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# Developmental and population growth rates of phosphine-resistant and -susceptible populations of stored-product insect pests

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#### ABSTRACT

Phosphine resistance positively contributes towards an individual's fitness under phosphine fumigation. However, phosphine resistance may place resistant individuals at a fitness disadvantage in the absence of this fumigant, which can be exploited to halt or slow down the spread of resistance. This study aimed to determine if there is a fitness cost associated with phosphine resistance in populations of the red flour beetle (Tribolium castaneum (Herbst)), the lesser grain borer (Rhyzopertha dominica (F.)) and the sawtoothed grain beetle (Oryzaephilus surinamensis (L.)). The developmental rate and population growth of phosphine-resistant and -susceptible populations of these three species of stored-product insects were therefore determined under phosphine-free environment. The majority of the phosphine-resistant populations exhibited lower developmental and population growth rates than the susceptible populations indicating that phosphine resistance is associated with fitness cost in all three species, which can potentially compromise the fixation and dispersal of the resistant genotypes. Nonetheless, some phosphine-resistant populations did not show a fitness cost. Therefore, resistance management strategies based on suppression of phosphine use aiming at eventual reestablishment of phosphine susceptibility and subsequent reintroduction of this fumigant will be useful only for insect populations exhibiting a fitness cost associated with phosphine resistance. Therefore recognition of the prevailing phosphine-resistant genotypes in a region is important to direct the management tactics to be adopted. © 2009 Elsevier Ltd. All rights reserved.

# 1. Introduction

The impairment of the reproductive performance of insecticideresistant individuals in insecticide-free environment is the result of fitness costs associated with pesticide resistance, which is often determined by resource allocation from a basic physiological process to the protection against insecticides, favoring survival at the expense of reproduction (Coustau et al., 2000; Guedes et al., 2006). Fitness costs are preliminarily recognized from demographic studies carried out with individual populations in pesticide-free environments, but the occurrence of such costs under this environmental condition is not universal, although frequent (Beeman and Nanis, 1986; Haubruge and Arnaud, 2001; Raymond et al., 2001; Fragoso et al., 2005; Oliveira et al., 2007). Fitness costs associated with resistance to grain protectants have received considerable attention lately (Fragoso et al., 2005; Guedes et al., 2006; Oliveira et al., 2007; Ribeiro et al., 2007; Araújo et al., 2008a, b). However, fitness costs potentially associated with phosphine resistance, the main fumigant currently used worldwide against stored-product insects, have received little attention and have yet to be the subject of demographic studies.

The previously high prominence of phosphine as a storedproduct fumigant has been further increased by the worldwide phasing out of methyl bromide as a fumigant (Zettler and Arthur, 2000; Bell and Hutton, 2002; Fields and White, 2002). The ever increasing overuse of phosphine since the 1960's has resulted in phosphine resistance, which was initially summarized in the FAO worldwide survey of 1976 (Champ and Dyte, 1976). Contrary to the early reports indicating low levels of phosphine resistance in Brazilian populations of stored-product insects (Champ and Dyte, 1976; Sartori et al., 1990), recent reports indicate moderate to high levels of phosphine resistance in field-collected Brazilian populations of Oryzaephilus surinamensis (L.) (Coleoptera: Silvanidae), Rhyzopertha dominica (F.) (Coleoptera: Bostrichidae), Tribolium castaneum (Herbst) (Coleoptera: Tenebrionidae), and Sitophilus zeamais Motschulsky (Coleoptera: Curculionidae) (Lorini et al., 2007; Pimentel et al., 2007, 2009).

Phosphine resistance positively contributes towards an individual's fitness under phosphine fumigation. However, phosphine resistance may place resistant individuals at a fitness disadvantage

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in the absence of this fumigant with implications for the management of these resistant populations. Fitness disadvantages associated with phosphine resistance have been inferred from genetic studies and from preliminary determinations (Lorini et al., 2007; Pimentel et al., 2007, 2009; Schlipalius et al., 2008), but have not yet been subjected to demographic studies. The objective of this study was to determine fitness costs associated with phosphine resistance in representative field-collected populations of *T. castaneum*, *R. dominica* and *O. surinamensis*. Fitness costs associated with phosphine resistance were expected to occur in the field-collected resistant populations studied, and consequences of these costs are important for the design of phosphine resistance management plans.

# 2. Materials and methods

#### 2.1. Insects

Two phosphine-resistant and two phosphine-susceptible populations of T. castaneum, R. dominica and O. surinamensis were used in the present study based on earlier studies (Pimentel et al., 2007; Sousa et al., 2008). These representative populations were collected from stored grains between June 2004 and September 2005. The phosphine-resistant populations of T. castaneum were collected at the counties of Alfenas (state of Minas Gerais) (here referred as resistant - A; 48× resistant) and Campos de Júlio (state of Mato Grosso) (resistant – CJ; 63× resistant), while the susceptible populations were from Água Boa (state of Mato Grosso) (susceptible -AB) and Branganca Paulista (state of São Paulo) (susceptible – BP). The phosphine-resistant populations of *R. dominica* were from Bom Despacho (Minas Gerais) and Palmital (São Paulo) (referred here as resistant - BD and resistant - P, with phosphine resistance levels of  $39 \times$  and  $71 \times$ , respectively), while the susceptible populations were from Nova Era (Minas Gerais) and Piracicaba (SP) (susceptible - NE and susceptible – P, respectively). The phosphine-resistant populations of *O. surinamensis* were from Astolfo Dutra (Minas Gerais) and Guaxupé (Minas Gerais) (resistant – AD and Resistant – G, with phosphine resistance levels of  $29 \times$  and  $32 \times$ , respectively), while the susceptible populations were from Uberlândia and Unaí (Minas Gerais) (susceptible – Ub and susceptible – Un). The insects from each population were individually reared on insecticide-free substrates in 1.5 L glass jars at 30  $\pm$  2 °C, 70  $\pm$  5% relative humidity (r.h.), and in continuous darkness after collection from the field (i.e., for *ca.* 10 generations). Coarsely ground maize was the feeding substrate for both T. castaneum and O. surinamensis, and whole wheat grains were the feeding substrate for R. dominica. Both feeding substrates were used at 13% moisture content and were maintained at -18 °C for at least a week before use to prevent cross-infestation.

# 2.2. Developmental rate until adult emergence

The experiments were carried out in Petri dishes  $(140 \times 10 \text{ mm})$  containing 35 g of the respective food substrates. Each Petri dish was infested with 20 non-sexed adult insects (1-3 weeks old) and maintained at the same conditions described for rearing them. All of these parental insects were removed after 13 days to allow relative standardization of progeny development (Trematerra et al., 1996; Fragoso et al., 2005). After the removal of the parental insects, the food substrate containing the developing progeny was maintained under the same controlled conditions until adult emergence. Four replicates (with 20 adults each) were used for each population of *T. castaneum* and *O. surinamensis*, and six replicates (also with 20 adults each) were used for each population units progenies were counted and removed from the experimental units

(i.e., Petri dishes) on alternate days starting after the first emergence, which took place 30, 28 and 33 days after first oviposition by the populations of *T. castaneum*, *O. surinamensis* and *R. dominica*, respectively. Daily and cumulative emergence were recorded and the cumulative data were normalized (Trematerra et al., 1996). Both data sets were subjected to non-linear regression analysis using the curve-fitting procedure of SigmaPlot (SPSS, 2001).

The analysis of the cumulative emergence data was the initial focus of attention since experimental errors are less likely with it than with the daily emergence data (Trematerra et al., 1996; Fragoso et al., 2005). In addition, since the relative trends in cumulative emergence are more important than the overall data (Trematerra et al., 1996), which are not as statistically reliable, the data for each population were normalized using the time of the first adult emergence in each replicate as the starting point (Trematerra et al., 1996; Fragoso et al., 2005). This procedure minimizes the intra- and inter-population variation in the rate of development. The regression analysis of emergence was initially restricted to the models proposed earlier by Trematerra et al. (1996), but the 3-parameter sigmoid model ( $y = a/(1 + \exp(-(x - b)/c))$ ) provided better fits for cumulative emergence of populations of T. castaneum and O. surinamensis, as also observed by Fragoso et al. (2005), and the 3-parameter Gompertz model ( $y = a \exp(-\exp(-(x-b)/c))$ ) provided better fits for populations of R. dominica. These models were therefore used.

# 2.3. Population growth

The experiment on population growth was carried out in plastic jars (95  $\times$  100 mm) containing 150 g of coarsely ground maize for *T. castaneum* and *O. surinamensis*, and 200 g of whole wheat grains for *R. dominica*. The grains were infested with 20 non-sexed adult insects (1–3 weeks old) under the same environmental conditions mentioned above. The insects were not removed in this experiment, in contrast with the experiments concerning developmental rate, and also employed four replicates for each population of *T. castaneum* and *O. surinamensis*, and six replicates for each population of *T. castaneum* and *O. surinamensis*, and six replicates for each population of *T. castaneum* and *O. surinamensis*, and six replicates for each population of *R. dominica*. The number of live adult insects was recorded 0, 35, 50, 65, 80, 95, and 110 days after starting the experiment for each insect population. The data were subjected to non-linear regression analysis using the curve-fitting procedure of SigmaPlot (SPSS, 2001).

## 3. Results

# 3.1. Developmental rate until adult emergence

#### 3.1.1. Cumulative emergence

The overlapping cumulative emergence from the phosphineresistant populations of T. castaneum was lower than those of both susceptible populations (Fig. 1a; Table 1). The total emergence was lower for both phosphine-resistant populations ( $62.6 \pm 2.2$  and  $77.7 \pm 2.1$  insects/dish for resistant – A and resistant – CJ, respectively), than for the susceptible populations of T. castaneum (113.6  $\pm$  3.5 and 94.1  $\pm$  2.7 insects/dish for susceptible – AB and susceptible - BP, respectively). A similar trend was observed for phosphine-resistant populations of O. surinamensis, which also exhibited slower development to adulthood, than the susceptible populations of this species (Fig. 1b; Table 1). Again the total emergence was lower for the phosphine-resistant - AD population  $(93.0 \pm 6.6 \text{ insects/dish})$ , followed by the susceptible – Ub and resistant – G populations (141.1  $\pm$  5.2 and 149.9  $\pm$  12.2 insects/ dish), which were statistically indistinguishable, and the susceptible - Un population, which exhibited the highest emergence  $(178.0 \pm 6.9 \text{ insects/dish}).$ 

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