus it is clear that rapid cooling may be used as an adjunct to fumigation which, by its very nature, confers no long-term protection. This approach exploits the physiological response of the insects to changing temperature.

Integrated Control - Residual Insecticide and Cooling

The cooling of grain, by means of aeration, is widely used in the grain handling industry in Australia and elsewhere to slow both the rate of breakdown of residual insecticides applied to the wheat and the rate of population growth of any insect species present. The philosophy behind this strategy is illustrated in Fig. 5, where it can be seen that the amount of Methacrifos needed at 20°C to yield a required residue of about 2 mg kg^{-1} after 10 months is less than 10% of that needed at 30°C; if the actual cooling process is taken into account this rises to 20% (Desmarchelier et al., 1979). This is simple chemical kinetics and widely cited as a major reason for using aeration (e.g. Desmarchelier et al., 1979; Desmarchelier and Bengston, 1979; Thorpe and Elder, 1980, 1982).

That the real situation is much more complex than this has been recognised by a number of authors (e.g. Desmarchelier, 1977; Tyler and Binns, 1982). This is because, in addition to the temperature-dependent kinetics of the insecticide, temperature affects the biology of the insect as we have already seen; and there is a marked interaction between temperature and toxicity of the insecticide. A number of authors have shown that the effect of cooling upon the action of an insecticide varies with the type considered. Amongst others, Iordanou and Watters (1969), Norment and Chambers (1970), Tyler and Binns (1982), Barson (1983) and Longstaff and Desmarchelier (1983) have shown that various organophosphorus insecticides have positive temperature-toxicity coefficients, i.e. they are more toxic at higher temperatures. In contrast, it would seem that pyrethroid compounds are more toxic at lower temperatures (e.g. Longstaff and Desmarchelier, 1983; Desmarchelier, 1984). These observations raise the question of whether both types of insecticide will benefit from being used with grain cooling (Longstaff, in press).

To assess the effect of cooling upon the efficacy of these two types of insecticide, the aforementioned simulation model was used. The effect of temperature upon the toxicity of the insecticide was derived from the data of Longstaff and Desmarchelier (1983) for deltamethrin and pirimiphos-methyl (Fig. 6). Because this data set was fairly small a range $\pm$ 10% of the derived values of the temperature-toxicity coefficient was used in the simulations.

In addition to the four temperature regimes shown in Fig. 2, two further constant temperature regimes were used (25°C and 30°C) which correspond to the temperatures used in studies that formed the basis for recommended application rates for these chemicals in Australia. The objective of the simulations was to find the dosage of insecticide required to achieve an adult population of less than 11% of the arbitrary detection level, after a period of 52 weeks of storage, for each temperature regime.

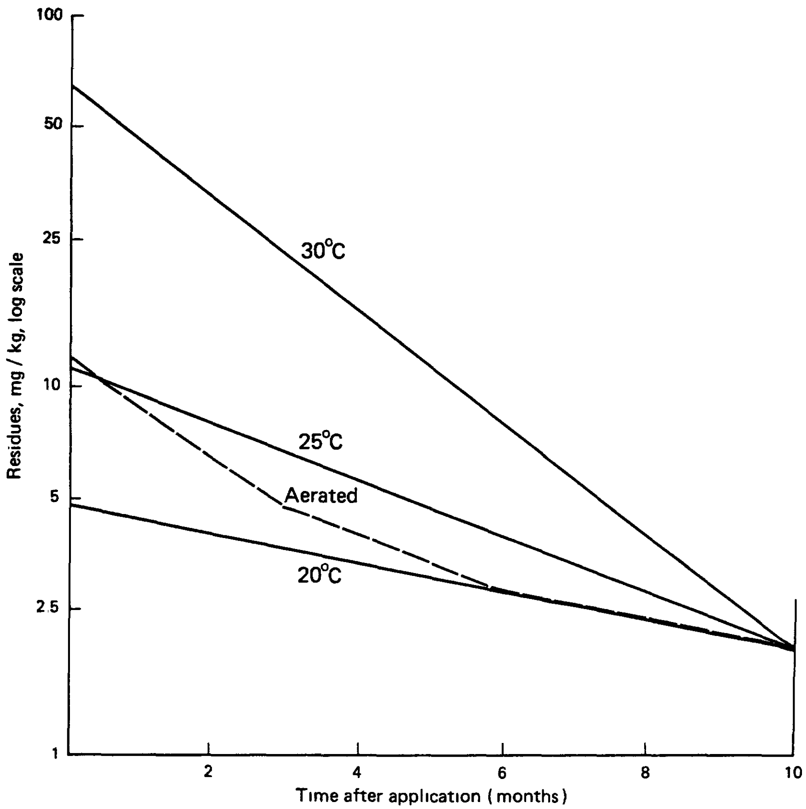

Fig. 5. The amount of methacrifos required to give 10 months protection at three constant temperatures and in aerated grain against time after application.

The results of the simulations are shown in Table II and indicate that the use of cooling with deltamethrin could reduce the dosage to about 10% of that necessary where no cooling was used. Furthermore the greater the rate of cooling the more favourable the results. Whilst the predicted dosages of pirimiphos-methyl at 25°C and 30°C are comparable with the recommended application rates in Australia i.e. 1 mg kg^{-1} for deltamethrin and 4-6 mg kg^{-1} for pirimiphos-methyl (Bengston and Desmarchelier, 1979; Hargreaves et al., 1982), the advantages of using cooling with pirimiphos-methyl would seem to be less obvious, with the model predicting much higher dosages when rapid cooling is employed. Such high dosages could prove hazardous to operators, as noted by Tyler and Binns (1982).

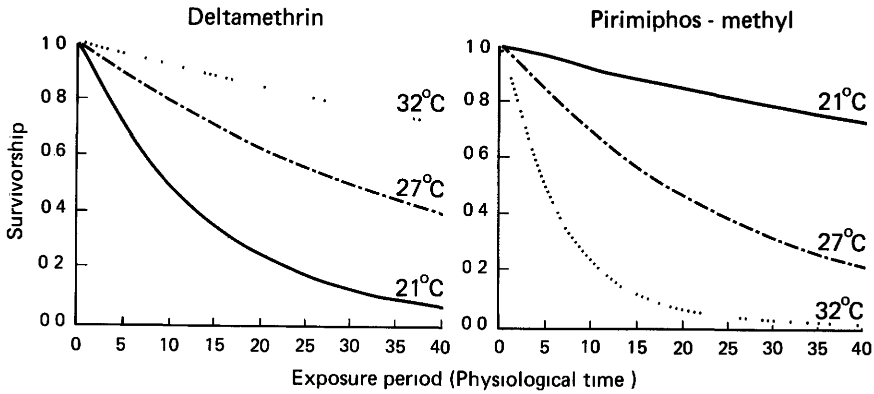

Fig. 6. The relationship between survivorship of S. oryzae and period of exposure to deltamethrin and pirimiphos-methyl at each of three constant temperatures.

The results for pirimiphos-methyl, which are similar to those of Tyler and Bins (1982), would appear to be in conflict with those of Desmarchelier (1977). He found that 6 mg kg^{-1} of pirimiphos-methyl provided a minimum of 30 weeks of protection against S. oryzae at both 20°C and 30°C. There are several possible explanations for this apparent conflict. First, the data set from which the temperature-toxicity relationship was derived was quite small and, as shown in Table II, errors in estimating the temperature-toxicity coefficient have a major effect upon the predicted dosages. Second, the model assumes that the infesting population has a stable age distribution, with many more immatures than adult insects. If one were to delay cooling for a period long enough to allow all stages to develop to maturity, they would be exposed to the insecticide under the conditions where it is most toxic. Subsequent rapid cooling would then be applied. A further series of simulation was carried out to assess the implications of this and it was found that a minimum period of about 9 weeks was required before cooling. The predicted dosages of pirimiphos-methyl required for control were significantly reduced under these circumstances, by as much as an order of magnitude in the case of rapid cooling (Table II).

The third point concerns the methodology adopted in these three studies. Tyler and Binns (1982) and this study assess the efficacy of the chemical over relatively short periods (24 hrs and 4 weeks respectively) whereas Desmarchelier (1977) uses 30 weeks). Whilst the model does allow for temperature-dependent breakdown of the insecticide it does not allow for loss of bioavailability (Champ et al., 1969; Rowlands, 1971; Desmarcheleir, 1978) which may also be temperature-dependent.

TABLE II. The results of simulations carried out to determine the amounts of pesticide (mg kg^{-1}) needed to achieve control (10% of detectable level of adults after 40 weeks) of Sitophilus oryzae. In addition, to the four temperature regimes described in the text, two other constant temperatures were employed (30 and 25°C).

Temperature Regime	Deltamethrin	Pirimiphos-methyl
Constant	1.93	0.53
Thorpe cooling regime	0.67	12.80
Cool to 25°C after 1 week	0.40	22.40
Cool to 20°C after 1 week	0.13	40.53
Constant 30°C	1.60	1.07
Constant 25°C	0.63	4.27

Integrated Control - the Management of Insecticide Resistance

It was mentioned earlier that at lower temperatures the rate of development of all insects is reduced and it is obvious that this means that fewer generations can be gone through in a given storage period. This is of great importance where one is concerned with management of stored grain susceptible to infestation by pest species containing insecticide resistant individuals. In uncooled grain of 30-32°C the generation time for S. oryzae is about 5-6 weeks and selection will be able to act on 8-10 generations of individuals in a storage period of a year. By contrast, at 15°C the generation time is about 30-32 weeks and selection will have at the most 2 generations to act upon. Thus, as pointed out by Heather (1979, 1982), the effects of lowered temperatures upon the biology of the insects are beneficial to the manager.

The aforementioned population growth model can be modified to include a relatively simple genetic submodel of resistance that describes the most common type of resistance observed, a single, incompletely dominant factor. A range of initial gene frequencies and resistance factors were employed, with the heterozygote having intermediate fitness. It was assumed that the resistance was expressed in terms of enhanced adult survival only. The objective of the simulations was to determine the amount of extra insecticide that would be needed to produce the same degree of control where resistance is absent. The results are shown in Table III for the two most extreme temperature regimes. In the "worst case" situation, where the initial gene frequency is 10^{-2} and the resistance factor is 64, the amount by which the dosage has to increase when no cooling is employed is more than double that where rapid cooling is employed, for both types of insecticide. Obviously, the earlier comments about the wisdom of using cooling with organophosphorus compounds must be considered in light of the probability of resistance occurring.

TABLE III. Proportional increase in the pesticide application rate necessary to achieve a similar level of control to that where resistance is absent.

1. No Cooling

Resistance factor	Initial Gene Frequency					
	10^{-4}	10^{-3}	10^{-2}	10^{-4}	10^{-3}	10^{-2}
4	1	1	1.05	1	1.02	1.05
8	1	1.02	1.2	1	1.05	1.2
16	1	1.05	1.55	1.01	1.1	1.6
32	1.04	1.25	2.2	1.05	1.25	2.3
64	1.1	1.65	3.3	1.1	1.55	3.6

2. Fast cooling

Resistance factor	Initial Gene Frequency					
	10^{-4}	10^{-3}	10^{-2}	10^{-4}	10^{-3}	10^{-2}
4	1	1.01	1.03	1	1	1.03
8	1	1.02	1.05	1	1.01	1.05
16	1.01	1.03	1.1	1	1.02	1.1
32	1.03	1.04	1.2	1	1.03	1.2
64	1.05	1.05	1.6	1	1.05	1.35

Apart from the effect upon required application rates of resistance being present, the temperature regime will effect the gene frequency.

The interaction between insecticide, temperature regime, resistance factor and initial gene frequency are shown in Table IV and the gene frequency trajectories for the "worst case" situation (resistance factor of 64 and initial gene frequency of 10^{-2}) with deltamethrin is shown in Fig. 7. Cooling the grain not only reduces the amount by which the application rate must be increased; the level of resistance at the end of the storage period may be as much as two orders of magnitude lower.

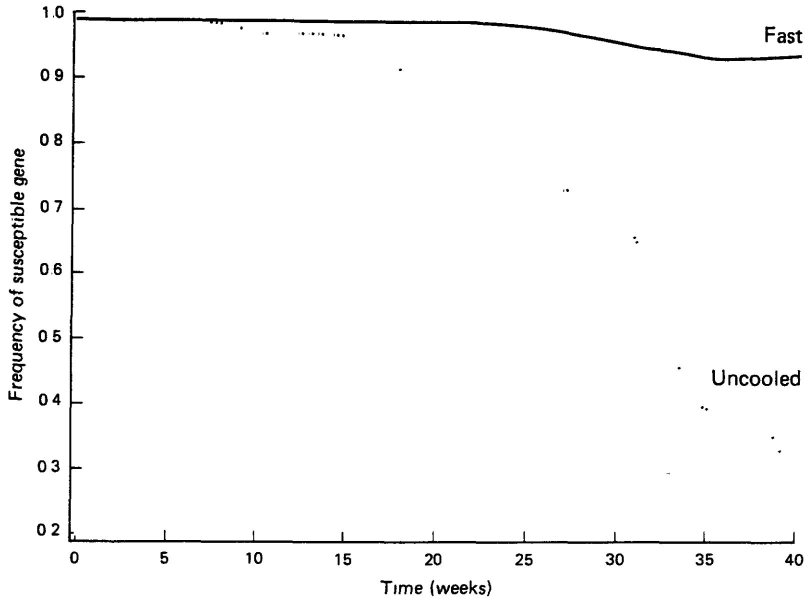

Fig. 7. The changes in frequency of the susceptible gene in populations subjected to no cooling and fast cooling.

Conclusion

From what has been said above it is apparent that the manipulation of certain aspects of the stored grain environment, namely temperature and relative humidity will adversely affect the physiology of the pest species, reducing both the population growth rate and the number of generations upon which selection can act. By itself, this sort of manipulation is unlikely to achieve total control of the pest population but it may be seen as part of more effective integrated strategies. There would appear to be scope for using grain cooling to follow

TABLE IV. Frequency of resistance gene in youngest adult age class after 40 weeks of storage.

1. No Cooling

Resistance factor	Initial Gene Frequency							
	Deltamethrin				Pirimiphos-methyl			
	10^{-5}	10^{-4}	10^{-3}	10^{-2}	10^{-5}	10^{-4}	10^{-3}	10^{-2}
4	0.0002	0.0011	0.0100	0.0915	0.0001	0.0001	0.0063	0.0578
8	0.0004	0.0032	0.0308	0.2345	0.0003	0.0020	0.0189	0.1358
16	0.0010	0.0096	0.0966	0.4444	0.00007	0.0062	0.0551	0.2415
32	0.0028	0.0270	0.2044	0.6278	0.0020	0.0195	0.1234	0.3142
64	0.0073	0.0680	0.3722	0.7241	0.0082	0.0511	0.1990	0.3310

2. Fast Cooling

Resistance factor	Initial Gene Frequency							
	Deltamethrin				Pirimiphos-methyl			
	10^{-5}	10^{-4}	10^{-3}	10^{-2}	10^{-5}	10^{-4}	10^{-3}	10^{-2}
4	0.00001	0.0002	0.0019	0.0187	0.00001	0.0002	0.0018	0.0173
8	0.00003	0.0003	0.0027	0.0259	0.00003	0.0003	0.0024	0.0234
16	0.00005	0.0004	0.0037	0.0356	0.00005	0.0004	0.0033	0.0312
32	0.00007	0.0006	0.0052	0.0481	0.00007	0.0005	0.0044	0.0410
64	0.0001	0.0008	0.0071	0.0635	0.0001	0.0006	0.0059	0.0532

fumigation of a grain bulk, to provide a measure of long-term, residue-free protection. It may also be combined with the use of residual insecticides, although it would seem that the situation with organophosphorus compounds is not clear. Where pyrethroid compounds are used, the combination of reduced fecundity, lowered immature survival and protracted development periods with enhanced toxicity of the chemical will result in major savings in application costs.

Whilst the use of grain cooling has obvious benefits for the manager, there are also risks. An assumption of the modelling exercise was that the temperature was uniform throughout the bulk, or at least that the temperatures used were the highest observed througout the bulk. This obviously puts a premium on the design of the aeration system and, particularly, the minimisation of the "edge effects".

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