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RESISTANCE — A THREAT TO THE USE OF CONTROLLED ATMOSPHERES FOR STORED-PRODUCT PROTECTION?

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ABSTRACT

According to data in the literature, adult stored-product insects could be selected for up to a ninefold increase in tolerance to controlled atmosphere (CA) treatments over the tolerance of unselected strains. Carbon dioxide (CO_2)-atmospheres with high residual oxygen (O_2) contents produced higher resistance factors than did hypoxic atmospheres. High moisture contents (m.c.) favoured insect survival. Tolerance to various CA's correlated with adult body weight. However, when developmental stages were examined, lethal times of the naturally most tolerant pupal stages could not clearly be prolonged by selection. In a comparison among ten *Sitophilus granarius* strains from three continents, including strains formerly resistant to methyl bromide, phosphine or CO_2, the LT_{99} values of pupal stages in the least susceptible strain were maximally double those of the most susceptible strain. At present we have no proof that resistance threatens the use of CA's for stored-product protection. To minimise the risk of resistance developing, the number of control treatments per commodity should be reduced and emphasis placed on preventive measures and early pest detection within the framework of integrated stored-product protection. All control techniques available, including the use of CA's and toxic fumigants, should be alternated, and incomplete control treatments must be avoided.

INTRODUCTION

Due to the very limited number of stored-product protection agents available today, potential insecticide resistance is a serious threat which increases the need for a sound resistance-management policy. The information available on the mode of action of toxic fumigants and development of resistance to them in stored-product pests was reviewed by Price (1986).

Controlled atmospheres (CA's) low in oxygen (O_2) and/or high in carbon dioxide (CO_2) have been registered in many countries during the last two decades for stored-product protection. On the one hand, users did not readily accept this technology which takes more time, requires a higher degree of gastightness and is often more costly than is fumigation with toxic substances. On the other hand, use of this technique may be increasing because it does not leave residues in the treated product, minor leaks do not produce health risks to exposed people and there is no unpredictable environmental risk in the use of nitrogen (N_2) or CO_2.

According to several laboratory studies, adults of some stored-product Coleoptera could be selected that were several times more tolerant to a given CA than random individuals. The present paper summarises current knowledge about resistance to CA's.

REVIEW OF CURRENT KNOWLEDGE

What is known about resistance to CA's? It is possible to experimentally select strains with an increased tolerance towards certain CA's (Table 1). Bond and Buckland (1979) exposed adult granary weevils *Sitophilus granarius* (L.) to an atmosphere of 42% CO_2, 46.4% N_2

TABLE 1
Literature data on the selection of stored product pests for tolerance to controlled atmospheres

Source	Species[1]	Temperature (°C)/r.h.(%)	Gas mixture	Selection (no. of generations)	Resistance factor/level
Bond and Buckland (1979)	*S. granarius* (A)	25/100	42% CO_2 46.2% N_2 11.6% O_2	7	3.3 (LT_{99})
Navarro *et al.* (1985)	*S. oryzae* (A)	26/100	75% CO_2 (rest air)	10	3.34 (LT_{95})
Navarro *et al.* (1985)	*S. oryzae* (A)	26/60	75% CO_2 (rest air)	10	2.87 (LT_{95})
Donahaye (1990a)	*T. castaneum* (A)	25/95	65% CO_2 15% N_2 20% O_2	40	9.2 (LT_{95})
Donahaye (1990b)	*T. castaneum* (A)	25/95	99.5% N_2 0.5% O_2	40	5.2 (LT_{95})
Annis (1991)	*S. oryzae* (P)	25/65	40% CO_2 (rest air)	7	–[2]
Annis (1991)	*S. oryzae* (P)	25/65	65% CO_2 (rest air)	7	–
Annis (1991)	*S. oryzae* (P)	25/65	95% CO_2 (rest air)	7	–

[1]In paranthesis, selected development stage: A = adults; P = pupae.
[2]No significant resistance was recorded.

and 11.6% O_2 (by volume) at 25°C and close to 100% r.h., until 60% mortality was achieved. After selecting six subsequent generations in this way, they determined that the tolerance factor was 3.3 at the LT_{99}-level as compared to an unselected population. Navarro *et al.* (1985), by selecting adult rice weevils *S. oryzae* (L.) for ten generations in an atmosphere of 75% CO_2 at 26°C and approximately 100% r.h., achieved a tolerance factor of up to 3.34 at the LT_{95} level. When this tolerant strain was exposed to the same gas mixture at 60% r.h., there was a tolerance factor of 2.87 (LT_{95}). Since O_2 content of up to 21% did not markedly change either the LT's or the tolerance levels, the authors attributed the tolerance to the action of CO_2. These data correspond to those of Adler (1994), suggesting that at least part of the toxic action of CO_2 is due to acidosis blocking the glycolytic pathway and thus inhibiting further metabolism even in the presence of sufficient O_2.

Donahaye (1990a, b) selected adult *Tribolium castaneum* (Herbst) for 40 generations at 25°C and 95% r.h. not only to a CO_2-enriched atmosphere (65% CO_2, 15%N_2 and 20% O_2) but also to a hypoxic atmosphere (99.5% N_2 and 0.5% O_2). While the level of tolerance against the hypoxic atmosphere reached a value of 5.2 after 26 generations and could not be increased thereafter (Donahaye, personal communication), the tolerance level against the hypercarbic gas mixture increased gradually from 6.3 to 9.2 after 40 generations of selection. This may indicate that physiologically it is easier to withstand the toxic effects of CO_2 in the presence of sufficient O_2 than the physiological stress caused by lack of O_2.

All laboratory selections were carried out at extremely high r.h., and Donahaye (1991) noted that such conditions were not to be expected in a practical situation. However, one has to keep in mind that condensation processes, leaky storage structures and heavy infestations in so-called "hot spots" may lead to very high local moisture contents (m.c.'s).

In a comparison of eight laboratory strains (-L) and two field strains (-f) of *S. granarius* from Australia (AUS), Canada (CN), France (F), Great Britain (GB), the United States of America (USA) and Germany (D), Adler (1991, 1993) found that there were differences in their susceptibility to certain atmospheric gas mixtures, i.e. 99% N_2, 1% O_2 (Atmosphere 1); 80% N_2, 1% O_2, 19% CO_2 (Atmosphere 2); and 4% N_2, 1% O_2, 95% CO_2 (Atmosphere 3).

LT_{99}-values among the strains, calculated by Probit analysis according to Finney (1971), showed up to a twofold difference in the pupal age group and up to a fourfold difference in adults (Tables 2–7, Figs. 1–3). However, no single strain was consistently more tolerant through all stages than were others. This may be due in part to differences in the average time needed by each strain for egg-to-adult development. The granary weevil is known for its unsynchronised development. At 25°C and 75% r.h., from eggs oviposited on the same day weevil emergence may be up to 21 d apart. A comparison of untreated cultures reared at 25°C and 75% r.h. showed differences in the average development times of the tested strains (Table 8). Therefore, developmental stage 5 (Table 6), treated 29–32 d after oviposition, may have contained a large number of relatively susceptible late larval stages in a slow-developing strain or some already very susceptible emerging weevils in a fast-developing strain. Both effects would reduce the LT_{99} to be

TABLE 2

Susceptibility of ten *S. granarius* strains (stage 1: eggs, reared at 25°C/75% r.h., exposed 1–4 days after oviposition) to three different CA's at 20°C/75% r.h.

	Atmosphere 1		Atmosphere 2		Atmosphere 3	
Strain	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits
GB-L2	14.8	14.0–15.8	**10.3**	9.7–10.9	14.1	13.2–15.1
D-L	15.6	14.6–16.7	14.7	13.7–15.8	**15.7**	14.5–17.1
CN-L2	12.3	11.7–13.0	13.2	12.5–13.9	**11.9**	11.4–12.5
CN-L1	**11.7**	11.0–12.4	12.4	11.6–13.2	12.1	11.5–12.7
GB-L1	13.0	12.4–13.6	14.6	13.9–15.2	15.0	14.2–15.9
D-f	13.0	12.2–13.9	13.4	12.7–14.1	13.2	12.6–13.9
USA-L	14.7	13.7–15.8	14.4	13.3–15.6	13.6	12.5–14.9
AUS-L	**17.2**	16.5–18.0	14.3	13.8–14.9	14.7	14.0–15.5
F-L	14.9	13.9–16.1	14.3	13.3–15.4	14.3	13.2–15.5
AUS-f	14.5	13.9–15.1	**14.9**	14.3–15.5	15.4	14.6–16.2

Atmosphere 1: 99% N_2, 1% O_2; Atmosphere 2: 80% N_2, 19% CO_2, 1% O_2; Atmosphere 3: 95% CO_2, 4% N_2, 1% O_2. Bold numbers indicate highest and lowest values. -L: laboratory strain; -f: field strain (e.g. CN-L1: laboratory strain from Canada).

TABLE 3

Susceptibility of ten *S. granarius* strains (stage 2: larvae, reared at 25°C/75% r.h., exposed 8–11 days after oviposition) to three different CA's at 20°C/75% r.h.

	Atmosphere 1		Atmosphere 2		Atmosphere 3	
Strain	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits
GB-L2	**10.6**	9.7–11.6	8.5	7.9–9.1	4.0	3.6–4.5
D-L	9.9	9.1–10.8	**8.6**	7.9–9.5	**2.5**	2.0–3.1
CN-L2	8.5	7.9–9.1	7.8	7.2–8.3	4.4	4.0–4.8
CN-L1	8.5	7.9–9.2	7.4	6.9–8.0	3.8	3.4–4.2
GB-L1	6.6	6.0–7.3	6.8	6.3–7.3	2.7	0.7–10.3
D-f	8.2	7.6–8.8	7.8	7.3–8.3	3.3	3.0–3.6
USA-L	**5.1**	4.6–5.8	7.2	6.4–8.1	3.0	2.4–3.7
AUS-L	6.0	5.5–6.6	6.8	6.3–7.4	**4.7**	3.7–5.9
F-L	7.6	6.6–8.7	**5.1**	4.5–5.7	2.6	2.1–3.3
AUS-f	7.8	7.2–8.5	6.9	6.4–7.4	3.2	2.3–4.3

Atmosphere 1: 99% N_2, 1% O_2; Atmosphere 2: 80% N_2, 19% CO_2, 1% O_2; Atmosphere 3: 95% CO_2, 4% N_2, 1% O_2. Bold numbers indicate highest and lowest values.

TABLE 4

Susceptibility of ten *S. granarius* strains (stage 3: larvae, reared at 25°C/75% r.h., exposed 15–18 days after oviposition) to three different CA's at 20°C/75% r.h.

	Atmosphere 1		Atmosphere 2		Atmosphere 3	
Strain	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits
GB-L2	14.1	13.0–15.3	11.6	10.8–12.4	5.0	0.4–59.0
D-L	**17.3**	16.0–18.7	**15.7**	14.4–17.1	5.8	5.2–6.5
CN-L2	12.5	11.8–13.2	10.6	10.0–11.5	**7.4**	6.9–7.8
CN-L1	11.7	11.0–12.5	11.2	10.6–11.8	6.5	6.1–6.9
GB-L1	**7.1**	6.7–7.6	**8.6**	8.4–9.4	5.0	4.4–5.8
D-f	13.2	12.4–13.9	12.9	12.0–13.9	4.7	0.8–26.7
USA-L	10.0	9.2–10.9	10.5	9.7–11.4	**4.3**	3.9–4.9
AUS-L	8.9	8.4–9.4	9.5	8.9–10.1	5.6	4.9–6.4
F-L	11.9	10.9–13.0	11.6	10.7–12.6	4.4	3.8–5.1
AUS-f	12.8	12.0–13.6	10.4	9.9–11.0	5.7	5.0–6.4

Atmosphere 1: 99% N_2, 1% O_2; Atmosphere 2: 80% N_2, 19% CO_2, 1% O_2; Atmosphere 3: 95% CO_2, 4% N_2, 1% O_2. Bold numbers indicate highest and lowest values.

TABLE 5

Susceptibility of ten *S. granarius* strains (stage 4: larvae, reared at 25°C/75% r.h., exposed 22–25 days after oviposition) to three different CA's at 20°C/75% r.h.

	Atmosphere 1		Atmosphere 2		Atmosphere 3	
Strain	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits
GB-L2	18.6	16.2–21.3	20.2	19.2–21.2	15.0	9.3–24.2
D-L	23.8	22.8–24.9	22.0	21.0–23.1	**19.9**	18.6–16.7
CN-L2	21.5	20.9–22.2	22.6	21.7–23.6	15.6	14.8–16.4
CN-L1	22.5	21.8–23.3	23.0	22.1–23.8	17.9	17.1–18.8
GB-L1	**14.7**	13.6–15.9	**15.2**	14.5–16.0	**9.2**	5.5–15.3
D-f	**28.4**	27.6–29.2	**26.3**	25.0–27.7	18.6	17.6–19.6
USA-L	18.6	17.6–19.7	20.9	19.9–22.0	14.0	12.9–15.3
AUS-L	17.2	16.3–18.2	17.9	17.0–18.8	13.0	11.7–14.5
F-L	19.1	18.3–20.0	20.4	19.4–21.5	15.5	14.5–16.7
AUS-f	22.5	21.5–23.5	25.8	24.3–27.3	15.0	14.0–16.2

Atmosphere 1: 99% N_2, 1% O_2; Atmosphere 2: 80% N_2, 19% CO_2, 1% O_2; Atmosphere 3: 95% CO_2, 4% N_2, 1% O_2. Bold numbers indicate highest and lowest values.

TABLE 6

Susceptibility of ten *S. granarius* strains (stage 5: mainly pupae, reared at 25°C/75% r.h., exposed 29–32 d after oviposition) to three different CA's at 20°C/75% r.h.

	Atmosphere 1		Atmosphere 2		Atmosphere 3	
Strain	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits
GB-L2	**19.5**	17.5–21.8	22.1	21.3–23.0	18.3	17.3–19.4
D-L	22.5	21.5–23.5	21.2	20.1–22.3	18.5	17.5–19.6
CN-L2	24.1	23.5–24.7	24.6	23.7–25.4	19.5	18.7–20.2
CN-L1	**28.8**	28.0–29.3	26.7	25.8–27.6	22.5	21.7–23.4
GB-L1	20.5	19.9–21.2	22.2	21.5–22.9	**11.3**	6.2–20.8
D-f	26.6	25.9–27.4	22.4	21.6–23.2	19.7	18.8–20.7
USA-L	22.2	21.2–23.3	23.3	22.4–24.4	20.2	19.0–21.5
AUS-L	21.8	21.0–22.5	20.7	20.0–21.5	19.3	18.3–20.4
F-L	20.4	19.3–21.5	**20.2**	19.1–21.4	15.5	14.5–16.5
AUS-f	28.4	27.3–29.5	**29.7**	28.1–31.4	**23.2**	22.1–24.2

Atmosphere 1: 99% N_2, 1% O_2; Atmosphere 2: 80% N_2, 19% CO_2, 1% O_2; Atmosphere 3: 95% CO_2, 4% N_2, 1% O_2. Bold numbers indicate highest and lowest values.

TABLE 7

Susceptibility of ten *S. granarius* strains (adults, reared at 25°C/75% r.h., exposed 1–3 weeks after emergence) to three different CA's at 20°C/75% r.h.

	Atmosphere 1		Atmosphere 2		Atmosphere 3	
Strain	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits	LT_{99} (d)	Fiducial limits
GB-L2	8.0	7.5–8.6	8.1	7.5–8.6	**8.1**	7.6–8.7
D-L	7.3	4.8–11.2	5.6	3.9–7.8	4.5	3.9–5.3
CN-L2	7.6	6.5–9.0	6.8	6.1–7.6	5.8	5.0–6.6
CN-L1	6.3	5.5–7.2	7.4	6.6–8.4	5.5	4.8–6.2
GB-L1	4.3	4.0–4.6	**2.5**	0.1–64.5	**3.4**	3.0–3.7
D-f	5.5	5.1–5.8	**10.3**	8.3–12.7	5.5	4.8–6.2
USA-L	6.6	4.5–9.6	5.2	3.8–7.0	4.4	3.8–5.1
AUS-L	**4.2**	3.9–4.4	3.2	2.9–3.5	4.0	3.6–4.4
F-L	**9.0**	1.1–23.5	6.6	1.3–32.9	4.4	3.8–5.1
AUS-f	4.3	4.0–4.6	2.9	0.7–11.4	3.8	3.4–4.2

Atmosphere 1: 99% N_2, 1% O_2; Atmosphere 2: 80% N_2, 19% CO_2, 1% O_2; Atmosphere 3: 95% CO_2, 4% N_2, 1% O_2. Bold numbers indicate highest and lowest values.

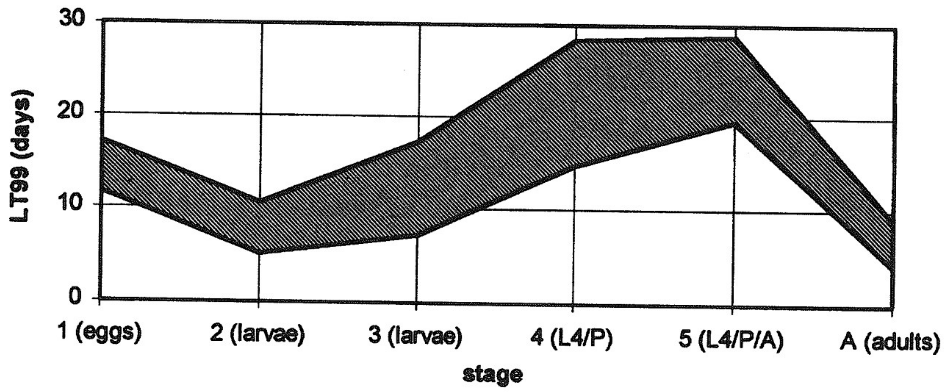

Fig. 1. Variations in the LT_{99} of ten *S. granarius* strains produced by an atmosphere composed of 99% N_2, 1% O_2.

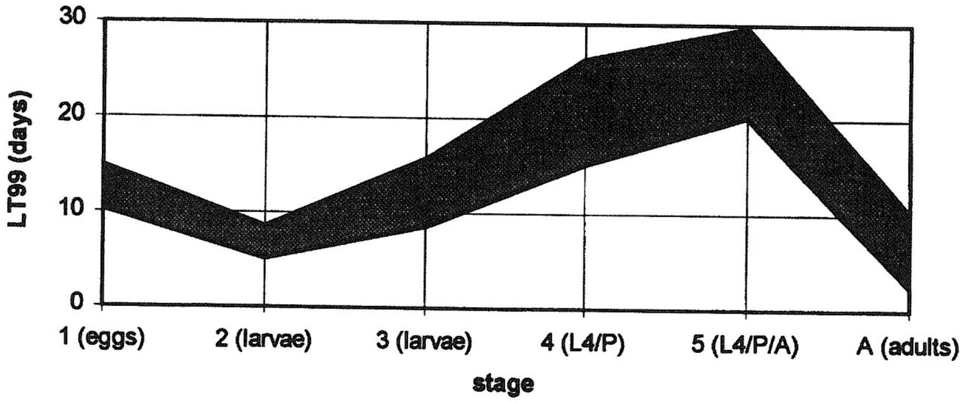

Fig. 2. Variations in the LT_{99} of 10 *S. granarius* strains produced by 80% N_2, 19% CO_2, 1% O_2.

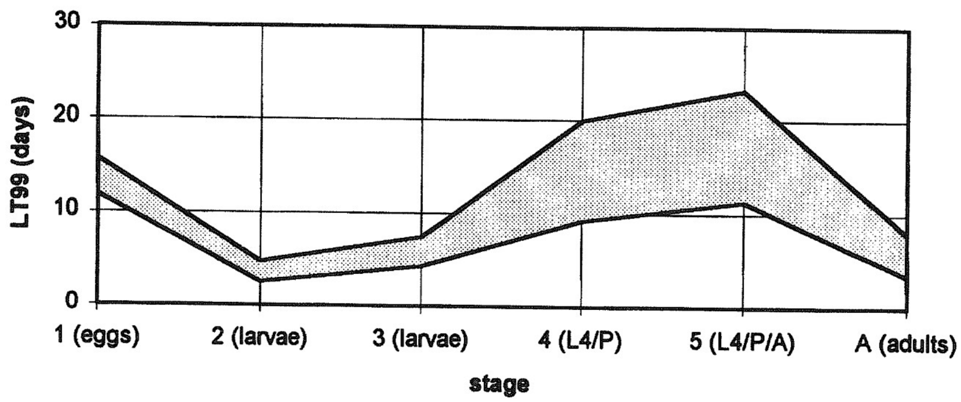

Fig. 3. Variations in the LT_{99} of 10 *S. granarius* strains produced by 95% CO_2, 4% N_2, 1% O_2.

TABLE 8
Mean development times of ten *S. granarius* strains

Strain	Mean development time (d)
GB-L2	43
D-L	38.5
CN-L2	41
CN-L1	38.5
GB-L1	47
D-f	38.5
USA-L	45
AUS-L	49
F-L	40
AUS-f	42

Time (days) from oviposition to adult emergence at 25 ± 1°C/75 ± 5% r.h., estimated by weekly examination of untreated samples.

expected from treatment of only young pupal stages. This complicates the comparison of mortality data of late juvenile stages in *Sitophilus* species.

Comparison of adults

Donahaye (1991) noted that both of his strains of *T. castaneum*, selected for tolerance against hypercarbia and hypoxia, respectively, were significantly heavier than the unselected strain.

When the LT_{99}-values and adult body weights of strains were compared using Spearman's ranks test, a significant correlation between body weight and tolerance to 95% CO_2 (Table 9, Atm. 3) could be found. Among adult weevils, the GB L-strain GB-L2 (originally named "methyl bromide (MB) resistant XXM 65 (51)") proved to be most tolerant to Atm. 3. According to information from the Slough Laboratory, this strain originally came from Canada and was described in Bond and Upitis (1976) as being resistant to MB. When it arrived in the United Kingdom in 1979, it was reported to be about 15 times more tolerant to MB than normal strains; since then no selection has been carried out. As early as 1973, Upitis *et al.* reported increased body weight coinciding with MB-resistance in granary weevils. The increased body weight found then has probably been retained ever since selection was carried out.

The Canadian "CO_2-selected" laboratory strain CN-L2 was the culture described in Bond and Buckland (1979). In their experiment it proved to be the strain the adults of which were the second most tolerant to Atm. 3 (Table 9). Both selected strains seem to have been, at least to some degree, genetically stable over many years without further selection. Moreover, it seems that resistance to MB in *S. granarius* could result in cross resistance to CO_2 even though the experiments of Donahaye (1991) with CO_2-selected *T. castaneum* did not reveal any sign of this.

TABLE 9
Body weight, LT_{99}-values (days) and rankings of adults of ten *S. granarius* strains

	Weight		Atmosphere 1		Atmosphere 2		Atmosphere 3	
Strain	g	Rank	LT_{99}	Rank	LT_{99}	Rank	LT_{99}	Rank
GB-L2	4.66 ± 0.03	1	8.0	2	8.1	2	8.1	1
D-L	4.29 ± 0.13	2	7.3	4	5.6	6	4.5	5
CN-L2	4.19 ± 0.07	3	7.6	3	6.8	4	5.8	2
CN-L1	3.87 ± 0.04	4	6.3	6	7.4	3	5.5	3
GB-L1	3.51 ± 0.04	5	4.3	8/9	2.5	10	3.4	10
D-f	3.35 ± 0.01	6	5.5	7	10.3	1	5.1	4
USA-L	3.33 ± 0.02	7	6.6	5	5.2	7	4.4	6/7
AUS-L	3.05 ± 0.03	8	4.2	10	3.2	8	4.0	8
F-L	2.62 ± 0.03	9	9.0	1	6.6	5	4.4	6/7
AUS-f	2.53 ± 0.02	10	4.3	8/9	2.9	9	3.8	9

Weight of 1000 live adult weevils, based on 3 replicates, and standard deviation. Spearman's ranks test gave the following values: Correlation of mean adult body weight to LT_{99}–Atmosphere 1, $r_s = 0.415$; correlation of mean adult body weight to LT_{99}–Atmosphere 2, $r_s = 0.479$; correlation of mean adult body weight to LT_{99}–Atmosphere 3, $r_s = 0.706$.
Threshold r_s value for significance ($p = 0.05$) is 0.55. Thus, medium adult body weight correlates significantly only to tolerance for the hypercarbic atmosphere.

The adults of the Australian field strain AUS-f, originally named "GSG 66, PH_3-resistant" had the lowest comparative body weight and were also quite susceptible to all tested gas mixtures.

Comparison of juvenile stages

Annis (1991) pointed out that analyses in resistance surveys should be carried out on the most tolerant developmental stage of the most tolerant species because dosage schedules for CA treatments are designed to control these pests. He suggested that the pupal stages of *S. oryzae* and *Trogoderma* spp. should be studied. Exposing groups of pupae of seven different strains of *S. oryzae* for seven generations to hypercarbic atmospheres of 40, 65 or 95% CO_2 in air at 26°C and 65% r.h., Annis found a significant increase in tolerance in one strain. Because of variations in the data, however, this increase was too small to enable its magnitude to be estimated.

In a later study, Donahaye *et al.* (1992) found that partial resistance was displayed by the eggs and larvae of both the high-CO_2 and the low-O_2 resistant strains of *T. castaneum*. However, the naturally most tolerant pupal stage did not display any increased tolerance in these strains selected in the adult stage.

The comparison of *S. granarius* strains is somewhat confusing because the AUS-f strain the adults of which were most susceptible to 95% CO_2 displayed pupal stages which were the most tolerant to this atmosphere (Tables 6 and 7). This could mean that the relative tolerance of pupal stages is independent of adult body weight. The variation in LT_{99}-values shown in Figs. 1–3 may be an indication of the genetic potential of each stage of development. The maximum ratio of the most susceptible to the most tolerant strain is 1:4 in adults (Atm. 2), but it is 1:2 in pupae (Atm. 3).

CONCLUSION

The development of resistant pest populations can be regarded as a natural response to selection by man's competitors for food resources. This process is comparable to the "arms race" in the co-evolution of wild plants and their pests. To keep the lead in the race with agricultural pests, man will have to minimize the chances for selection.

The striking tolerance of certain pest species to CA's raises the question of whether this could be the result of long-term hermetic storage carried out in many agricultural countries since ancient times. Up till now, no treatment failures due to resistant strains have been reported from practical applications, and no tolerant stages of tolerant species could be selected to a sufficient degree to allow defined resistance factors to be estimated. It should be kept in mind that high m.c. favours the selection of tolerant populations, and such tolerance could be stable for an extended period. More research needs to be done to gain a better understanding of the mode of action of CA's and the potential of arthropods to develop resistance to them. The data available today, however, do not prove that the development of resistance is an immediate threat to the use of CA's for stored-product protection.

In order to minimise the risk of resistance developing, such methods for pest prevention as insect-proof structural design, hygiene, cold storage and product drying should be used together in an integrated stored-product protection system (Fig. 4). Today's informa-

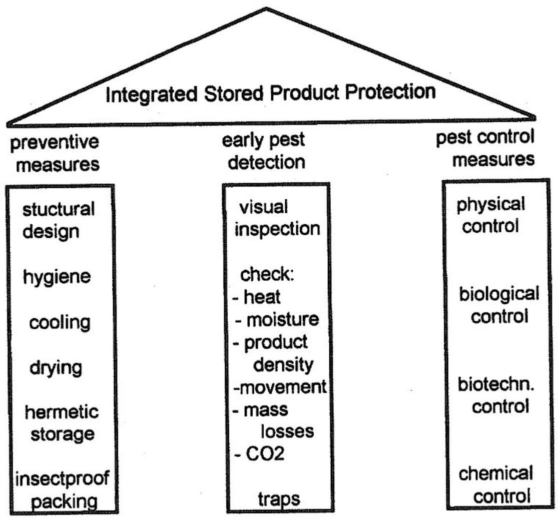

Fig. 4. The three columns of integrated stored-product protection.

tion technology could also support a logistical approach to the handling of stored products, reducing storage durations and shortening the routes between producer, manufacturer and consumer. Early pest detection methods in combination with hygiene and limited control treatments could help to reduce the number of large scale fumigations. The efficacy of each control treatment should be assured, and inadequate treatment methods must be avoided. Surface treatments may be dangerous because insects below the surface would be exposed to sublethal doses. Finally, the different pest-control methods available should be alternated in order to reduce the chance of accidental selection of resistant populations.

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