J. Appl. Entomol.

Deltamethrin-induced feeding plasticity in pyrethroid-susceptible and -resistant strains of the maize weevil, *Sitophilus zeamais*

N. M. P. Guedes, R. N. C. Guedes, L. B. Silva & E. M. G. Cordeiro

Departamento de Biologia Animal, Universidade Federal de Viçosa, Viçosa, Brazil

Keywords
behavioural resistance, feeding behaviour, food conversion, insecticide avoidance, insecticide resistance, stored grains

Correspondence
Raul Narciso C. Guedes (corresponding author), Departamento de Biologia Animal, Universidade Federal de Viçosa, Viçosa, MG 36571-000, Brazil.
E-mail: guedes@ufv.br

Received: November 26, 2008; accepted: January 20, 2009.

doi: 10.1111/j.1439-0418.2009.01391.x

Abstract

Phenotypic plasticity contributes to the adaptative evolution of populations exposed to new or altered environments. Feeding plasticity is a component of phenotypic plasticity not usually considered in insect strains adapted to insecticide-altered environments, but which may either accentuate or mitigate insecticide resistance. This is a concern in the pyrethroid-resistant strains of the maize weevil *Sitophilus zeamais* Motsch. (Col., Curculionidae), and the reason for this study. A pyrethroid-susceptible and two pyrethroid-resistant strains of maize weevil were subjected to free-choice and no-choice tests with maize grains sprayed with increasing doses of the pyrethroid, deltamethrin. The insects from the pyrethroid-resistant strains exhibited higher feeding avoidance with increased deltamethrin doses than insects from the susceptible strain when subjected to free-choice tests. The strains of maize weevil physiologically resistant to pyrethroids were also behaviourally resistant to deltamethrin – an additional management concern. The resistant strains avoid deltamethrin-sprayed grains and are less nutritionally affected by this compound, with divergent responses from the susceptible strain with increased doses of deltamethrin. Furthermore, the higher relative growth rate and consequently higher efficiency of food conversion observed in the insecticide-resistant strains were significant even without insecticide exposure, indicating that these traits are stimulus-independent and may persist even without further insecticide selection, potentially limiting the options available for their management.

Introduction

Insecticide resistance is a phenomenon of economical and environmental concern and it is also important as a model system for the study of the evolution of newly adapted phenotypes (Lockwood et al. 1984; Haynes 1988; Mallet 1989; Hoy et al. 1998). Insects may withstand insecticide applications either through the evolution of physiological mechanisms allowing them to cope with high insecticide levels on or within the body, or through behavioural mechanisms minimizing their exposure to insecticides (Gould 1984; Hoy et al. 1988; Jallow and Hoy 2005). Interest in the latter was stimulated by the use of pyrethroid insecticides exhibiting irritant and repellent effect in insects (Lockwood et al. 1984; Mallet 1989). However, studies correlating physiological and behavioural resistance to insecticides are rare (Suiter and Gould 1994; Renou et al. 1997; Kongmee et al. 2004; Jallow and Hoy 2005).

Insecticide resistance is recognized as a pleiotropic trait, the expression of which may vary with the individual genotype and its environment (Chevillon et al. 1997; Boivin et al. 2001; Oliveira et al. 2005; Ribeiro et al. 2007). Such plasticity of expression of insecticide resistance may contribute to the adaptative evolution of populations exposed to new or altered environments (Pagliucci and Muren 2003;

Price et al. 2003; Ghalambor et al. 2007). Feeding plasticity is a component of phenotypic plasticity not usually considered in insect strains adapted to insecticide-altered environments, but which may either accentuate or mitigate insecticide resistance. This is a concern in pyrethroid-resistant strains of the maize weevil *Sitophilus zeamais* Motsch. (Col., Curculionidae), a major insect pest of stored grains (USDA 1980; Rees 1996; Araújo et al. 2008a; Guedes and Pereira 2008) and the reason for the present study.

The over-reliance on insecticide use against stored grain insect pests led to the widespread evolution of insecticide resistance in these pest species (Champ and Dyte 1976; Badmin 1990; Subramanyam and Hagstrum 1996; Pimentel et al. 2007). The maize weevil is no exception and high levels of insecticide resistance, particularly pyrethroid resistance, have been reported (Guedes et al. 1994, 1995; Perez-Mendoza 1999; Fragoso et al. 2003; Ribeiro et al. 2003). The neurotoxic activity of pyrethroids and their reported association with avoidance behaviour in insects are indications of the potential importance of the behavioural response elicited by this group of insecticides in pyrethroid-resistant populations of insect pests (Dethier et al. 1960; Gammon 1978; Lockwood et al. 1984; Pekár and Haddad 2005). Insecticide-induced behavioural responses have also been reported in stored-product insects (Watson and Barson 1986; Cox et al. 1997), but not their plasticity and association with insecticide resistance. Here we explored the feeding plasticity of pyrethroid-susceptible and -resistant strains of the maize weevil when exposed to deltamethrin-sprayed maize grains at increasing rates in free-choice and no-choice tests. We expected to learn if there is any association between physiological and behavioural resistance to pyrethroids in strains of maize weevil and we were expecting divergence of response (i.e. feeding plasticity) between the susceptible and resistant strains with exposure to increased doses of deltamethrin.

Material and Methods

Insects and insecticides

Three strains of *S. zeamais* were used in the present investigation, which were termed here as 'susceptible', 'resistant cost' and 'resistant no-cost'. The susceptible strain was collected by mid-1980 in Sete Lagoas County (state of Minas Gerais, Brazil) (Guedes et al. 1994, 1995). The resistant cost strain was collected in Juiz de Fora County (state of Minas Gerais, Brazil) in 1999. It is resistant to pyrethroids, but has reduced fitness (reproductive output) in the absence of pyrethroid exposure (Fragoso et al. 2003; Guedes et al. 2006; Oliveira et al. 2007). The resistant no-cost strain was collected in Jacarezinho County (state of Paraná, Brazil) in the late 1980s (Guedes et al. 1994, 1995). It is also resistant to pyrethroids, but does not exhibit fitness cost (reduced reproductive output) associated with insecticide resistance (Fragoso et al. 2005; Guedes et al. 2006; Oliveira et al. 2007). Both insecticide-resistant strains (i.e. resistant cost and resistant no-cost) exhibit high levels of pyrethroid resistance (>100×) (Guedes et al. 1994, 1995; Ribeiro et al. 2003; Araújo et al. 2008a). The two resistant strains share the same major insecticide resistance mechanism – altered target-site sensitivity (mutation T929I in the sodium channel, following the housefly numbering; R.A. Araújo personal communication) with secondary involvement of enhanced activity of glutathione *S*-transferases (Guedes et al. 1995; Fragoso et al. 2003, 2007; Ribeiro et al. 2003). The three strains were replicated and maintained in large numbers (to minimize the effects of genetic drift) in whole maize grains (13% moisture content) free of insecticides under controlled temperature (25 ± 2°C), relative humidity (70 ± 5%) and photoperiod (12 : 12 h light : dark). The experiments were all carried out under the same conditions used for insect rearing.

The commercial formulation of the pyrethroid insecticide deltamethrin ([cyano-(3-phenoxyphenyl)-methyl] 3-(2,2-dibromoethenyl)-2,2-dimethyl-cyclopropane-1-carboxylate); K-Obiol® 25 CE; emulsifiable concentrate at 25 g a.i./l; Bayer CropScience Brasil, São Paulo, Brazil) was purchased at the local market. Deltamethrin was sprayed in batches of 1 kg of maize using manual sprayers with their nozzles directed down towards the grains at 20 cm height. Different batches were used for each replicate and the sprayed grains were manually shaken to ensure coverage over the kernels. A volume of 1 ml was used to spray each grain batch at 3 bar pressure. The manual sprayers were changed for each insecticide application to prevent residual contamination. The sprayed grains were left drying overnight before use and the sprayed doses of deltamethrin ranged from 0 to 5 p.p.m. depending on the experiment and insect strain, as subsequently detailed.

Free-choice test of preference

Pair-wise free-choice tests were carried out using white plastic trays (25 × 15 × 6 cm), with one half containing water-sprayed grains (50 g) and the other half containing deltamethrin-sprayed grains (50 g) at increasing doses (0.05, 0.25, 0.50, 1.00, 1.50, 2.00, 4.00 and 5.00 p.p.m.). A control with water-sprayed grains on both sides was also used to normalize the results. The trays were coated with Teflon® PTFE (DuPont, Wilmington, DE, USA) to prevent insect escape and covered with a fine fabric (organza) to prevent insect flight. Fifty non-sexed adult insects (1 to 2 weeks old) were released in the centre of the tray and insect preference was assessed after 1 h by determining the proportion of insects present on the deltamethrin-sprayed grains. The results obtained with 1 h exposure were similar to those obtained with extended exposure (up to 24 h) based on preliminary tests. No insect mortality was observed during the test. Five replicates were used for each combination of deltamethrin dose and maize weevil strain.

No-choice feeding test

Batches of 10 g of sprayed maize grains were placed in glass jars (0.5 l) with the upper portion of their inner walls coated with Teflon® PTFE. The grains were previously weighed and their moisture content determined. Thirty non-sexed adult insects (1 to 2 weeks old) were weighed and subsequently released in each jar. After 10 days, the (live) insects were removed and weighed once more. The grain batches were also weighed and their moisture content determined to estimate the loss of grain mass because of water loss within the period. Three to five replicates were used for each combination of strain and deltamethrin dose. The deltamethrin doses used (i.e. 0.00, 0.0005, 0.005, 0.05, 0.25, 0.50 p.p.m.) were within the sub-lethal range for each strain, as determined in preliminary tests and estimates of the lowest observed effect dose (LOED) established for the susceptible strain (0.1 p.p.m.) and the pyrethroid-resistant strains (0.5 and 1.0 p.p.m. for the resistant no-cost and resistant cost strain, respectively). The following nutritional indexes were calculated for each combination of deltamethrin-sprayed dose and maize weevil strain, as described elsewhere (Isman et al. 1990; Huang et al. 1997): relative growth rate (daily weight gain per unit of insect weight), relative consumption rate (daily consumption rate per unit of insect weight), conversion efficiency of ingested food [(relative growth rate/relative consumption rate) × 100], and feeding deterrence index (proportion of grain mass not consumed by the insects).

Statistical analysis

The avoidance and nutritional data were subjected to analyses of covariance with insect strain as independent variable and deltamethrin dose as covariate (PROC GLM; SAS Institute 2002). Subsequent regression analyses were carried out whenever necessary, using the software TABLECURVE 2D to fit the regression lines (SPSS 2000). The regression models were tested from the simplest (linear and quadratic) to the alternative models of increasing complexity (nonlinear peak models). Model selection was carried out based on simplicity, high F-values (and mean squares) and steep increase in R^2 with model complexity. The overall nutritional results of both strains without insecticide exposure were also subjected to multivariate analysis of variance (PROC GLM with MANOVA statement; SAS Institute 2002), and subsequent individual analyses of variance for each nutritional parameter were carried out, if appropriate (PROC GLM; SAS Institute 2002). Assumptions of normality and homogeneity of variance were checked (PROC UNIVARIATE; SAS Institute 2002), but no data transformation was necessary.

Results

Free-choice test of preference

The model of analysis of covariance for the proportion of insects avoiding deltamethrin-sprayed grains was significant ($F_{26,135} = 7.46$; $P < 0.0001$). The effects of strain and deltamethrin dose were significant ($F_{2,135} = 12.90$, $P < 0.0001$ and $F_{8,135} = 18.32$, $P < 0.0001$, respectively), but not the strain–dose interaction ($F_{16,135} = 1.36$, $P = 0.7$). Subsequent regression analysis provided the avoidance curves for all three insect strains, which followed a similar trend, with the proportion of insects avoiding deltamethrin-sprayed grains increasing with the increase in insecticide dose until reaching a plateau (fig. 1). Therefore, deltamethrin avoidance was stimulus-dependent and differed among maize weevil strains. The insects from both insecticide-resistant strains showed higher deltamethrin avoidance than the insecticide-susceptible insects, which is evident for doses lower than the recommended label rate (<0.5 p.p.m.), where the resistant strains exhibited an about six-fold higher deltamethrin avoidance than the susceptible strain (30.00 ± 4.35% and 35.79 ± 7.07% for the resistant no-cost and resistant cost strains, and 5.69 ± 3.69% for the susceptible

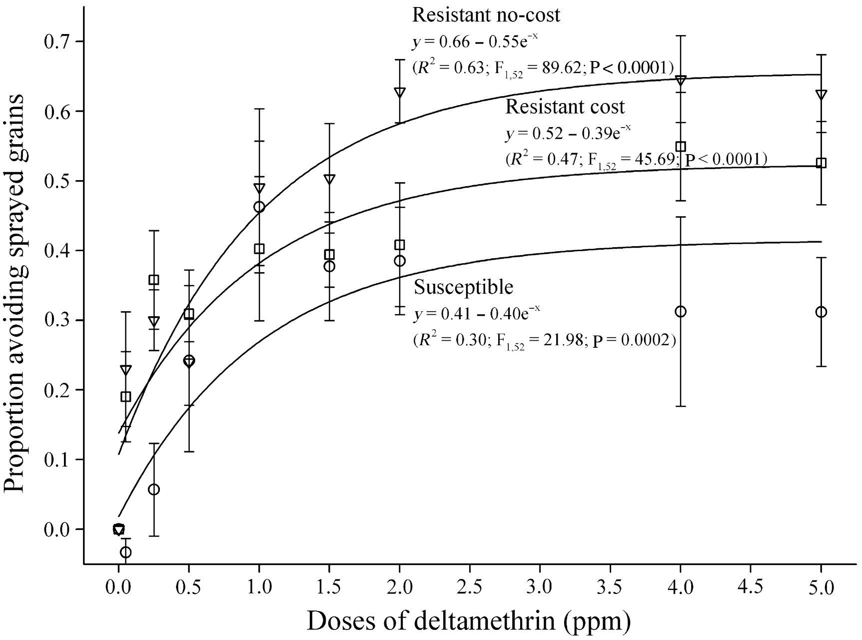

Fig. 1 Proportion of adults of one pyrethroid-susceptible (○) and two pyrethroid-resistant strains [resistant cost (□) and resistant no-cost (▽)] of maize weevil (*Sitophilus zeamais*) avoiding maize grains sprayed with increasing doses of the pyrethroid insecticide deltamethrin. Each symbol represents the mean of five replicates.

strain). The resistant no-cost strain exhibited the highest deltamethrin avoidance, with over 60% of the insects avoiding grains with higher residue levels (≥2 p.p.m.), while the resistant cost strain exhibited about 50% of insects avoiding the same residue levels and the susceptible strain exhibited little over 30% of avoiding insects.

No-choice feeding response

Nutritional indexes were calculated for the maize weevil strains exposed for 10 days to maize grains sprayed with increasing doses of deltamethrin to verify if the insects from different strains differ in their food conversion and if they employ any strategy to either minimize or compensate insecticide ingestion.

Strain differences without insecticide exposure

The multivariate analysis of variance for the nutritional parameters indicated significant differences among strains without insecticide exposure (Wilks' lambda = 0.1616; $F_{6,20} = 4.96$; $P = 0.002$), a likely result of their different genetic make-up. The univariate analysis of variance for the individual nutritional parameters indicated significant strain differences in relative growth rate ($F_{2,12} = 20.44$; $P < 0.0001$) and efficiency of conversion of ingested food ($F_{2,12} = 16.92$; $P = 0.0003$), but there was no significant difference in relative consumption rate among strains (0.72 ± 0.01 mg/mg day; $F_{2,12} = 1.53$; $P = 0.26$); as feeding deterrence was standardized based on the control, the strain differences without insecticide exposure were not considered. The relative insect growth rate was higher for the insecticide-resistant strains (0.016 ± 0.0004 and 0.013 ± 0.001 mg/mg day for the resistant cost and resistant no-cost strains, respectively) than for the insecticide-susceptible strain (0.0089 ± 0.0009 mg/mg day). A similar trend was observed for the efficiency of food conversion (2.17 ± 0.05%, 1.89 ± 0.09% and 1.30 ± 0.15% for the resistant cost, resistant no-cost and susceptible strains, respectively), which was expected as there was no significant strain variation in relative consumption rate and therefore the variation in food conversion was basically determined by the strain differences in relative growth rate.

Feeding plasticity with increased (sub-lethal) doses of deltamethrin

The analyses of covariance models for each nutritional parameter were all significant ($F_{12,40} \geq 3.08$; $P \leq 0.004$). The strain–dose interaction was significant for the relative growth rate ($F_{5,40} = 3.08$; $P = 0.002$), relative consumption rate ($F_{5,40} = 5.93$; $P = 0.0003$), efficiency of conversion of ingested food ($F_{5,40} = 4.17$; $P = 0.004$) and also for feeding deterrence ($F_{5,40} = 4.85$; $P = 0.001$). The sub-lethal feeding effects of deltamethrin-sprayed grains were therefore significantly plastic among strains for insect growth and consumption rates, food conversion and feeding deterrence.

Subsequent regression analyses complementing the analyses of covariance were carried out to recognize the trends of each nutritional parameter as influenced by deltamethrin dose in each insect strain. The coefficients of determination (R^2) of the estimated regression models showed low to moderate values (between 0.20 and 0.78), and therefore were of limited predictive value, but good enough to allow the trend recognition of the deltamethrin effect in weevil nutrition. Deltamethrin did not affect the relative growth rate of the susceptible and the resistant no-cost strains, but at doses of 0.05 p.p.m. and higher the insecticide led to a steady declining trend of relative growth rate for the resistant cost strain (fig. 2). The relative consumption rate of the susceptible strain declined with increase in deltamethrin dose at 0.05 p.p.m., in contrast with the increased relative consumption observed with increased deltamethrin dose for the resistant no-cost strain (fig. 3). The trend for the resistant cost strain was similar to that of the susceptible one, but with the decline in consumption rate taking place only at a 10× higher insecticide dose (i.e. 0.5 p.p.m.).

The efficiency of conversion of ingested food, which is obtained from the ratio of relative growth rate and relative consumption rate, showed an overall trend for the pyrethroid-resistant strains analogous to those of the relative growth rate with the deltamethrin dose not affecting the resistant no-cost strain, but decreasing the efficiency of food conversion of the resistant cost strain (fig. 4). The deltamethrin dose did not affect the efficiency of food conversion of the resistant no-cost strain, but such conversion improved for the susceptible strain at 0.05 p.p.m. deltamethrin. The resistant cost strain exhibited the highest efficiency of food conversion for deltamethrin doses of up to 0.05 p.p.m., when its decline in efficiency dropped to levels lower than those exhibited by the resistant no-cost strain at 0.25 p.p.m. deltamethrin. Feeding deterrence increased with deltamethrin dose, particularly at 0.005 p.p.m. (fig. 5). Such an increase took place between 0.005 and 0.05 p.p.m. deltamethrin for the susceptible strain and around 0.25 p.p.m. for the deltamethrin-resistant strains.

Discussion

Here we reported divergence of feeding response between insecticide-susceptible and -resistant strains of the maize weevil exposed to increased residues of deltamethrin in sprayed maize grains. This finding characterizes feeding plasticity with increased insecticide doses sprayed on the food source, which may further compromise the management of the resistant insects and provide them with further possibilities of adapting to new environments.

An insect's chance of survival to an insecticide may be greatly increased if its behaviour is modified to avoid insecticide-sprayed surfaces (Watson and

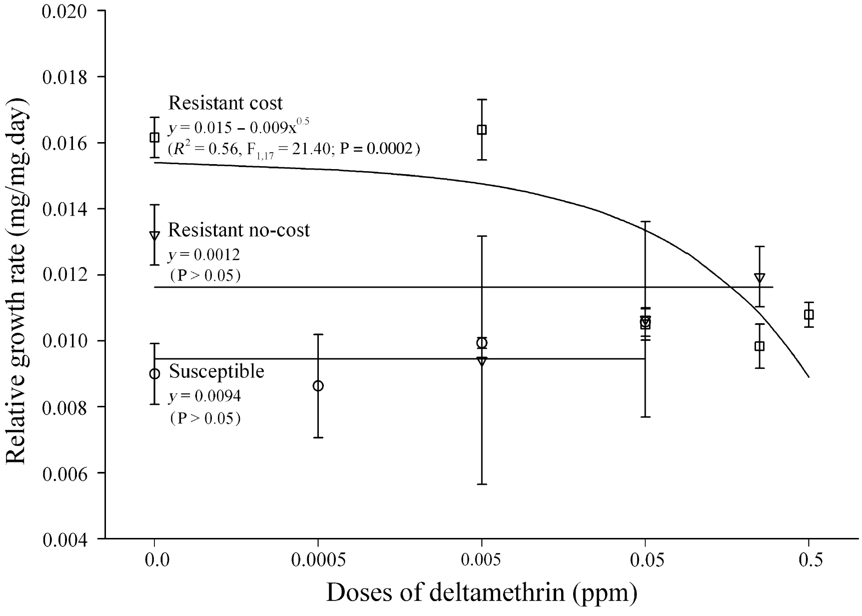

Fig. 2 Relative growth rate (mg/mg.day) of one pyrethroid-susceptible (○) and two pyrethroid-resistant strains [resistant cost (□) and resistant no-cost (▽)] of maize weevil (*Sitophilus zeamais*) exposed to maize grains sprayed with increasing doses of the pyrethroid insecticide deltamethrin. Each symbol represents the mean of three to five replicates.

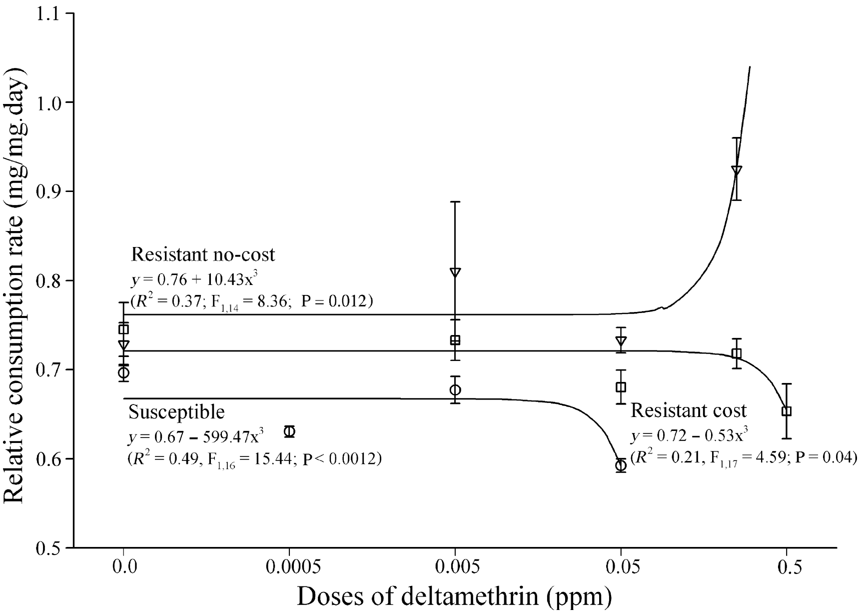

Fig. 3 Relative consumption rate (mg/mg) of one pyrethroid-susceptible (○) and two pyrethroid-resistant strains [resistant cost (□) and resistant no-cost (▽)] of maize weevil (*Sitophilus zeamais*) exposed to maize grains sprayed with increasing doses of the pyrethroid insecticide deltamethrin. Each symbol represents the mean of three to five replicates.

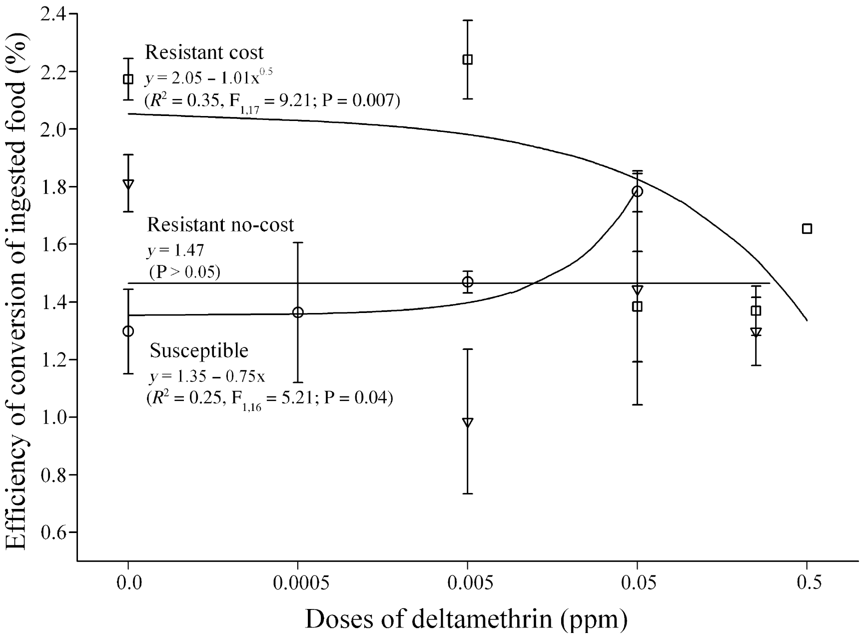

Fig. 4 Efficiency of conversion of ingested food (%) of one pyrethroid-susceptible (○) and two pyrethroid-resistant strains [resistant cost (□) and resistant no-cost (▽)] of maize weevil (*Sitophilus zeamais*) exposed to maize grains sprayed with increasing doses of the pyrethroid insecticide deltamethrin. Each symbol represents the mean of three to five replicates.

Barson 1986; Cox et al. 1997). The detection of insecticide presence in the environment may be achieved through the insect learning ability or through genetic modifications in its peripheral receptors or central processing systems leading to the evolution of behavioural resistance to insecticides in some species (Georghiou 1972; Haynes 1988; Mallet 1989; Gould 1991; Hoy et al. 1998). Our results with strains of maize weevil in free-choice tests of feeding preference (or avoidance) with insecticide-sprayed maize grains indicate that the physiologically resistant strains are better capable of detecting the deltamethrin-sprayed grains than the susceptible strain and even more so with higher insecticide residues on the grain. Therefore, the physiologically resistant strains are also behaviourally resistant to deltamethrin further compromising the efficacy of this compound, which may also extend to other

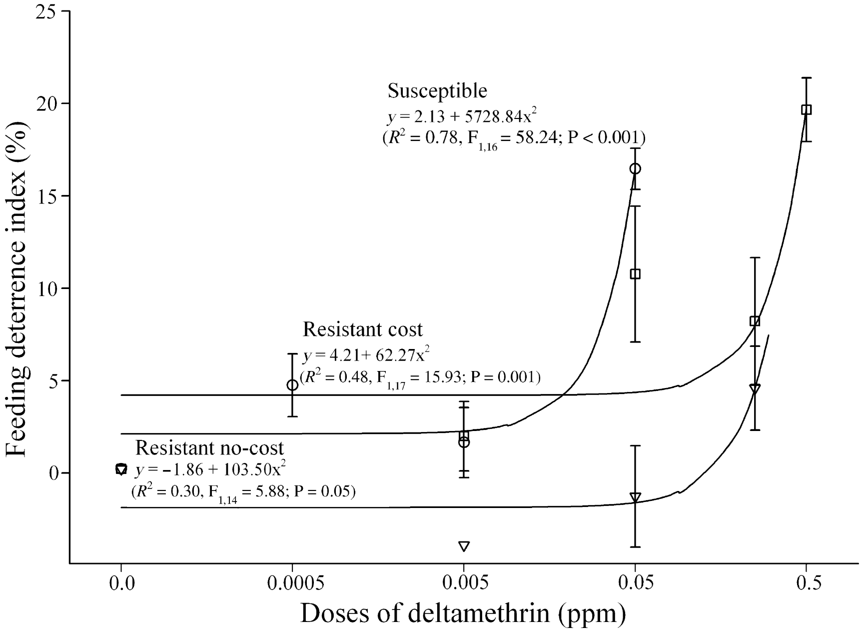

Fig. 5 Feeding deterrence of one pyrethroid-susceptible (○) and two pyrethroid-resistant strains [resistant cost (□) and resistant no-cost (▽)] of maize weevil (*Sitophilus zeamais*) exposed to maize grains sprayed with increasing doses of the pyrethroid insecticide deltamethrin. Each symbol represents the mean of three to five replicates.

pyrethroids. Furthermore, the plasticity of response observed among strains suggests that high-dose management tactics, based on use of high doses of insecticides to increase mortality and turn the resistance functionally recessive (Tabashnik and Croft 1982; Mallet 1989), is not promising in such case. This is so because the use of higher doses of insecticide will only increase the avoidance behaviour exhibited by the already physiologically-resistant insects minimizing the intended mortality. The use of insecticide rotation or mixtures seems more promising management tactics in this case.

The forced exposure of insects from three strains of maize weevil in no-choice feeding tests with maize grains indicated a higher relative growth rate and consequently higher efficiency of food conversion in the insecticide-resistant strains. Such differences were significant even without insecticide exposure indicating that these are stimulus-independent traits probably resulting from the different genetic make-up of each strain and may persist even without further insecticide selection, potentially limiting the tactics available for their management. In addition, such forced exposure of the insects to deltamethrin-sprayed grains also indicated phenotypic plasticity with divergence of feeding response between insecticide-susceptible and -resistant strains subjected to grains with increased insecticide residues.

An insecticide may interfere with insect food consumption if it is able to affect one of the following behavioural components: feeding likelihood, feeding frequency, ingestion efficiency and feeding duration (Simpson 1995). Insecticide-resistant strains of maize weevil are less likely to feed on insecticide-sprayed grains than the insecticide-susceptible strain, if given a choice, as previously discussed. Deltamethrin deterred feeding by the resistant strains at the highest doses used (≤0.25 p.p.m.) on no-choice tests, but drastically deterred feeding by the susceptible strain at 0.05 p.p.m. deltamethrin. The consumption of insecticide-sprayed grains by the resistant no-cost strain increased at the higher doses of deltamethrin, in contrast with a decrease in consumption by the susceptible and resistant cost strains, as a likely strategy of the resistant no-cost strain to compensate the energy expended for protection against the insecticide (Guedes et al. 2006; Araújo et al. 2008a,b). In addition, the conversion efficiency of insecticide-sprayed grains is more seriously compromised in the resistant cost than in the resistant no-cost strain, particularly at higher doses of deltamethrin. Furthermore, the food conversion efficiency of the resistant no-cost strain is not affected by the deltamethrin doses in the range here considered.

In summary, we reported here that pyrethroid-resistant strains of maize weevil better avoid deltamethrin-sprayed grains and are less nutritionally-affected by this compound with divergent responses from the susceptible strain with increased doses of deltamethrin. The resistant population without fitness costs associated with insecticide resistance exhibited even higher behavioural resistance and was also even less nutritionally affected by deltamethrin than the resistant strain with fitness disadvantage. Such responses observed against deltamethrin may also extend to other pyrethroids as well, which deserves attention. The potential pyrethroid-induced plasticity of behavioural responses should also be considered in insecticide resistance assessments since it does have important pest management implications. The management of these resistant strains is further compromised by their deltamethrin-induced feeding plasticity and management tactics based on the high-dose approach are unlikely to succeed. The same can be said regarding the temporary suppression of deltamethrin use aimed at the reestablishment of susceptibility due to fitness disadvantage, because it will not occur for strains not exhibiting fitness disadvantage associated with insecticide resistance, as one of the strains used in the present study. Tactics involving insecticide rotation or mixtures seem more promising.

Acknowledgements

The authors thank the Minas Gerais State Foundation for Research Aid (FAPEMIG), the CAPES Foundation (Brazilian Ministry of Education) and the Brazilian National Council of Scientific and Technological Development (CNPq) for the financial support provided for the present study. The authors also thank Dr J Santos for providing two of the initial insect stock strains used in the present study. Comments and editing by Drs J.E. Throne, J.F. Campbell and K.Y. Zhu on an early draft of the manuscript were greatly appreciated, as were the comments and suggestions provided by Prof. S. Vidal and two anonymous reviewers.

References

Araújo RA, Guedes RNC, Oliveira MGA, Ferreira GH, 2008a. Enhanced activity of carbohydrate- and lipid-metabolizing enzymes in insecticide-resistant populations of the maize weevil, *Sitophilus zeamais*. Bull. Entomol. Res. 98, 417–424.

Araújo RA, Guedes RNC, Oliveira MGA, Ferreira GH, 2008b. Enhanced proteolytic and cellulolytic activity in insecticide-resistant strains of the maize weevil, *Sitophilus zeamais*. J. Stored Prod. Res. 44, 354–359.

Badmin JS, 1990. IRAC survey of resistance of stored grain pests: results and progress. In: Proceedings of the 5th international working conference on stored product protection. Ed. by Fleurrat-Lessard F, Ducom P, INRA/SDPV, Bordeaux, 973–981.

Boivin T, D'Hières CC, Bouvier JC, Beslay D, Sauphanor B, 2001. Pleiotropism of insecticide resistance in the codling moth *Cydia pomonella*. Entomol. Exp. Appl. 99, 381–386.

Champ BR, Dyte CE, 1976. FAO global survey of pesticide susceptibility of stored grain pests. FAO/UN, Rome.

Chevillon C, Bourguet D, Rousset F, Pasteur N, Raymond M, 1997. Pleiotropy of adaptative change in population: comparisons among insecticide resistance genes in *Culex pipiens*. Gen. Res. 68, 195–203.

Cox PD, Fleming DA, Atkinson JE, Bannon KL, Whitefield JM, 1997. The effect of behaviour on the survival of *Cryptolestes ferrugineus* in an insecticide-treated laboratory environment. J. Stored Prod. Res. 33, 257–269.

Dethier VG, Barton-Brown L, Smith CN, 1960. The designation of chemicals in terms of the responses they elicit from insects. J. Econ. Entomol. 53, 134–136.

Fragoso DB, Guedes RNC, Rezende ST, 2003. Glutathione *S*-tranferase detoxification as a potential pyrethroid resistance mechanism in the maize weevil, *Sitophilus zeamais*. Entomol. Exp. Appl. 109, 21–29.

Fragoso DB, Guedes RNC, Peternelli LA, 2005. Developmental rates and population growth of insecticide-resistant and susceptible populations of *Sitophilus zeamais*. J. Stored Prod. Res. 41, 271–281.

Fragoso DB, Guedes RNC, Oliveira MGA, 2007. Partial characterization of glutathione *S*-transferases in pyrethroid-resistant and -susceptible populations of the maize weevil, *Sitophilus zeamais*. J. Stored Prod. Res. 43, 167–170.

Gammon DW, 1978. Neural effects of alethrin on the free walking cockroach *Periplaneta americana*: an investigation using defined doses at 15 and 32°C. Pestic. Sci. 9, 79–91.

Georghiou GP, 1972. The evolution of resistance to pesticides. Annu. Rev. Ecol. Syst. 3, 133–168.

Ghalambor CK, McKay JK, Carroll SP, Reznick DN, 2007. Adaptative versus non-adaptative phenotypic plasticity and the potential for contemporary adaptation in new environments. Funct. Ecol. 21, 394–407.

Gould F, 1984. Role of behavior in the evolution of insect adaptation to insecticides and resistant host plants. Bull. Entomol. Soc. Am. 30, 34–41.

Gould F, 1991. Arthropod behavior and the efficacy of plant protectants. Annu. Rev. Entomol. 36, 305–330.

Guedes RNC, Pereira EJG, 2008. Maize weevil x insecticides: pyrethroid resistance, associated fitness costs and mitigation, and management implications. In: Crop protection research advances Ed. by Columbus F. NOVA Science, Hauppauge, NY, pp. 119–144.

Guedes RNC, Lima JOG, Santos JP, Cruz CD, 1994. Inheritance of deltamethrin resistance in a Brazilian strain of maize weevil (*Sitophilus zeamais* Mots.). Int. J. Pest Manage. 40, 103–106.

Guedes RNC, Lima JOG, Santos JP, Cruz CD, 1995. Resistance to DDT and pyrethroids in Brazilian populations of *Sitophilus zeamais* Motsch. (Coleoptera: Curculionidae). J. Stored Prod. Res. 31, 145–150.

Guedes RNC, Oliveira EE, Guedes NMP, Ribeiro BM, Serrão JE, 2006. Cost and mitigation of insecticide resistance in the maize weevil, *Sitophilus zeamais*. Physiol. Entomol. 31, 30–38.

Haynes KF, 1988. Sublethal effects of neurotoxic insecticides on insect behavior. Annu. Rev. Entomol. 33, 149–168.

Hoy CW, Head GP, Hall FR, 1998. Spatial heterogeneity and insect adaptation to toxins. Annu. Rev. Entomol. 43, 571–594.

Huang Y, Tan JMWL, Kini RM, Ho SH, 1997. Toxic and antifeedant action of nutmeg oil against *Tribolium castaneum* (Herbst) and *Sitophilus zeamais* Motsch. J. Stored Prod. Res. 33, 289–298.

Isman MB, Koul O, Luczynski A, Kaminski J, 1990. Insecticidal and antifeedant bioactivities of neem oils and their relationship to azadiractin content. J. Agric. Food Chem. 38, 1406–1411.

Jallow MFA, Hoy CW, 2005. Phenotypic variation in adult behavioral response and offspring fitness in *Plutella xylostella* (Lepidoptera: Plutellidae) in response to permethrin. J. Econ. Entomol. 98, 2195–2202.

Kongmee M, Prabaripai A, Akratanakul P, Bangs MJ, Chareonviriyaphap T, 2004. Behavioral responses of *Aedes aegypti* (Diptera: Culicidae) exposed to deltamethrin and possible implications for disease control. J. Med. Entomol. 41, 1055–1063.

Lockwood JA, Sparks TC, Story RN, 1984. Evolution of insect resistance to insecticides: a reevaluation of the roles of physiology and behavior. Bull. Entomol. Soc. Am. 30, 41–51.

Mallet J, 1989. The evolution of insecticide resistance: have the insects won? Trends Ecol. Evol. 4, 336–340.

Oliveira EE, Guedes RNC, Corrêa AS, Damasceno BL, Santos CT, 2005. Resistência *vs* susceptibilidade a piretróides em *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae): há vencedor? Neotrop. Entomol. 34, 981–990.

Oliveira EE, Guedes RNC, Tótola MR, De Marco P, 2007. Competition between insecticide-susceptible and –resistant populations of the maize weevil, *Sitophilus zeamais*. Chemosphere 69, 17–24.

Pagliucci M, Muren CJ, 2003. Genetic assimilation and a possible evolutionary paradox: can macroevolution sometimes be so fast as to pass us by? Evolution 57, 1455–1464.

Pekár S, Haddad CR, 2005. Can agrobiont spiders (Araneae) avoid a surface with pesticide residues? Pest Manage. Sci. 61, 1179–1185.

Perez-Mendoza J, 1999. Survey of insecticide resistance in Mexican populations of maize weevil, *Sitophilus zeamais* Motschulsky (Coleoptera: Curculionidae). J. Stored Prod. Res. 35, 107–115.

Pimentel MAG, Faroni LRD'A, Tótola MR, Guedes RNC, 2007. Phosphine resistance, respiration rate and fitness consequences in stored-product insects. Pest Manage. Sci. 63, 876–881.

Price TD, Qvarnstrom A, Irwin DE, 2003. The role of phenotypic plasticity in driving genetic evolution. Proc. R. Soc. London Ser. B 270, 1433–1440.

Rees DP, 1996. Coleoptera. In: Integrated management of insects in stored products Ed. by Subramanyam Bh, Hagstrum DW, Marcell Dekker, NY, USA, pp. 1–39.

Renou M, Henninot-Rodes E, Delorme R, Augé D, Touton P, 1997. Oviposition of resistance and susceptible strains of *Drosophila melanogaster* in the presence of deltamethrin. Entomol. Exp. Appl. 84, 173–181.

Ribeiro BM, Guedes RNC, Oliveira EE, Santos JP, 2003. Insecticide resistance and synergism in Brazilian populations of *Sitophilus zeamais* (Coleoptera: Curculionidae). J. Stored Prod. Res. 39, 21–31.

Ribeiro B, Guedes RNC, Corrêa AS, Santos CT, 2007. Fluctuating asymmetry in insecticide-resistant and insecticide-susceptible strains of the maize weevil, *Sitophilus zeamais* (Coleoptera: Curculionidae). Arch. Environ. Cont. Toxicol. 53, 77–83.

SAS Institute, 2002. SAS/STAT User's guide, v. 8. SAS, Cary, NC.

Simpson SJ, 1995. Regulation of a meal: chewing insects. In: Regulatory mechanisms on insect feeding Ed. by Chapman RF, De Boer G. Chapman and Hall, New York, pp. 137–156.

SPSS, 2000. TableCurve 2D user's guide. SPSS, Chicago, IL.

Subramanyam Bh, Hagstrum DW, 1996. Resistance measurement and management. In: Integrated management of insects in stored products Ed. by Subramanyam Bh, Hagstrum DW. Marcel Dekker, New York, pp. 331–397.

Suiter KA, Gould F, 1994. Physiological and behavioral avoidance responses to residues of four pesticides by six spider mite populations. Entomol. Exp. Appl. 71, 1–14.

Tabashnik BE, Croft BA, 1982. Managing pesticide resistance in crop-arthropod complexes: interactions between biological and operational factors. Environ. Entomol. 11, 1137–1144.

USDA, 1980. Stored-grain insects. ARS-USDA, Washington, DC.

Watson E, Barson G, 1986. A laboratory assessment of the behavioural responses of three strains of *Oryzaephilus surinamensis* (L.) (Coleoptera: Silvanidae) to three insecticides and the insect repellent N,N-diethyl-m-toluamide. J. Stored Prod. Res. 32, 59–67.