Journal of Stored Products Research xxx (2014) 1–15

Contents lists available at ScienceDirect

Journal of Stored Products Research

journal homepage: www.elsevier.com/locate/jspr

Review

A review of insect responses to variations encountered in the managed storage environment

C.H. Bell

Fellow Emeritus, Food and Environment Research Agency, Sand Hutton, York YO41 1LZ, UK

ARTICLE INFO

Article history:
Accepted 10 June 2014
Available online xxx

Keywords:
Temperature and concentration thresholds
Stored product protection
Insect activity
Resistance
Insect development

ABSTRACT

In combating infestation in the storage environment the choice of control method and appropriate setting of dose or exposure level needs to take into account how long it is likely to take for the applied measure to reach the site of infestation, and then the local environmental conditions of temperature and humidity before deciding how long is needed for insects to be controlled. Other factors such as the physical properties of the stored product, the nature of the packaging, the time of year and the lighting conditions, may also be of critical importance. This review examines some of the defence mechanisms insects employ and environmental niches they utilize when confronted by control measures.

The responses of insects to natural or induced environmental stimuli may be divided into behavioural and metabolic responses. Behavioural responses include orientation towards more favourable conditions or attractants, and avoidance measures such as retreating from treated surfaces into a refuge or descending a concentration gradient of a repellent gas or fumigant. Metabolic responses include aspects of increased metabolism such as when a toxicant is actively excluded from entering the body or the activation of enhanced detoxification pathways following uptake, and aspects of reduced metabolism such as the shutting down of activity, an induced delay in development prolonging a tolerant stage, or a switch to less active biochemical pathways such as anaerobiosis. The response of insects to physical and chemical gradients, treated surfaces, their temperature-related activity responses, their survival at temperature extremes and survival thresholds in toxic atmospheres are discussed in the context of pest survival and the development of resistance in the storage environment.

1. Introduction

A basic property of any ecosystem is the process of continual adjustment to maintain stability, a reflection of the universal law of energy transfer from a higher zone to a lower one. All living organisms have survived by adopting strategies for survival in their ecosystem. For mankind the primary strategy has been one of attempting to manage the environment; for insects and mites it has been one of keeping pace with environmental change. To this end the evolutionary trend in insects has been towards small size, a rapid breeding cycle and close links between environmental cues and specific responses. Economy in size leads to economy in the number of cells available to comprise vital organ systems and sensors. The insect nervous system is a wonder of creation in its simplicity and efficiency, enabling the most subtle of environmental stimuli received by a range of finely tuned sensors (Anderson and Hallberg, 1990; Kučerová et al., 2014; Ndomo-Moualeu et al., 2014) to elicit precise metabolic or behavioural responses that are designed to be of potential advantage to the individual.

Many factors are involved in the successful maintenance of a safe storage environment. Environmental conditions can be radically altered by the arrival or increase of insect populations. The application of control measures, whether by using a chemical pesticide or altering the physical environment by manipulation of temperature, humidity or oxygen level, brings about further changes. In any environment upper and lower temperature limits for survival exist for each pest species, in close relationship with those for humidity, individuals differing in their response. Besides taking into account the dosage or application levels needed for effective control, pest management programmes also need to consider temperature thresholds for insect development, mobility and flight which control population growth and dispersal.

The control of insect infestations in food stores has required much effort over the years and remains a major problem in the modern world. Insects and mites can tolerate some extreme conditions much better than mammals or birds. Control intervention

---

E-mail addresses: chris.bell@fera.gsi.gov.uk, candv@bellhuntington.fsnet.co.uk.

http://dx.doi.org/10.1016/j.jspr.2014.06.004
0022-474X/© 2014 Elsevier Ltd. All rights reserved.

Please cite this article in press as: Bell, C.H., A review of insect responses to variations encountered in the managed storage environment, Journal of Stored Products Research (2014), http://dx.doi.org/10.1016/j.jspr.2014.06.004

by any procedure has the objective of rendering the environment unsuitable for survival of pest species while not endangering humans or livestock. The success of treatments is often challenged by the ability of insects and mites to respond by activating various defence mechanisms. Insects are potentially vulnerable to a wide range of adverse chemical and physical environments but the threshold levels for effective action of these may differ widely from one species to another, between the developmental stages of a particular species and even between individuals of the same species and stage.

In food stores there are limitations in applying measures to combat infestation as the food itself might be adversely affected. For bulk stored food, fumigation has long been chosen as the most practical control option for dealing with an active infestation. Here the key for success is in obtaining an adequate concentration level of the toxic gas for a sufficient time at the actual site the pests are present. This will include penetration to voids and crevices in the retaining structure where local temperature differences may combat the ingress of gas. The difficulty of obtaining an even distribution of a fumigant gas may be compared to the reaching of a target level of temperature in heat treatments, particularly in bulk commodities where heat transfer becomes a major obstacle, but also in food processing facilities where obtaining an even distribution is always a problem. Where structural heat treatments are carried out, the time taken to reach the target temperature at all points always greatly exceeds the time needed to eradicate the incipient infestation which at, say, 50 °C may be less than 1 h (Banks and Fields, 1995; Burks et al., 2000).

The ability of insects to respond to gradients of temperature, humidity and various gas concentrations enhances their chance of survival (Section 2). Other behavioural responses that can be of advantage include the seeking of locations away from treated surfaces such as crevices or food residue layers (Section 3) and activity responses linked to diurnal rhythms and aggregation cues (Section 4). Temperature controls insect mobility in addition to survival and development extremes (Section 5) and there are metabolic responses related to raised temperature and other control procedures (Section 6), the enhancement of which can rapidly lead to pest resistance (Section 7). Metabolic responses include mechanisms excluding uptake of a toxicant, the shut-down of activity or the development of an increased capacity to detoxify or eliminate a toxicant after uptake. Active sites might become desensitised and there are also developmental aspects such as the induced prolonging of a tolerant stage or entry into diapause. In this review the various responses of insects that can increase the potential for survival in managed storage environments are explored.

2. Response to gradients

2.1. Gradients encountered in practice

Insects are finely tuned to locate food sources, food odours providing the principal attractant, but in each of the different storage or food processing environments that are encountered in practice, local microclimates exist and give rise to gradients, gradients of temperature, moisture or humidity, light intensity and even gradients of atmospheric gases set up by the respiration of stored products or the pest populations present. When a building or silo is sealed, or a bag stack or cereal bulk sheeted prior to a fumigation or controlled atmosphere treatment, some of these gradients may be buffered or modified but they still exist.

The optimum requirements of insects and mites for active development are well known and much information has been gathered on their capacity to locate environments supplying the right conditions for breeding. Many species produce pheromones which at very low levels are effective in attracting other individuals to assist the rapid colonisation of a food source. Besides the biological responses to food odours, kairomones and pheromones, in grain bulks insects have been shown to respond to gradients of temperature (Surtees, 1964; Hagstrum et al., 1998; Jian et al., 2003, 2005; Flinn and Hagstrum, 2011; Throne and Flinn, 2013), moisture content (Yinon and Shulov, 1969; Parde et al., 2004), oxygen (Navarro et al., 1981; Adler, 1992), carbon dioxide (Navarro et al., 1981; Parde et al., 2004) and light (Smereka and Hodson, 1959). In chamber tests they have also been shown to respond to moving gas fronts of the fumigants methyl bromide and phosphine (Bell, 1987). Table 1 lists some of the species for which some strains have been shown to respond to different gradients.

2.2. Temperature and humidity

The response to a particular gradient in different insects may differ widely. Most insects ascend temperature gradients as long as the top end of the range is well below 40 °C, but the rate at which they respond varies greatly according to mobility within the medium. Hence in grain *Cryptolestes ferrugineus* (Stephens) will move towards a 1 °C temperature rise within an hour while the less mobile *Rhyzopertha dominica* (F.) may take several days to respond (Flinn and Hagstrum, 1998, 2011). With respect to intermediate levels of humidity, while *Trogoderma granarium* (Everts) will descend a moisture gradient in grain bulks, *Sitophilus granarius* (L.) and *C. ferrugineus* will move towards zones of higher moisture (Yinon and Shulov, 1969; Smereka and Hodson, 1959; Parde et al., 2004).

In the course of random dispersal insects may seem to show a preference for moving up or down in grain bulks and the response to gradients might be overridden by this response (Parde et al., 2004; Jian et al., 2009). The apparently positive geotropic movement of *C. ferrugineus* in wheat required the combined effect of high moisture and low CO_2 concentration gradients to be completely overcome (Parde et al., 2004).

There are other factors which may enhance the effect of movement in response to a gradient. The release of semiochemicals is an obvious example. Semiochemicals have been extensively used for infestation detection in mills and warehouses and also for mating disruption at higher concentration levels (Trematerra et al., 2013; Burks and Kuenen, 2012). When several insects responding to a stimulus arrive in one locality, sex or aggregation pheromones may be released that cause an increased level of aggregation, very possibly drawing in individuals that were not responding to the original gradient. A temperature gradient may then be set up by the local activity which may act as a further attractant and arrestant for other pests.

2.3. Gases

One of the problems associated with the assessment of insect responses to a gas concentration gradient or treated surfaces is how to differentiate between what is simply an excitory response, whereby activity is increased causing non-directional random movement, and what is a true movement away or towards the stimulus. When examining the effect of treated surfaces in choice tests, a general increase in activity will tend to cause fewer insects to be present at any one time in the treated half of an arena than in the untreated half simply because movement is faster where the activity level is increased. However, when activity is increased on encountering a gas front, there is the additional possibility that insects moving at random may become immobilised if their movement does not quickly take them away from the increasing gas concentration, and this can create the impression of attractancy

Please cite this article in press as: Bell, C.H., A review of insect responses to variations encountered in the managed storage environment, Journal of Stored Products Research (2014), http://dx.doi.org/10.1016/j.jspr.2014.06.004