Time to population recovery as a means for specifying low oxygen dosages

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Abstract
Dosage regimes for gaseous toxicants are usually given in terms of concentration and an exposure time. These regimes are conveniently based on the effective dose known to give some defined level of mortality (EDx). The EDx can be closely defined and confidence intervals calculated when experimental conditions are well controlled. While the EDx is useful scientifically it is not so useful for grain managers. Their task is to integrate treatments with a range of operational considerations. This paper describes the integration of a model of mortality of Sitophilus oryzae under low oxygen atmospheres (<1% O2) with demographic models of this species. The purpose of the combined model is to allow grain managers to optimise exposure periods in terms of available time and grain temperature. This allows them to determine the minimum duration insect-free storage expressed as time to population recovery.

Introduction
One of the aims of a grain manager is to have grain of known provenance and quality available for dispatch when required. In many cases this means having grain free of detectable insects at the time it leaves the storage facility. It is a difficult task to predict when, and if, insect numbers will become detectable by outturn inspection procedures at some time in the future. The task is made harder because of gaps in our knowledge of insect population dynamics at very low densities. Furthermore, the detection of no insects at inspection is at best semi-quantitative. In stored-product insects, densities of 1500/t are about the lowest useable with reasonable population models (Longstaff 1981), whereas the average insect density entering the Australian bulk handling system has been estimated to be about 8 insects/t (White 1985).

The mortality response of insects to toxicants is conventionally described by probit analysis, on the assumption that there is a linear relationship between the probit of mortality and some transformation (normally logarithmic or linear) of an expression of dosage applied (time, concentration or the product of concentration and time). Therefore, if the original population number is known, it should be possible to combine models of population dynamics with the results of probit analysis to predict population numbers at any time after treatment. Although this is theoretically possible and its use has been reported previously (Banks 1986), there are several simplifying assumptions required that may limit its practical use.

This paper discusses the process used to determine times of low oxygen exposure required that should ensure that no insects will be detected when the grain is presented for inspection some time later. The effects of simplifying assumptions are considered, along with gaps in our overall knowledge, and the potential effects these may have on the outcome are discussed.

In Australia there are about 10 species of insects most likely to be found during outturn inspection of grain. There are very few comprehensive dosage-response data for the effects of low oxygen atmospheres for these insects. There are, however, enough data to suggest that pupae of Sitophilus spp. and Rhyzopertha dominica are the most difficult to kill under low oxygen conditions (Annis and Dowsett 1993). There are sufficient data on these species to make crude estimates of probit response lines at temperatures in the range 21–27°C. The demography of Sitophilus oryzae is well documented (Longstaff and Evans 1983) and it is possible to model the time of occurrence and duration of the immature stage (Annis and Banks 1993).

There are no single or adequate sets of data that relate all the processes needed to make the necessary models which will give the interactions between initial population, projected population size, percentage kill, temperature and relative humidity. There are, however, several individual studies that may be linked and approximations that can justifiably be made. The aim of the study reported here was to make conservative estimates of the maximum probable number of live insects that may occur at a specified time after treatment. This means that all assumptions must be conservative in terms of the estimated period of insect-free storage.

The major assumptions are as follows:

- Any infestation will include S. oryzae, a species known to be highly tolerant of low oxygen atmospheres.

- Any treatment giving substantial mortality in S. oryzae pupae will give complete mortality in all other stages and species.

- At the time of treatment, even if no insects were detected, the actual number would be just below the limit of detection.

- The same low level infestation (i.e. just below the limit of detection) will be acceptable at a future outturn.

- It is known that the number of eggs produced per insect is reduced at low population densities (Longstaff 1981), and that there is likely to be a time lag until widely dispersed pairs of insects find each other. As this effect is not quantified, it is not considered in the population models used, and reproduction rates at low population densities are always assumed to be at optimum levels.

- Temperature/time/mortality data are far from comprehensive, therefore a common slope is assumed for the time/mortality, and a second common slope for the temperature/mortality, curves.

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Data Sources

Effects of temperature on the duration of immature stages

Eastham and Segrove (1947) present a comprehensive set of data on the duration of immature stages of S. granarius over the temperature range 15–30°C and 40–70% r.h. As no similar data exists for S. oryzae, the data for S. granarius was used. The duration of the immature stages in this data set could be well represented by the equation

\[ P_i = 10(0.6833 + 27.441/T - 0.0002r - 0.072330r/T) \]  \( \text{(1)} \)

where \( P_i \) is the duration of the immature stages (days), \( T \) is temperature in °C and \( r \) is the relative humidity. The immature period was taken as the basis for a physiological time period, and used to scale a beta function that described the survivorship curve of Birch (1953). Time is corrected to physiological time units on the basis of \( P_i \) compared to 28 days (a nominal standard immature period), by a scaling factor \( f_P \) where \( f_P = 28/P_i \) and therefore the corrected physiological time \( t_c = f_P t_f \)

\[ f = 1 - \text{BETADIST}(t_f, 3.155, 3.802, A, B) \]  \( \text{(2)} \)

where \( f \) is the fraction of the whole population surviving at \( t_c \) (in weeks), BETADIST is a Microsoft Excel spreadsheet function that returns the cumulative beta probability density, \( t_c \) is the value at which to evaluate the function over the interval \( A < t_c < B \), \( A \) and \( B \) lower and upper bounds to the interval of \( t_c \).

Fecundity based on temperature and relative humidity

The composite data in Longstaff (1981) which cover the number of eggs laid over the reproductive life of S. oryzae are well fitted by the polynomial in \( T \) and \( r \) given below. These data cover the range 45–70% r.h. and 15–35°C. The original data are corrected to a uniform population density of 1 female/500 grains.

\[ L = 10.85 + 155.1r - 2.235r^2 + 0.01103r^3 - 495.7T + 23.91T^2 - 0.3727T^3 + 0.000109rT^2 \]  \( \text{(3)} \)

Where \( L \) is the lifetime egg production per female at population density of 1 female/500 grains, \( T \) is the temperature, \( r \) is the relative humidity.

Density dependent fecundity

The equation relating fecundity to population density is from Longstaff 1981 and applies to S. oryzae.

\[ F = 6.821(\log_{10}N)^2.322N^{-0.3992} \]  \( \text{(4)} \)

This function has been shown to be applicable from approximately 10–10^7 weevils/million grains. The assumption used in the model is that, below 10 weevils/million grains, the fecundity remains at 18.9 eggs/female/week; the value calculated at a density of 10 weevils/million grains. This assumption is conservative and presumes that no matter what the initial distance between insects mating will occur immediately (no searching time involved). This equation was derived from data collected at 27°C and 65% r.h. (14% m.c. grain).

Time mortality data

There are three sets of data available with useable information on pupal survival of S. oryzae under low oxygen conditions (Lindgren and Vincent 1970; Storey 1975a; Annis and Dowsett 1993). Most other published data lack adequate definition of developmental stages and/or results to allow their incorporation into any model. The reported LT50 and LT95 from the useful papers are shown in Figure 1, which indicates that the gradient between log(time) and probit mortality does not vary widely no matter what the developmental stage or temperature. It was possible to model the LT values of pupae as a surface with a probit mortality axis, a linear temperature axis, a logarithmic time axis and an interaction term between log time and temperature. The fit was not perfect but was well

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Fig. 1. LT50 and LT95 for Sitophilus oryzae adults and pupae at various temperatures reported by several authors: a. Annis (1987); l. Lindgren and Vincent (1970); sa Storey (1975a); sb Storey (1975b).
within the needs of the model (Fig. 2). The resulting equation was:

\[
M = 100 \cdot \text{NORMSDIST}[-15.57 + 0.2201 \cdot T + 1.871 \\
\quad \log_{10}(t) + 0.1080 \cdot \log_{10}(t) - 5]
\]  

...(5)

Where \( M \) is the calculated percentage mortality in the pupal stage, \( T \) is the temperature in °C, \( t \) is the exposure period in hours and NORMSDIST is the Excel function that returns the standard normal distribution function.

The component parts of the model were combined to calculate the number of live individuals in 1-day age cohorts. This was updated in 7 day time steps for natural mortality, egg production and mortality, if a treatment has taken place. An Excel spreadsheet was used as a convenient framework for calculation but many other computer applications and language packages would be equally applicable.

Results and Discussion

Combination of the empirical models allows estimates of the minimum time until a population returns to its original size (see Fig. 3). This gives the grain manager an indication of the minimum safe storage period. It can be seen that this period remains more or less constant for any given exposure time over the range 22–32°C and tends to give longer protection as temperatures fall below 22°C. Because this model is purely empirical it cannot be used outside the range of data used to create its components which was 17.5–32.5°C.

A major limitation of this analysis is that no allowance is made for a lag in reproduction or reduction in fecundity due to very low population densities. These phenomena have been reported for *Sitophilus granarius* by Maclagan (1932) who stated that at population densities below 1 insect/200 grains the number of progeny per weevil began to fall. These findings were confirmed (and some additional data added) by Longstaff (1981) who showed that this phenomenon probably continues down to densities of about 1 insect/20000 grains (about 1 insect/750 g of wheat). There is no information for less than this density although it is likely that it will continue until some very low population densities where reproduction will no longer occur. There is, unfortunately, no information on which to model what happens at the low densities expected after an effective treatment. This means that in real treatments, it could be expected that the protection will be somewhat longer than that estimated.

Conclusions

It is possible to produce a mathematical model of population growth following treatment with low oxygen atmospheres at different temperatures. This model relies on combining a
series of empirical equations that describes mortality and the components that determine subsequent population growth. There are obvious limitations to this approach, but it provides more information than was previously available for determining exposure regimes for different temperatures. There are still important gaps in the knowledge required to complete the modelling process. Until these are filled there is little value in improving the model or setting up experiments to validate its output.

The current model, while having many limitations, will be useful because it gives grain managers an idea of the minimum period of effective protection given by an exposure to a low oxygen (<1%) treatment. Predictions by the model will be conservative in terms of the period of protection and this period is likely increase as more knowledge becomes available.

References


