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The Combined Influence of Temperature and Modified Atmospheres on *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae)

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Abstract—In laboratory experiments, egg, larval, pupal, and adult stages of the red flour beetle *Tribolium castaneum* (Herbst) were exposed to three low oxygen concentrations realistically obtainable under hermetic storage conditions, at three temperatures of 26, 30, and 35°C. The gas concentrations were: 1% O_2, 85% N_2, 14% CO_2; 2% O_2, 84.7% N_2, 13.3% CO_2; 3% O_2, 85% N_2, 12% CO_2 (all at 75% relative humidity). When exposed to the 3% O_2 level at 26°C, adults were most tolerant with a mortality of 70.5% when exposed for 10 d. To obtain 99% mortality at 35°C with the atmosphere containing 1% O_2, a maximum of only 44 h was required for the most tolerant stage, namely the pupa. Comparison of exposure times required to produce 50% kill (LT_{50}) showed that the effect of temperature on mortality rates was pronounced at all three levels of O_2; for all the insect stages, values of LT_{50} at 35°C ranged between 0.16 and 0.5 times those at 26°C. The insects were also submitted to a gas mixture containing 1% O_2 in 99% N_2 representing a mixture obtainable by N_2 flushing techniques. At the higher temperatures, differences in mortality from those obtained on exposure to 1% O_2:85% N_2:14% CO_2 were not significant. However, at 26°C, mortality levels of insects exposed to this mixture were lower, particularly for adults and eggs. Copyright © 1996 Published by Elsevier Science Ltd

Key words—Tribolium castaneum, hypoxia, temperature, hermetic storage, modified atmospheres

INTRODUCTION

In the recent past, the preservation of cereals and other durable agricultural products in storage has relied heavily upon insecticides to control storage pests. However, the present trend is towards alternative non-toxic control methods that pose no threat to the health of operator or consumer, and which are environmentally friendly. The use of modified atmospheres (MA) is one of the most promising alternatives. The technology has been developed, and is suitable particularly for industrially advanced countries (Longstaff, 1994). However, in developing countries and in situations where prolonged storage is required, the use of naturally modified atmospheres produced by respiration of insects or micro-organisms in well-sealed structures, and termed traditionally as hermetic storage, is an alternative of great potential that is being re-evaluated (Navarro *et al.*, 1994; Varnava *et al.*, 1995).

Oxygen (O_2) depletion and carbon dioxide (CO_2) enrichment of the intergranular atmosphere form the basis for insect infestation suppression and control in the hermetic storage of dry grain.

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However, our knowledge of the sensitivities of insects to atmospheres obtainable in 'real-life' hermetic-storage situations is only partial. The important role of low O_2 concentration rather than high CO_2 in causing mortality of stored-product insects in hermetic storage was demonstrated by Bailey (1965). Only later was the importance of the synergistic effect of concomitant O_2 depletion and CO_2 accumulation for insect control clearly demonstrated (Calderon and Navarro, 1979, 1980). These synergistic and combined effects contribute to successful insect control, as shown by studies of the effects of incomplete air-tightness upon insect populations (Oxley and Wickenden, 1963; Burrell, 1980). Furthermore the lower the grain moisture content (m.c.) and corresponding intergranular humidity, the higher the mortality, due to the desiccation effect on insects caused by low O_2 (Navarro, 1975, 1978), or elevated CO_2 concentrations (Navarro and Calderon, 1973). The influence of temperature on insect respiration implies that in warm climates characteristic of developing countries, O_2 intake by insects is very intensive and O_2 reduction may be rapid. Conversely in temperate climates, insect metabolism is much slower, depletion of O_2 may be lower than its ingress, and insect control may not be achieved. This led Burrell (1980) to postulate that for light infestations of cool grain, residual populations would provide an inoculum for reinfestation after the grain is removed from hermetic storage.

Of the few published studies on the influence of low O_2 concentrations on stored product insects, that by Annis and Dowsett (1993) compared the sensitivity of all stages of *T. castaneum* to O_2 concentrations of 1–3% O_2 in N_2 at 25°C with those of *Rhyzopertha dominica* (F.) and *Sitophilus oryzae* (L.). Exposure periods lasted up to 53 d with very high mortalities recorded for *T. castaneum* at 3% O_2 after 30 d.

In recent studies Soderstrom *et al* (1992) combined heat with MA regimes with the objective of reducing exposure times for MA treatments. They showed that the sensitivity of *Tribolium castaneum* to hypoxia and hypercarbia is strongly influenced by temperature.

In contrast, this laboratory study was undertaken to investigate exposure times required to kill *T. castaneum* at three low oxygen concentrations realistically obtainable under hermetic storage conditions, at three temperatures covering the range of storage temperatures commonly encountered in warm climates. To account for extreme conditions that may arise in hermetic storage as a result of moisture migration, and the development of high-moisture pockets, a humidity level of 75% relative humidity (r.h.) was chosen in order to minimise the known combined effect of low humidity and hypercarbia mentioned above. For comparison, one MA concentration obtainable by N_2 flushing was also examined.

MATERIALS AND METHODS

Modified atmospheres

Three combinations of atmospheric gases were chosen to cover the range of atmospheres frequently produced in well-sealed containers by naturally modified atmospheres. For comparison, a nitrogen (N_2) rich MA, obtainable under N_2 flushing treatment was evaluated.

The chosen MAs and gas levels achieved are set out in Table 1.

These compositions were obtained from supply cylinders of O_2, N_2 and CO_2 using a gas-mixing apparatus described by Donahaye (1990). This consisted of component gases supplied in tubing at rates regulated by a series of valves and gas-flow meters, which enabled the components to be mixed in the desired combinations. After the gas supplies converged, gas in the common supply-line was led to temperature controlled incubators, adjusted to the desired temperature, and passed through a wash-bottle containing sulphuric acid to obtain a constant r.h. of 75%. This humidity, although higher than that present in the intergranular atmosphere of grain bulks stored at safe

Table 1. Targeted and actual atmosphere compositions recorded from thermal conductivity measurements

Targeted			Recorded		
$\%O_2$	$\%CO_2$	$\%N_2$	$\%O_2 \pm SD$	$\%CO_2 \pm SD$	$\%N_2 \pm SD$
1	14	85	1.05 ± 0.11	13.95 ± 0.19	84.98 ± 0.44
2	13.3	84.7	1.94 ± 0.10	13.11 ± 0.48	84.94 ± 0.41
3	12	85	2.94 ± 0.10	12.16 ± 0.25	84.89 ± 0.33
1		99	1.06 ± 0.08		99.94 ± 0.08

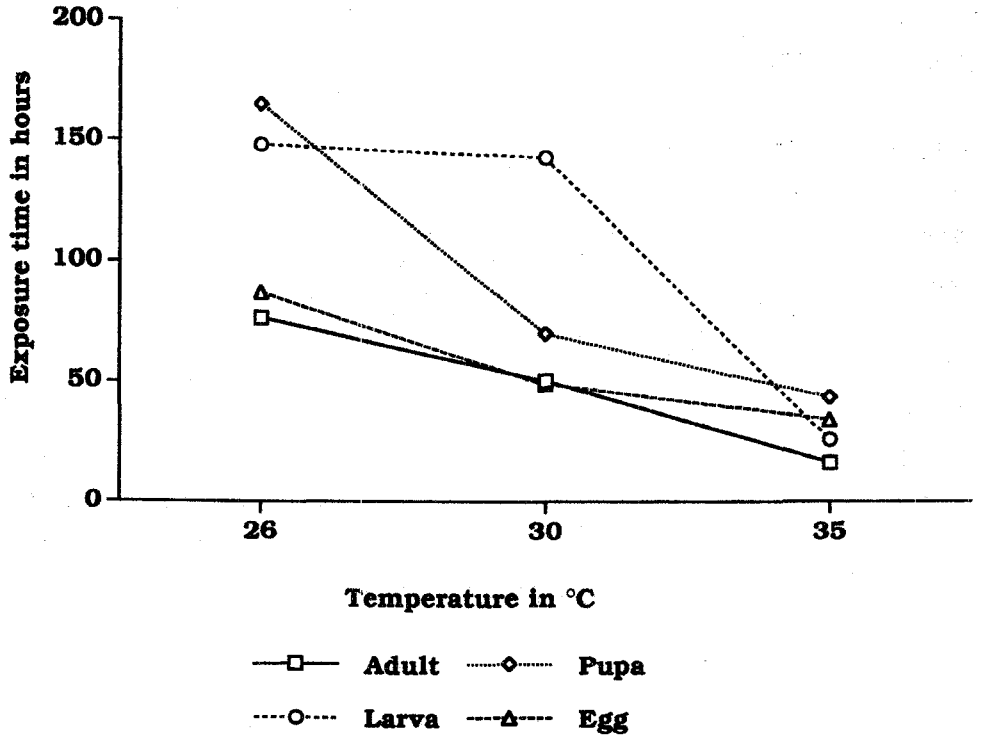

Fig. 1. Times of exposure required to produce 99% mortality (LT_{99}) of all stages of *Tribolium castaneum* to 1% O_2, 85% N_2, 14% CO_2 at 75% r.h., at three temperatures.

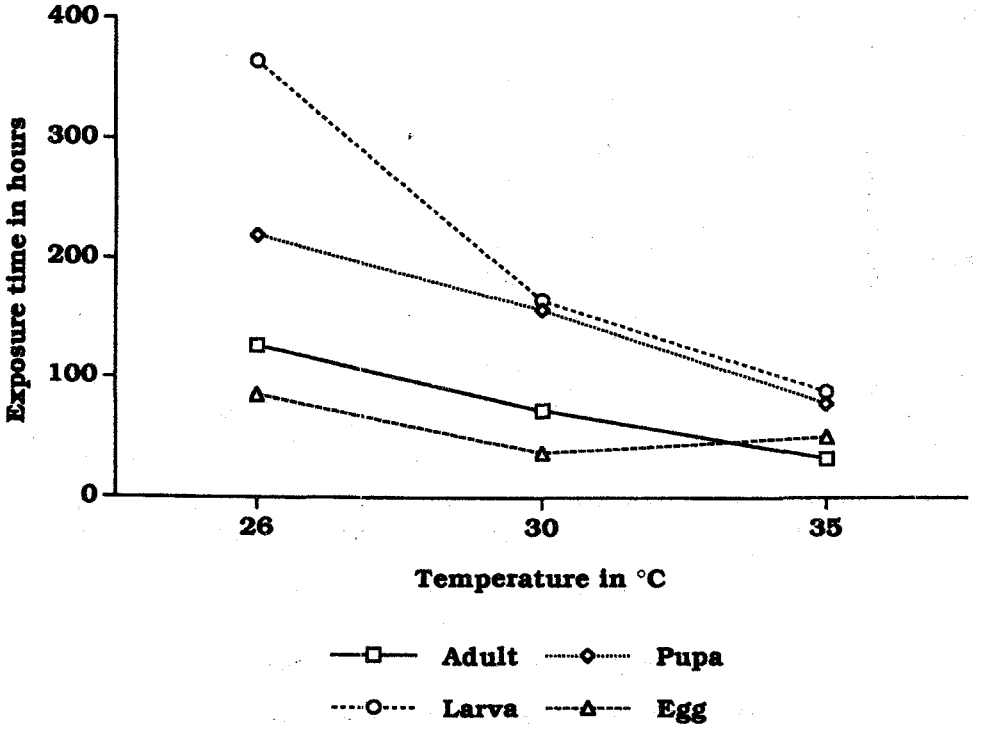

Fig. 2. Times of exposure required to produce 99% mortality (LT_{99}) of all stages of *Tribolium castaneum* to 2% O_2, 84.7% N_2, 13.3% CO_2 at 75% r.h., at three temperatures.

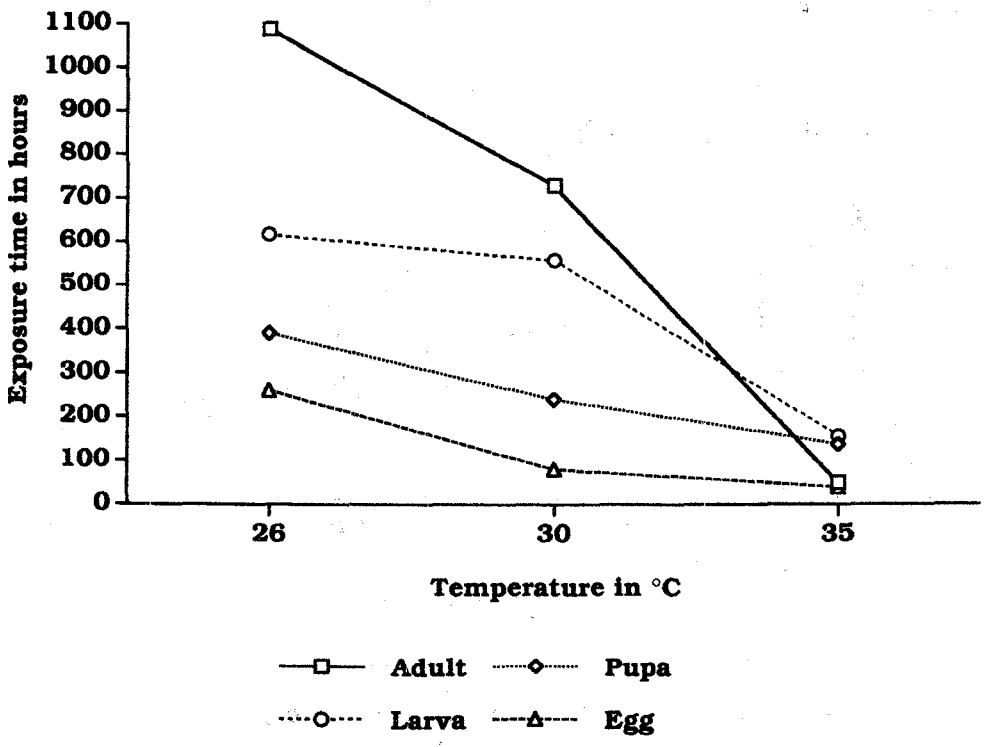

Fig. 3. Times of exposure required to produce 99% mortality (LT_{99}) of all stages of *Tribolium castaneum* to 3% O_2, 85% N_2, 12% CO_2 at 75% r.h., at three temperatures.

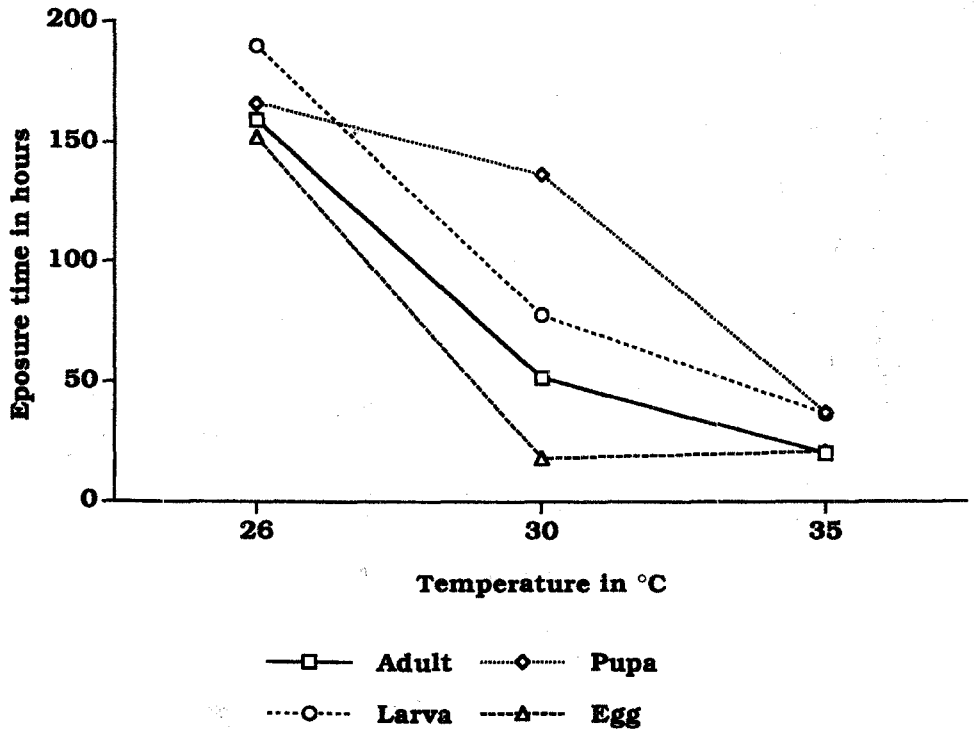

Fig. 4. Times of exposure required to produce 99% mortality (LT_{99}) of all stages of *Tribolium castaneum* to 1% O_2, 99% N_2 at 75% r.h., at three temperatures.

Table 2. Summary of mortality responses of *Tribolium castaneum* to 1% O_2, 85% N_2, 14% CO_2 at three temperatures

Stage	Temp °C	chi-square	df	Slope	SE slope	LT_{50} (h)	LT_{50} *conf. limits	LT_{99} (h)	LT_{99} *conf. limits
Egg	26	11.1	6	2.16	0.36	7.2	4.5–10.6	86.7	40–567
	30	12.5	7	1.85	0.14	2.75	2.4–3.1	49.2	34–79
	35	11.1	9	1.8	0.4	1.9	1.0–2.0	34.3	13–653
Larva	26	14.1	8	4.15	0.79	40.7	34–46	147.9	100–410
	30	15.5	9	4.19	0.64	39.9	35–45	143	101–288
	35	19.7	12	8.2	1.4	13.5	12–15	25.8	22–37
Pupa	26	15.5	9	4.64	1.55	52.2	33–87	165	94–8643
	30	9.4	5	8.5	1.13	37.5	34–40	70.2	62–84
	35	19.6	9	7.6	1.6	21.4	18–25	43.6	34–83
Adult	26	22.3	14	7.67	1.38	38.0	33–43	76.4	63–114
	30	21	13	11.58	0.78	31.9	31–33	50.7	47–55
	35	28.9	19	14.0	3.3	11.1	10–12	16.3	14–24

* 95% confidence limits.

moisture contents, was selected in order to minimise the known combined effect of low humidity and hypercarbia on desiccation and mortality (Navarro, 1975; Navarro and Calderon, 1973). Finally the gas mixtures were delivered via a distribution chamber to a series of 100 ml Erlenmeyer flasks that served as exposure chambers arranged in parallel. Gas supply was designed to provide a flow rate through the exposure chambers of 7.5–10 ml/min. Gas samples were withdrawn periodically from the exposure chambers and analysed using a gas chromatograph equipped with twin thermal conductivity cells and dual columns packed with 'Poropak Q' and 'molecular sieve 5a'.

Temperatures

The three exposure temperatures of 26, 30 and 35°C, were chosen to span the temperature range of freshly harvested grain entering storage in warm climates.

Insects

All stages of *T. castaneum* were obtained from cultures reared at 30°C and 70% r.h. on a diet of ground wheat and yeast using standard culture techniques (Donahaye, 1990). Cultures were of a malathion-susceptible strain obtained from the Pest Infestation Control Laboratory, Slough, U.K. in 1979. Cultures were started from eggs obtained by sieving from oviposition jars containing adults in wheat flour.

Preparation of stages before exposure to treatments. Eggs were separated from oviposition jars by sieving daily; eggs aged 24–48 h were exposed to the treatments.

Larvae were removed from culture jars and exposed 12 d after oviposition.

Pupae were obtained by daily separation from culture jars and held in wheat flour for 24 h before exposure.

Newly emerged adults were held in pre-exposure jars containing wheat flour, and were exposed 7–14 d after emergence.

Table 3. Summary of mortality responses of *Tribolium castaneum* to 2% O_2, 84.7% N_2, 13.3% CO_2 at three temperatures

Stage	Temp. °C	chi-square	df	Slope	SE slope	LT_{50} (h)	LT_{50} *conf. limits	LT_{99} (h)	LT_{99} *conf. limits
Egg	26	14.1	8	2.16	0.34	7.2	4.2–10.4	85.0	46–301
	30	16.9	7	2.44	0.19	4.15	3.5–4.9	37.2	27–60
	35	7.8	6	2.2	0.2	1.9	1.0–2.0	34.3	13–653
Larva	26	14	8	2.6	0.33	46.4	40–52	364.0	253–660
	30	16.9	10	5.13	0.82	58.1	48–66	164.8	127–227
	35	16.9	10	3.6	0.7	19.9	16–24	88.0	55–289
Pupa	26	14.1	8	6.16	0.71	91.8	87–96	218.9	185–285
	30	21.0	13	6.24	0.31	66.5	62–73	157.0	126–230
	35	16.9	10	4.5	1.1	23.8	14–30	78.1	54–217
Adult	6	27.6	18	8.72	0.86	68.4	65–72	126.4	114–147
	0	21	13	6.38	0.83	31.4	27–35	72.6	62–95
	35	19.7	12	10.3	1.7	19.3	18–21	32.5	28–42

* 95% confidence limits.

Table 4. Summary of mortality responses of *Tribolium castaneum* to 3% O_2, 85% N_2, 12% CO_2 at three temperatures

Stage	Temp. °C	chi-square	df	Slope	SE slope	LT_{50} (h)	LT_{50}*conf. limits	LT_{99} (h)	LT_{99}*conf. limits
Egg	26	19.6	12	1.9	0.29	15.5	11–20	259	128–1059
	30	11.1	6	2.08	0.15	6.0	5.2–6.8	78.2	57–117
	35	16.9	10	2.3	0.2	3.7	3.0–4.4	37.9	24–74
Larva	26	15.5	9	3.61	0.59	139.9	120–177	615	377–1755
	30	23.7	15	2.43	0.62	61.9	41–83	557.7	261–6813
	35	16.9	10	3.4	0.3	31.6	28–35	154.7	121–220
Pupa	26	12.9	7	5.86	1.59	156	131–218	389.3	254–3011
	30	21.0	13	5.44	1.54	89.5	67–104	239.6	168–996
	35	11.1	6	5.9	0.7	55.0	51–59	136.7	111–185
Adult	26	26.3	17	2.71	0.89	151.9	108–190	1090	491–83429
	30	26.3	17	3.26	0.41	141.7	123–172	730	469–1549
	35	15.5	9	9.5	1.1	27.0	25–29	48.0	42–58

* 95% confidence lim.ts.

Experimental procedure

Six groups of 50 insects were placed in six exposure flasks together with approximately 2 g medium, and linked to the gas mixture apparatus. An additional flask exposed to air served as a control. Periodic removal of flasks was based on preliminary trials to cover the time ranges over which insect mortality was found to occur for each stage, gas mixture, and temperature. The maximum exposure period employed was 10 d. Due to heterogeneity of response, each set of exposures was repeated at least five times.

At the end of each exposure time a flask was removed from the apparatus. Eggs were transferred to an apparatus designed to enable incubation and periodic inspection of egg-hatch (Donahaye *et al.*, 1992). Larvae, pupae, and adults were retained in the exposure flasks, food medium was added and the flasks were incubated in a constant temperature room at 30 ± 1°C and 70 ± 5% r.h.

Mortality of all stages was determined after 10 d, with eggs that failed to hatch, larvae that failed to pupate, and pupae that failed to reach adult emergence being considered as dead. Experimental results were subjected to probit analysis using a program written by Daum (1979).

RESULTS AND DISCUSSION

The exposure times required to produce 99% mortality at each MA and at the three temperatures are given in Figs 1 – 4. For comparison of sensitivity among developmental stages to the different treatments, LT_{50} and LT_{99} levels are given in Tables 2–5.

From the figures and tables it can be seen that in the experimental atmospheres chosen, mortality rates were strongly influenced by both the O_2 concentration present and the ambient temperature. At 3% O_2, 99% mortality of all stages at 26°C would have been achieved after 45 d, with adults being the most tolerant (Fig. 3, Table 4), though this figure was obtained from the probit line since the maximum exposure time was 10 d when mortality was only 70.5%. In

Table 5. Summary of mortality responses of *Tribolium castaneum* to 1% O_2, 99% N_2 at three temperatures

Stage	Temp °C	chi-square	df	Slope	SE slope	LT_{50} (h)	LT_{50} *conf. limits	LT_{99} (h)	LT_{99} *conf. limits
Egg	26	14	6	1.39	0.14	3.2	2.2–4.2	152	77–439
	30	15.5	9	2.49	0.24	2.1	1.6–2.5	17.9	13–30
	35	15.5	9	2.1	0.2	1.6	1.2–1.9	20.5	13–39
Larva	26	15.5	9	3.78	0.64	46.0	33–56	189.7	136–385
	30	15.5	9	3.55	0.44	17.2	13.8–19.9	77.7	63–106
	35	15.5	9	6.4	2.0	15.7	6–19	36.3	29–140
Pupa	26	18.3	11	4.61	1.42	52.0	29.9–67.5	166.3	105–1557
	30	12.6	7	2.86	0.58	21.0	12.0–28.0	136.6	79–609
	35	15.5	9	10.8	3.9	22.5	14–26	36.9	29–301
Adult	26	16.9	11	7.96	0.64	81.4	77–85	159.4	144–184
	0	19.6	12	10.48	0.54	31.1	30–32	51.8	49–55
	35	16.9	10	13.3	2.6	13.1	12–14	19.7	17–27

* 95% confidence limits.

comparison, at 35°C, only 6.4 d exposure were required. When the O_2 concentration in the 'hermetic storage atmosphere' was reduced to 1% (Fig. 1, Table 2), exposure times needed to achieve 99% kill decreased to 6.8 d at 26°C and 44 h at 35°C. Exposure to 1% O_2 in N_2 revealed longer exposure periods required to produce 99% mortality at 26°C than those in the 1% O_2:85% N_2:14% CO_2 atmosphere, particularly for adults and eggs. At 30 and 35°C differences between the two atmospheres were not consistent and not significant. The figures show that for all the atmospheres employed, and for all four insect stages, there was a very sharp reduction in exposure times required to produce 99% mortality between exposures at 26 and 35°C. However, the difficulty in comparing exposure times required to produce 99% mortality is exacerbated by the fact that, as shown in the tables, confidence limits at the higher mortality levels are very wide, particularly for exposure at 26°C. This finds expression in several anomalous recordings such as the low larval LT_{99} in Fig. 1, and pupal LT_{99} in Fig. 4 at 26°C. Clearly it is more convenient to compare times required to produce 50% mortality where the confidence limits are narrowest. For example, at 35°C, the LT_{50} of all stages exposed to the three simulated hermetic storage atmospheres were between 0.16 and 0.5 times those at 26°C.

These findings may be compared with several studies on the influence of MAs on *Tribolium* spp., though MAs identical to the above have not been covered. Navarro (1975) investigated the interaction between very low O_2 concentrations in N_2 and r.h., at 26°C, on the mortality of *T. castaneum* adults. His findings at 1.1% O_2 produced an LT_{50} of 2.6 d at 54% r.h., and 10 d at 96–100% r.h. as opposed to our results of LT_{50} of 3.4 d at 75% r.h. A similar study on *T. castaneum* eggs by Tunç and Navarro (1983) included 2% O_2 in N_2 at 20%, 50% and 95% r.h. at 26°C. The findings indicated that r.h. affected egg mortality only slightly with complete mortality after 96 h at all humidities. An earlier study by Jay and Cuff (1981) investigated the influence of several MAs including 1% O_2 in N_2, on *T. castaneum* larvae, pupae and adults at 26.7°C and 50% r.h. They obtained complete mortality after 48–72 h and correlated this rapid kill with weight loss resulting from dessication. Comparison may also be made between our results and those of Tunç (1983) who exposed *T. confusum* adults to atmospheres with the following ratios of O_2:CO_2:N_2, i.e. 1.4:9.9:88.6, 2.3:10.6:87.1, and 3.0:10.4:86.6 at 20°C and 60% r.h. He recorded 100% mortality at the 1.4% O_2 level after 4 d, while 3% O_2 exposure for 7 d resulted in 3% mortality. This may be compared with our LT_{99} results at 26°C which for 1% O_2 and 14% CO_2 were 3.2 d, while for 3.0% O_2 and 12% CO_2, mortality at 7 d was 54%.

The study by Annis and Dowsett (1993) was designed to evaluate low O_2 concentrations obtained by MA techniques as alternatives to conventional fumigations where treatment period is a critical factor. All stages were exposed together making statistical analysis difficult. However their findings revealed that at 3% O_2, high mortalities of all stages of *T. castaneum* were obtained after 30 d. For *R. dominica* and *S. oryzae*, exposure to 2–3% O_2 only caused some mortality after 50 d. Conclusions were that low O_2 is not suitable for rapid control requirements. Comparison with our study is only relevant for the 1% O_2 in N_2 treatment where similar findings were obtained for *T. castaneum*, namely very low survival after 1 week.

A similar study to this one, on the sensitivity of two nitidulid beetle species to low O_2 concentrations (Donahaye *et al.*, 1995), showed that the effect of temperature was most pronounced at the 1% O_2 and 2% O_2 levels, where in most cases, at 35°C, less than half the time was required to produce 95% mortality than at 26°C. At the 3% O_2 level, adult mortalities of both species were hardly affected by temperature with more than 12 d exposure required to produce LT_{95}. Possibly the fact that the nitidulid beetles are also field pests that develop normally at high temperatures, had an attenuating influence on the effect of temperature on insect mortality at low O_2 concentrations.

Soderstrom *et al.* (1992) examined the influence of temperature over the range from 38 to 42°C on the influence of hypoxia and hypercarbia on *T. castaneum* adults for 6 h exposures. Their results confirm that raised temperatures significantly reduce exposure times required to obtain kill. They also noted that temperature preconditioning had an inhibitory effect on the influence of atmospheres containing 0.5 and 1% O_2.

The results of these findings could contribute to the formation of a database for a predictive model that would incorporate the variables of the hermetic storage ecosystem. This would enable storage operators to estimate the time required for hermetic storage conditions to kill initial insect infestations.

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