

Review : Resistance to Insecticides in Stored-product Insects and Its Mechanisms

Sebastien Boyer¹, Xiong Heming², Wang Xiaoqing³, Zhou Tianzhi³ and Zhang Hongyu^{1*}

Abstract: In this review, we briefly describe the major species of stored-product insects. We concentrate particularly on the economic importance of the control of these insect pests, highlighting a final cost of more than one billion of dollars world-wide. Then we describe in detail and focus our review on the different mechanisms of resistance described in these species. This work is centred on the main ways the resistances described most recently in these insects. First, we detail common description of species resistance throughout the world. We observed 27 recurrent species involved in resistance cases occurring on 5 continents. Resistance is commonly expressed as a factor. Field-collected strains expressed 1.3 to 1 194 fold resistance compared with sensitive strains according to the considered species and insecticide. Described resistance mechanisms include: behavioral resistance, particularly described with *Oryzaephilus surinamensis*, the involvement of detoxifying enzymes (particularly esterases, monooxygenases and transferases) and studies on the genetic resistance, involving the Kdr mutation mechanisms, the transmission of the genes of resistance. We detail all these mechanisms and give some advice on the need for further research some possible future studies, emphasising the need for more collaboration between laboratories from different countries. We dedicate a section to cross-resistance and the multiple resistance due to the many mistakes and different meaning we can find in several articles. Finally, we conclude with pathways that could be followed to increase our knowledge of the development of resistance. We think that studies on genetic diffusion in species and populations of stored-product pests are necessary. These studies are needed to understand the development and the diffusion of the resistance to insecticides.

Key words: stored-product insects, resistance, insecticides

Introduction

Somta *et al* described the problem of the Mungbean, *Vigna radiata* (L.) Wilczek, attacked by one species of stored-product insect^[104]. Mainly produced in Asia, the Mungbean infestation can result to a total destruction within 3 – 4 months^[6]. And knowing that this crop is a major source of dietary protein for poor people and an important nitrogen-fixing legume in tropical cropping systems, we can measure the several consequences related to this insect diseases. Unfortunately, this example is only one among several others.

Classical argumentation to highlight stored-product articles was an economic argue. But with the actual world-wide repartition of the majority of the major pests and with the resistance development to all tested insecticides, the stakes are at least double today. First, we have a real competition between several species for a

raw material which the food, included the species *Homo sapiens sapiens*. The second argue, more and more taking in account by necessity, is the environmental problem. Develop here in some words: find environmental importance^[19]. The stake of these researches is simple to understand: decrease diseases of stored-product insects to increase the quantity of food. With the actual scenario of lack of food in several country on several continent and the future scenario about the feeding of the world wide population, the argument is not necessary to be presented again for the necessity of all these works. Existing projections indicate that future population and economic growth will require a doubling of current food production, including an increase from 2 billion to 4 billion tons of grains annually^[110]. The economic cost is always remains to us at the beginning of each article but it remains difficult to have an idea about the real cost of these pests and or the real disease.

1. Institute of Urban Pests, College of Plant Science and Technology, Huazhong Agricultural University, Wuhan, Hubei, 430070, China.

2. Hubei Branch of China Grain Reserves Corporation, No. 786 Minzhu Road, Wuhan, Hubei, 430071, China.

3. Jingmen Grain Depot of China Grain Reserves Corporation, No. 22 Shenzhen Avenue, Development Area of Duodao, Jingmen, Hubei, 448124, China.

[* hongyu.zhang@mail.hzau.edu.cn]

We can find, here or there, some estimations. Insects and mites are responsible for deterioration of stored food and they cause yearly losses estimated at about 30% of 1800 million tons of stored grain^[52]. Another one talk aboutbut we didn't find any study treating about the total cost (treatment, lost, lack of food for human). In spite of all the pesticide used/misused, insects still destroy over 30% of the world's food crops each year. Over 2 billion tons of grains are produced yearly for food and feed, providing roughly two-thirds of total direct and indirect protein intake^[110]. When we observed the stock market values exchanges for maize or wheat in the American continent or in Europe, the price tonnage lies beyond the 200 \$/ton (i. e., tender wheat reached 385 \$/ton in January 2008). Although we are unable to give a precise number, we can estimate a global worldwide cost of at least one hundred billion dollars.

About 300 different species of stored product pests may be encountered with only about 18 species of primary economic importance.

Stored product insects are adapted to infesting raw grains and cereal products, and present a constant threat to these commodities worldwide. These insect pests survive on dry, stored cereals and legumes in raw or processed form, and they are maintained year after year in storage systems by residual grain remaining in bins, poor sanitation in mills, food-processing facilities and warehouses, and storage, and immigration form natural (rodent caches, bird nests, wooded areas) and other infested sites. Two major groups of insects harbour the mostly economically important post-harvest insect pests: Coleoptera (beetles) and Lepidoptera (moths and butterflies). To notice that several Coleopteran and Lepidopteran species attack crops both in the field and in store. Post-harvest insect pests may be primary, i. e. able to attack intact grains such as the genus *Sitophilus*, while others are secondary pests, attacking already damaged grains or grain products such as the genus *Tribolium*. The Table 1 is a list of the most studied pests until 1995.

Table 1. List of stored-product species and their location in the recent studies coming from 2 major journal treating the resistance in stored-product insects: Journal of Stored Products Research (1995 - 2007) and Journal of Economic Entomology (1997 - 2007)

Order	Family	Species	Location of studied populations
Coleoptera	Anobiidae	<i>Lasioderma serricorne</i>	UK
	Anthribidae	<i>Araecerus fasciculatus</i>	India
	Bostrichidae	<i>Prostephanus truncatus</i>	Benin, Mexico
		<i>Rhyzopertha dominica</i>	Australia, Brazil, India, Morocco, China, USA
	Bruchinae	<i>Callosobruchus chinensis</i>	Uganda, Nigeria, Thailand
		<i>Callosobruchus maculatus</i>	India, Nigeria, Ghana, Uganda, Brazil, Burkina Faso, Cameroon
		<i>Acanthoscelides obtectus</i>	Mexico, Greece, Colombia
		<i>Zabrotes subfasciatus</i>	Mexico
	Cucujidae	<i>Oryzaephilus surinamensis</i>	Australia
	Curculionidae	<i>Cylas formicarius elegantus</i>	India
		<i>Sitophilus granarius</i>	former Yugoslavia
		<i>Sitophilus oryzae</i>	Australia, Brazil, Ethiopia, Morocco, India, USA, Greece
		<i>Sitophilus zeamais</i>	Australia, Brazil, Benin, Mexico, Togo, USA
	Dermestidae	<i>Trogoderma granarium</i>	Asia/Africa
Laemophloeidae	<i>Cryptolestes ferrugineus</i>	China, Australia, USA	
	<i>Cryptolestes pusillus</i>	USA	
Silvanidae	<i>Oryzaephilus surinamensis</i>	Australia, Wales, England, USA, Turkey, Israel	
Tenebrionidae	<i>Tribolium castaneum</i>	Australia, England, Ivory Coast, Brazil, Israel, Nigeria, Morocco, India, Belgium, France, USA, Turkey	
	<i>Tribolium confusum</i>	Israel, Greece	
Hymenoptera	Ichneumonidae	<i>Diadegma insulare</i>	Mexico and USA

Order	Family	Species	Location of studied populations
Lepidoptera	Pyralidae	<i>Amyeolis transitella</i>	USA
		<i>Cadra cautella</i>	Korea
		<i>Ephestia cautella</i>	Australia, Turkey, Israel
		<i>Ephestia kuehniella</i>	Greece
		<i>Plodia interpunctella</i>	USA
	Tortricidae	<i>Cydia pomonella</i>	USA
Psocoptera	Liposcelididae	<i>Liposcelis bostrychophila</i>	China, USA, UK

To illustrate local diseases, we chose to cite just few examples coming from 3 different continents, Africa, South America and Asia. In East Africa, infestation of pigeonpea by *Callosobruchus chinensis* starts in the field and, once infested seeds are stored, there is rapid pest multiplication and destruction of seeds which may reach 100% within a very short time^[101]. In Nigeria, about 30 000 tons is lost annually due to only one pest, *Callosobruchus maculatus* (F.) (Coleoptera: Bruchidae). To notice that under traditional storage conditions, 100% infestation of cowpea occurring within 3 to 5 months of storage is common^[67]. In Asia, rice is an important staple food where paddy fields are harvested 1–3 times in a year and then stored before consumption. India produces hundred millions tons of paddy rice annually which is stored for 3–12 months as paddy by farmers, traders and by the public sector agencies. Only a small fraction of the paddy rice is stored in silos, which do not have the facilities for aeration and drying^[14]. Outdoor storage of paddy rice is common in China^[89] and other Asian countries^[99,88]. Again, outdoor storage does not give the same advantage as the silo, and losses are difficult to estimate. In Latin America, losses in maize caused by *Prostephenus truncatus* is well studied and varied from 9 to 45% depending upon the period of storage^[39,59,81,76,66]. Latin America produced nearly half the world's supply of dry beans^[18]. But almost 80% of beans are produced on small-scale farms without silos. Post-harvest crop losses are predominantly caused by coleopteran species from the family Bruchidae.

Actually the easiest method of controlling insects is with insecticides. In fact, insecticides are generally the most effective management tool and in many instances provide the only feasible method of reducing insect pest populations or reducing them to acceptable levels^[50,84]. We can observe than less and less experiments

were done with Organochlorine and organophosphorous insecticides, 1st generation of chemical insecticides. Historically, they were replaced by pyrethroids, especially deltamethrin, very efficient against arthropods. Two fumigants are currently used for the protection of stored foods: phosphine and methyl bromide. However, the use of methyl bromide was restricted due to its ozone depleting properties^[121] and it must be used after careful consideration because of its very high toxicity to warm-blooded animals^[28]. Phosphine remains one the most used insecticide. In parallel, carbon dioxide is an important factor affecting the efficacy of controlled atmosphere treatments for pest mortality^[115]. More recently, scientists have tested natural oils, which demonstrated a great and new interest of scientists and partners for environmental compounds in the recent future. Essential oils are an alternative to the currently used of fumigants. Papachristos and Stamopoulos^[82] insisted on the different methods we can use them, i. e. as fumigants^[108], contact insecticides^[94], repellents^[91], antifeedants^[51] and also affect some biological parameters such as growth rate, life span and reproduction^[47]. The other used insecticides finding in the literature are diverse: microbial pesticides, insect growth regulator, synergist^[27]. Integrated pest management system to control insect pests should combine the parasitoid and host plant resistance^[98].

Most recent research advances in insect topics, especially in resistance domain and in molecular and genetic advances, are well done on Diptera, particularly on *Drosophila*, the model, and on mosquitoes, the most injury. And reviews on resistance to insecticides in insects existed, especially developed on Diptera. For example, the two articles from Hemingway and Ranson^[55] on one hand and Li *et al*^[74] on the other hand described precisely biochemical and molecular mechanisms developed by insects. Hemingway and Ranson^[55] described mecha-

nisms resistance based on mosquitoes studies involving esterase, glutathion-S-transferase and monooxygenases activities, target site modification, acetylcholinesterase activities, GABA receptor modification and sodium channels, also enhancing the mutation in structural genes, gene amplification and transcriptional regulation. Li *et al*^[74] described these mechanisms more in depth with the involvement of transposable elements, allochemical tolerance and several molecular mechanisms of metabolic resistance (upregulation, coding sequences changes, catalytic site). In parallel, stored-product insects do not lack research too; several articles were published and a journal, Journal of Stored Products Research, was created in 1965. Unfortunately, we can't find synthesis of resistance mechanisms to insecticide on insect stored products.

Described Resistances

In recent years, more than 504 species of insects and mites with insecticide resistance have been recorded and there is still a steady increase in resistance to specific chemicals, with many species now resistant to several groups of insecticides^[38,68]. Insects have successfully adapted to most insecticides by becoming physiologically or behaviorally resistant to them^[93]. In post-harvest ecosystems, the development of insecticide resistance is of great concern to many people. Cases of resistance of insect-stored products to grain protectants^[3,29], and fumigants^[21,72] have been classically documented.

Resistance to insecticides such as malathion, pirimiphos-methyl, fenitrothion has been reported, for example, in *Rhyzopertha dominica* (F.), *Sitophilus oryzae* (F.), *Sitophilus zeamais* (Motschulsky), *Tribolium castaneum* (Herbst)^[41,42]. *S. zeamais* is resistant to DDT and deltamethrin too^[75]. Resistance to DDT and pyrethroids was reported in the early 1990s and in recent years a few instances of organophosphate as well as pyrethroid resistance have been reported^[36,90]. Insecticide resistance has a patchy distribution in Brazilian populations of maize weevil without significant spread, suggesting that the grain trade within the country and local selection are probably major forces driving the evolution and spread of insecticide resistance in this case^[42,36,90,35]. Perez-Medzoa^[84] described also resistance in strains of *S. zeamais* in Mexico. But in this country, maize weevil resistance to deltamethrin and permethrin is in its

initial stages because these insecticides were registered as grain protectants in Mexico only after 1992^[84]. Another example could be *Oryzaephilus surinamensis* (L.) in Australia. This insect was described resistant to commonly used pesticides such as fenitrothion, pirimiphos-methyl and chlorpyrifosmethyl^[9]. The field-collected strains showed resistance to DDT (1.3 – to 14.1 – fold), lindane (4.7 – to 20.9 – fold), malathion (1.6 – to 31.4 – fold), pirimiphos-methyl (3.0 – to 3.7 – fold), deltamethrin (1.2 – to 1.8 – fold), and permethrin (2.3 – to 3.5 – fold). In Morocco, 50 of 51 studied insect populations have been detected resistant^[13]. Several other workers also detected resistance to this fumigant in different parts of the world^[107,77,112,126,5]. Cases of resistance to used fumigants (phosphine but also methyl bromide and ethylene dibromide) has been well documented^[21,72,58]. Similarly, extensive use of controlled atmosphere in insect control could lead to selection of insect populations resistant to hypercarbia and hypoxia^[30,31,115]. At least 11 species of stored-product insects are now known to have developed resistance to phosphine^[23], which has been linked to selection pressures exerted by repeated ineffective fumigations in situations where phosphine gas was rapidly lost due to leakage^[49,112,13].

But generally, insecticide resistance studies are frequently involve only detection bioassays, with folder of resistance. Unfortunately, in the majority of these descriptions of insecticide resistance, we are unable to find experiments on the involved resistance mechanisms.

Behavioral Resistance

This last years, few studies dealt with this method of resistance. Experiments were principally done with *Oryzaephilus surinamensis* and several insecticides. Barson *et al*^[8] demonstrated that avoidance behaviour in *O. surinamensis* was not only dependent on the relative sensitivity of each strain to the toxicant, but also to the quality of the diet in terms of nutritional value and egg-laying sites. Sparks *et al*^[106] identified the role of insect mobility in avoidance behaviour and Wildey^[120] demonstrated the importance of insecticide formulation on contact repellency. At least, Watson and Barson insisted on the effects of the high insecticide concentrations on a avoidance behaviour of *O. surinamensis*^[116]. When applied at the highest tested doses, permethrin, pirimiphos-methyl and etrimfos

caused disorientation. Tested insects demonstrated evidence of avoidance behaviour to high insecticide concentrations^[116]. But, studies of behavioral resistance on stored-product insects, principally due to the non application of their results on the field, were not further developed.

Detoxifying Enzymes

Resistance suppression by a particular synergist suggests detoxification enzymes are involved in the resistance mechanism. The use of insecticide synergists for providing preliminary evidence on the resistance mechanism has seldom been fully explored in stored-grain insect pests (e. g. , (Guedes et al. ^[41] ; Guedes and Zhu^[45]) and in resistance studies with *S. zeamais*. Classical involved enzyme studies in other field research, the 3 most studied families : esterases, monooxygenases and glutathione transferases.

Esterases

Considerable focus on the role of esterases have been described in pyrethroid tolerance. A clear link was shown between the levels of esterases and populations of *Nilaparvata lugens* from pyrethroid treated and non-treated areas^[53]. Kranthi et al. ^[65] and Gunning et al^[48]. described the same correlations for *Helicoverpa*, respectively in India and Australia. Esterases have been involved in German cockroach pyrethroid resistance^[86,95,83]. Lee and Clark^[69,71] suggested that the pyrethroid was being sequestered in the haemolymph through a high affinity binding site on carboxylesterases. In other cases no relationship has been found between esterase levels/patterns and pyrethroid resistance^[79,7,46,1]. Despite the high level of variability in the esterases among the populations of *Liposcelis bostrychophila*, Ali and Turner^[1] were unable to link this variability with the permethrin tolerance. The involvement of esterases in resistance to organophosphorus insecticides in *Tribolium castaneum* was shown early by Dyte and Rowlands^[33]. Triphenyl phosphate, a carboxylesterase inhibitor, was used as an indicator for carboxylesterase involvement in malathion resistance in laboratory tests^[33]. Malathion resistance in most *T. castaneum* strains is due to this mechanism^[80,118,109]. To terminate, grain storage and warehouse operators should be aware that controlled atmosphere (CA) treatments can induce the esterase enzymes which in turn can promote selection of pest strains resistant to CA

treatments^[16] and the rates of development of CA resistance are similar to those recorded for laboratory induced resistance to fumigants^[30]. Many similarities exist between CA resistance and resistance to methyl bromide^[78,113,115].

Glutathione-S-transferases

In the same way, glutathione-S-transferases are often described in insect resistance to insecticides. The involvement of GSTs in the defense against not only organophosphates, but also organochlorines and cyclodienes, is widely reported and continues to attract attention^[123,124,34]. Some involvement of glutathione-S-transferase has been suggested in German cockroach^[122] and the mite *Varroa jacobsoni* Oud. ^[56] resistance. Kranthi et al^[65] suggested that the synergist insensitive tolerance of *Helicoverpa armigera* (Hubner) was due to some sort of nerve insensitivity and a similar mechanism was suggested by Yu and Nguyen^[125] for *Plutella xylostella* (L.) ^[1]. GST activity levels towards the substrate chlorodinitro benzene (CDNB) were always higher, but not always significantly in the resistant populations when compared with the susceptible population. The usually higher GST activity of the resistant population is a likely consequence of their distinct selection history^[42,90,34], which also seems to lead to differences in fitness cost associated with insecticide resistance in these populations^[36,44,34]. The higher catalytic activity of GSTs provides support for the hypothesis of their involvement in the resistance to this insecticide group in some maize weevil populations. GSTs may act as binding proteins increasing the activity of other pyrethroid detoxification enzymes such as esterases^[40,64]. An alternative explanation for the GST role as a binding protein is that the higher GST activity levels in pyrethroid resistant populations of maize weevil, as reported here, may be favoring their direct catalytic activity over pyrethroids as earlier recognized^[125], or their activity as antioxidant agents decreasing the oxidative stress initiated by pyrethroids as more recently suggested^[114]. Either way, there seems to be an involvement of enhanced GST activity in pyrethroid resistance in Brazilian populations of maize weevil, but this resistance mechanism is apparently secondary in importance to altered target site^[42,36,90], and is not as stable based on demographic and physiological studies with these same populations of *Sitophilus zeamais* ^[35,44,34].

Monoxygenases

The monoxygenases are a complex and a large family of enzymes, known to be involved in adaptation of insects and active in the metabolism of all known – insecticides. A number of mechanisms have been suggested recently to explain tolerance or resistance to pyrethroid insecticides. Microsomal cytochrome P450 dependent mono-oxygenases have been shown to be important in some Lepidoptera^[2,65], house flies^[63], headlice^[54] and *Blattella germanica* (L.)^[95,96]^[112]. Cyt P450 is a well-known and well-described enzyme against used-insecticides. For example, the indirect synergist-based evidence of Turner *et al.*^[111] suggested that the detoxification mechanisms in *L. bostrychophila* are of the microsomal mono-oxygenase type^[1]. But more interesting in our area of investigation, recent studies turned towards the possible involvement of Cyt P450 on natural insecticides. A large number of essential oils extracted from various spice and herb plants have already been screened for toxicity as potential fumigants. Monoterpenes rich in essential oils also showed their strong fumigant toxicities against several different stored-grain insect pests^[100]. Monoterpenes can be degraded by the cytochrome P450 – dependent monoxygenase system. In insects, 1, 8 – cineole was metabolised to 2b – hydroxycineole when the pyrgo beetle, *Paropsisterna tigrina* Chapuis, was fed leaves of the Australian tea tree, *Melaleuca alternifolia* (Maiden and Betche) Cheel^[105]. Essential oils or monoterpenes can induce the concentration and aldrin epoxidase activity of cytochrome P450 – dependent monoxygenase in rats and insects^[17,57,70]. Collins *et al.*^[26] also reported the 21.9 – fold higher aldrin epoxidase activity and 12.5 – fold higher concentration of cytochrome P450 in a CM – resistant strain, VOSCM in comparison to VOS48. Therefore, cytochrome P450 monoxygenase activity is presumably related to the detoxification of essential oil or monoterpenes in *O. surinamensis*^[70,68]. Against botanical insecticides, previous cited examples suggested that the cyt P450 monoxygenases are involved with the appearance of resistance to essential oil vapour. Pretreatment of the insects with diethylmaleate, an inhibitor of the glutathione S-transferases^[87,117], caused a partial suppression of resistance to lavender essential oil vapour. Conversely, triphenyl phosphate, an esterase inhibitor^[41,45], did not show any degree of synergism indicating that these enzymes are not in-

involved in the detoxification of lavender essential oil vapour by *Acanthoscelides obtectus*^[82]. These studies suggested that Cyt P450 and GST play a role in the resistance to lavender essential oil vapour, but not the esterases.

Acetylcholinesterase

The mode of action of fumigant toxicity of essential oil or monoterpene against insects may also be the inhibition of acetylcholinesterase (AChE)^[91]. They determined that five monoterpenes inhibited AChE activity in the electric eel and killed adults of the red flour beetle, *Tribolium castaneum* (Herbst). The enhanced carboxyl esterase and anti-oxidation enzymes (superoxide dismutase and catalase) activities could reduce the effects of these toxic products on insects resulting in the insects' resistance to CO₂ increasing. Although the resistance mechanisms of dichlorvos have not been elucidated, it is well known that organophosphate pesticides exert their neurotoxic effects by inhibiting the enzyme acetylcholinesterase (AChE), thereby prolonging the residence time of acetylcholine at cholinergic synapses and producing hyperexcitation of cholinergic pathways. Recent study by Leong and Ho^[73] showed that the AChE activity was inhibited by DDVP in both *L. bostrychophila* and *Liposcelis entomophila*^[29].

Genetic Resistance

Genetic results on insecticide resistance of stored-product insects are not so abundant as in mosquitoes and drosophila studies. *Tribolium castaneum* and *Rhyzopertha dominica* are the two species given us the more recent results, in part due to the work of Beeman and Collins.

Malathion-specific resistance has been particularly described in *T. castaneum*. Even if most studies concluded that this resistance is controlled by a single factor^[10,118], evidences were described involving a second allele giving a weaker resistance to malathion, also segregated at this locus^[11].

On the same way of scientific contradictions, Lindane resistance has been reported as being multifactorial and, later, this resistance was described as controlled by a single semi-dominant gene located on chromosome III.^[11,24] This two examples reflect the lack in the genetic knowledge on the resistance of stored-product insects.

Resistance to pyrethroids in *T. castaneum* strains was finally described to be controlled by at least two incompletely dominant, autosomally

inherited factors^[24]. In this same article except, the inheritance of this resistance was lightly studied too. Collins suggested that resistance was autosomally inherited and maternal effects were absent, estimating that independent genes controlling response from the response of F1 backcrosses were two or three^[24]. Assie *et al.*^[4] showed that the increase in the high malathion-specific resistant strains is due to a genetic background and could depend also to changes occurred in environmental parameters. They also suggested that two generations of selection may be sufficient to detect the potential for the increase of resistance^[4].

As suggested by Collins, extra resistance genes, with different characteristics, may have evolved in different regions. Resistance to phosphine in *R. dominica* species is complex and Collins is not sure about the number of involved genes, writing “least two, and possibly five, different genes”^[25,97]. These limited data are a real lack in our research field. Contrary to other disciplines where genetic resistance is strongly studied as the same as the population genetic of insects inside a country, a continent, even the world, we can't find actually works and cooperation about this subject. I insist too about the phylogeography problem. No data exist about a possible relationship between resistance evolution and genetic polymorphism on stored-product species. These data could be helpful to understand where these species are originating from, to define some natural enemies in the original area, to understand the world-wide spread of a species, to study the differences of the resistance evolution between the different geographical areas.

In this way, the very detailed article of Black and Vontas^[15] could be very useful. They described in details all the actual sequencing methods used nowadays (more than 20). They explained single nucleotide polymorphism mechanisms involved in each methods, their individual advantages and lacks, with a cost study of each of this techniques. As write before, to study the involved genes among some populations, or some species, more cooperation between laboratories from developed countries, able to have the most recent techniques and able to currently use them, and laboratories from developing countries, more involved in sampling and resistance studying, need to set up. For example, our laboratory just defined some RFLP primers and finished our first study on *R. domi-*

nica and we ought to use them on several populations coming from the 5 continents.

Cross Resistance or Multiple Resistance

Example: Kdr Resistance

Actually, an observed resistance to one insecticide is often related to a (some) previous used one(s). And we can read everywhere that it is a cross resistance. For example, one study on the more known resistance mechanisms in stored-product species on *Sitophilus zeamais* coming from Brazil^[42]. “The knockdown resistance is due to the alteration in the site of action of insecticides in the resistant insects. Cypermethrin and permethrin were never used against stored grain pests in Brazil. The detection of resistance bioassays using pyrethroids synergized with piperonyl butoxide and pirimiphos-methyl provided further evidence that KDR is the resistance mechanism involved. Therefore, population of *S. zeamais* seems to have a pyrethroid target site alteration that provides cross-resistance (i. e., resistance to two or more insecticides due to the same mechanism) to the three pyrethroids. These results support the contention that cross-resistance to pyrethroids in Brazilian populations of maize weevil usually occurs in seed storage facilities which were subjected to heavy DDT use in the past”^[42].

Other Citations

In the literature, concerning the stored-product insects, we found different used of the expressions cross-resistance. Guedes *et al.*^[42] wrote “This cross-resistance between DDT and pyrethroids became known as knockdown resistance” instead of talking about the involved mechanism. We can also find some supposition about a cross-resistance mechanism without any explanation; “The increased tolerance for the essential oil may be the result of cross-resistance”^[70]. Again we can wonder if talking about cross-resistance is relevant between an essential oil and one of its compounds; “a chlorpyrifos-methyl resistant strain was cross-resistant to essential oil obtained from *Eucalyptus globulus* (Labill) and its primary monoterpene, 1,8 - cineole”^[68]. Often, assumptions about involvement of some cross-resistance were expressed to explain some observed resistance, without any evidence and mechanism explanations; “our results suggest that the resistance to these compounds is likely caused by cross-resistance from another compound used as a grain protectant in

Brazil”^[90]. We also can find cross-resistance between insecticide families, and no insecticides themselves: “were either highly resistant to malathion or were cross-resistant to organophosphates and pyrethroids”^[62].

Some times, we can find some precaution in the used of cross-resistance and multiple resistance expressions. Fragoso *et al*^[34] called to mind “*the possibility of cross and multiple resistance*” and introduced us a important notion for field observation with an observed resistance probably due to “a result of cross-selection by another insecticide”.

Definitions

With these several examples, we can observe that authors used “cross-resistant” to describe as well the resistance itself, the resistance to insecticide or its mechanisms. No more rigor is observed concerning the use of cross-resistant, cross-resistance, multiple resistance and cross-selection. Definitions about cross-resistance and multiple resistance have evolved since 1979, date of the first finding of these words. Chapman and Penman described cross-resistance as a resistance to one compound conferring resistance to other compounds of the same group, and multiple resistance was described when resistance has been developed to compounds from a number of structurally different groups^[22]. In herbicide resistance, we have two other definitions for cross-resistance and multiple resistance. A cross-resistant weed biotype possesses resistance to several herbicides through a single resistance mechanism. An altered site of action does not necessarily provide cross-resistance to all herbicides with the same site of action. A weed biotype with multiple resistance possesses two or more distinct resistance mechanisms. A water hemp biotype has been identified that has altered binding sites for both the triazine and amino acid synthesis herbicides^[85].

In stored-product articles, cross-resistance is described occurs when a population (or strain) of insects that has developed resistance to one insecticide exhibits resistance to one or more insecticide(s) it has never encountered. Cross-resistance is different from multiple resistance, which occurs when insects develop resistance to several compounds by expressing multiple resistance mechanisms. Here we are far away from the first definitions. Although I am almost agree with this multiple resistance defi-

inition, even if it is incomplete, I prefer to define the cross-resistance as defined by Ishaaya^[60] describing the cross-resistance as following. Cross-resistance appeared when a selected strain (or population, or species) with insecticide A become resistant to an insecticide B; in parallel, this strain selected by the insecticide B must become resistant to the insecticide A. Then, we have a complete description of a cross-resistance, and we are able to work on the involved mechanisms into cross-resistance. About the field strain, we’d better use the term of multiple resistance, including the developed resistance to one insecticide leading to the resistance to one or more insecticide(s) with a single or multiple resistance mechanisms. Finally, agree or not with this definition is not the final point we wanted to highlight here. We though it is dangerous to use, in science, some bad words for good ideas. We need to be vigilant about our word choices.

Conclusions

Lateness in Fundamental Knowledges

This review gave a state on our current knowledge on the resistance of stored-product insects to insecticides. Involved laboratories, published articles and dedicated newspapers, or in part, to this discipline are numerous. Work that has been performing in each laboratory, on each species with each of insecticides is consequent. But we can deplore some lack in the fundamental accumulated knowledge. As an excuse, often, laboratories have contact with administrators or farmer, expecting applied and rapid results with precise data useful in the field. We can understand the importance of immediate results of resistance study for associates, but as scientists, we needn’t forget the importance of knowledge about species history, wide spread, development of genetic tools, evolution of pest management.

The solving of the problem of resistance (after first acknowledging its existence, which is unfortunately the major published article on the resistance in stored product insects) includes accurate forecasting based on the previous history of pesticide use and making available research data on resistance parameters^[37,103,61].

As the number of insecticides and fumigants for insect control have decreased, low cost, convenient to use and environmentally friendly alternatives need to be developed^[82]. But knowledge on resistance need to evolve fas-

ter than this new discoveries. Actually, this is an hypothesis from a utopia.

Considering the mechanisms described, the involved enzymes in the biochemical resistance, the discovered genes in the genetic resistance, we can obviously conclude that, indeed necessary, the made works are not innovative. Nothing new has been discovered compared to drosophila, mosquito and even crop insects. Considering the consequent use of phosphine in close space in stored-products, we can fairly wonder why were we unable to be so innovative. With Phosphine ; innovative method of resistance All species resist by the same way Resistance due to fumigant or to phosphine ; what about the next generation of botanical fumigants with the integrated pest management.

Collaborations, a Way for the Genetic Diffusion of Resistance

I want to insist of the lack of cooperation between laboratories from different countries working on the same species and insist on the need to create some collaborations between us. The other major relevant deficiency is the absence of phylogeny and phylogeography studies on the stored-product insects, to determinate the origin point of these species and to determinate whether a natural enemy exists or if biological compounds from this geographical origin, due to the co-evolution plant-insect, could be used. Furthermore, the study of insecticide resistance should employ evolutionary and ecological approaches to explore its genetic basis, together with the way selection acts to bring genetic changes, and the use of this knowledge to delay the onset of resistance^[4].

The other lack is the absence of the use of new techniques in the stored-product studies. As explained before, fundamental and applied studies of stored-product diseases can't go one without the other. The price of these methods in the developing countries need to be compensate by the laboratory from developed countries with more collaborations. The complete review of Black and Vontas^[15] could help laboratory to choose the involved method and also the laboratory. Indeed, with method keywords and clearest laboratory website, to find some scientists to collaborate has become easier. On the way of the new tools, modelling of the evolution of the resistance need to be considered. With insecticide treatment archives, cases of insecticide resistances, number of studied species and insecticides, involved mechanisms and future genetic results, we should be helpful to predict the rate

of development of resistance to insecticide. Moreover, the effect of population density, plant/insect interaction on the resistance level could be integrated into theoretical models^[4].

Acknowledgements

This work was supported by a China Postdoctoral Science Foundation, China National Science and Technology Project of the 11th Five-Year Plan (2006BAD02A18 - 03 and 2006BAI09B04 - 06) and Hubei Key Project of Science and Technology.

References

- [1] Ali, N. , Turner, B. Allozyme polymorphism and variability in permethrin tolerance in British populations of the parthenogenetic stored product pest *Liposcelis bostrychophila* (Liposcelidae, Psocoptera). Journal of Stored Products Research, 2001, 37:111 - 125
- [2] Armes, N. J. , Wightman, J. A. , Jadhav, D. R. , Rao, G. V. R. Status of insecticide resistance in *Spodoptera litura* in Andhra Pradesh, India. Pesticide Science, 1997, 50:240 - 248
- [3] Arthur, F. H. Grain protectants: Current status and prospects for the future. Journal of Stored Products Research, 1996, 32:293 - 302
- [4] Assie, L. K. , Francis, F. , Gengler, N. , Haubruge, E. Response and genetic analysis of malathion-specific resistant *Tribolium castaneum* (Herbst) in relation to population density. Journal of Stored Products Research, 2007, 43:33 - 44
- [5] Athie, I. , Gomes, R. A. R. , Bolonhezi, S. , Valentini, S. R. T. , De Castro, M. F. P. M. Effects of carbon dioxide and phosphine mixtures on resistant populations of stored-grain insects. Journal of Stored Products Research, 1998, 34:27 - 32
- [6] Banto, S. M. , Sanchez, F. F. The biology and chemical control of *Callosobruchus chinensis* (L.) (Coleoptera: Bruchidae). Philippine Entomologist, 1972, 2:167 - 162
- [7] Barber, M. D. , Moores, G. D. , Tatchell, G. M. , Vice, W. E. , Denholm, I. Insecticide resistance in the currant-lettuce aphid, *Nasonovia ribisnigri* (Hemiptera : Aphididae) in the UK. Bulletin of Entomological Research, 1999, 89:17 - 23
- [8] Barson, G. , Fleming, D. A. , Allan, E. Laboratory assessment of the behavioural responses of residual populations of *Oryzaephilus surinamensis* (L.) (Coleoptera: Silvanidae) to the contact insecticide pirimiphos - methyl by linear logistic modelling. Journal of Stored Products Research, 1992, 28:161 - 170
- [9] Beckett, S. J. , Evans, D. E. , Morton, R. A comparison of the demographies of pesticide susceptible and resistant strains of *Oryzaephilus surinamensis* (L.) (Coleoptera: Silvanidae) on kibbled wheat. Journal of Stored Products Research, 1996, 32:141 - 151

- [10] Beeman, R. W. Inheritance and Linkage of Malathion Resistance in the Red Flour Beetle. *Journal of Economic Entomology*, 1983, 76: 737 – 740
- [11] Beeman, R. W. , Nanis, S. M. Malathion Resistance Alleles and Their Fitness in the Red Flour Beetle (Coleoptera, Tenebrionidae). *Journal of Economic Entomology*, 1986, 79: 580 – 587
- [12] Beeman, R. W. , Stuart, J. J. A Gene for Lindane + Cyclo-diene Resistance in the Red Flour Beetle (Coleoptera, Tenebrionidae). *Journal of Economic Entomology*, 1990, 83: 1745 – 1751
- [13] Benhalima, H. , Chaudhry, M. Q. , Mills, K. A. , Price, N. R. Phosphine resistance in stored – product insects collected from various grain storage facilities in Morocco. *Journal of Stored Products Research*, 2004, 40: 241 – 249
- [14] Birewar, B. R. Improved methods for paddy storage at high moisture level in India. *Bulletin of Grain Technology*, 1987, 25: 256 – 266
- [15] Black, W. C. , Vontas, J. G. Affordable assays for genotyping single nucleotide polymorphisms in insects. *Insect Molecular Biology*, 2007, 16: 377 – 387
- [16] Bond, E. J. , Buckland, C. T. Development of resistance to carbon dioxide in the granary weevil. *Journal of Economic Entomology*, 1979, 7: 770 – 771
- [17] Brattsten, L. B. , Wilkinson, C. F. , Eisner, T. Herbivore-Plant Interactions-Mixed-Function Oxidases and Secondary Plant Substances. *Science*, 1977, 196: 1349 – 1352
- [18] Cardona, C. Insects and other invertebrate pests in Latin America. *Bean Production Problems in Tropics*. H. F. Schwartz and M. A. Pastor-Corrale. CIAT, Cali; 1989, 505 – 570
- [19] Carlson, R. *Silent spring*. Boston, Massachusetts, USA, 1962
- [20] Caswell, G. H. , Akibu, S. The use of pirimiphos-methyl to control bruchids attacking selected varieties of stored cowpea. *Tropical Grain Legume Bulletin*, 1980, 17/18: 9 – 11
- [21] Champ, B. R. , Dyte, C. E. *Fao Global Survey of Pesticide Susceptibility of Stored Grain Pests*. *Fao Plant Protection Bulletin*, 1977, 25: 49 – 67
- [22] Chapman, R. B. , Penman, D. R. Negatively Correlated Cross-Resistance to a Synthetic Pyrethroid in Organo-Phosphorus-Resistant *Tetranychus-Urticae*. *Nature*, 1979, 281: 298 – 299
- [23] Chaudhry, M. Q. Phosphine resistance: a growing threat to an ideal fumigant. *Pesticide Outlook*, June 2000, 2000, 88 – 91
- [24] Collins, P. J. Inheritance of resistance to pyrethroid insecticides in *Tribolium castaneum* (Herbst). *Journal of Stored Products Research*, 1998, 34, 395 – 401
- [25] Collins, P. J. , Daghli, G. J. , Bengston, M. , Lambkin, T. M. , Pavic, H. Genetics of resistance to phosphine in *Rhyzopertha dominica* (Coleoptera : Bostrichidae). *Journal of Economic Entomology*, 2002, 95: 862 – 869
- [26] Collins, P. J. , Rose, H. A. , Wegecsanyi, M. Enzyme-Activity in Strains of the Sawtoothed Grain Beetle (Coleoptera, Cucujidae) Differentially Resistant to Fenitrothion, Malathion, and Chlorpyrifos-Methyl. *Journal of Economic Entomology*, 1992, 85: 1571 – 1575
- [27] Daghli, G. J. , Eelkema, M. , Harrison, L. M. Chlorpyrifos-methyl plus either methoprene or synergized phenothrin for control of Coleoptera in maize in Queensland, Australia. *Journal of Stored Products Research*, 1995, 31: 235 – 241
- [28] Dansi, L. , Van Velson, F. L. , Vander, Heuden, C. A. Methyl bromide; carcinogenic effects in the rat fore stomach. *Toxicology and Applied Pharmacology*, 1984, 72: 262 – 271
- [29] Ding, W. , Wang, J. – J. , Zhao, Z. – M. , Tsai, J. H. Effects of controlled atmosphere and DDVP on population growth and resistance development by the psocid, *Liposcelis bostrychophila* Badonnel (Psocoptera : Liposcelididae). *Journal of Stored Products Research*, 2002, 38: 229 – 237
- [30] Donahaye, E. Laboratory Selection of Resistance by the Red Flour Beetle, *Tribolium Castaneum* (Herbst), to a Carbon Dioxide – Enriched Atmosphere. *Phytoparasitica*, 1990a, 18: 299 – 308
- [31] Donahaye, E. Laboratory Selection of Resistance by the Red Flour Beetle, *Tribolium castaneum* (Herbst), to an Atmosphere of Low Oxygen Concentration. *Phytoparasitica*, 1990b, 18: 189 – 202
- [32] Donahaye, E. The potential for stored – product insects to develop resistance to modified atmosphere. *Proceedings of the 5th International Working Conference on Stored Product Protection*, Bordeaux, France. 1990c
- [33] Dyte, C. E. , Rowlands, D. G. The metabolism and synergism of malathion in resistant and susceptible strains of *Tribolium castaneum* (Coleoptera : Tenebrionidae). *Journal of Stored Products Research*, 1968, 4: 157 – 173
- [34] Fragoso, D. B. , Guedes, R. N. C. , Goreti A. , Oliveira, M. Partial characterization of glutathione S – transferases in pyrethroid-resistant and-susceptible populations of the maize weevil, *Sitophilus zeamais*. *Journal of Stored Products Research*, 2007, 43: 167 – 170
- [35] Fragoso, D. B. , Guedes, R. N. C. , Peternelli, L. A. Developmental rates and population growth of insecticide-resistant and susceptible populations of *Sitophilus zeamais*. *Journal of Stored Products Research*, 2005, 41: 271 – 281
- [36] Fragoso, D. B. , Guedes, R. N. C. , Rezende, S. T. Glutathione S – transferase detoxification as a potential pyrethroid resistance mechanism in the maize weevil, *Sitophilus zeamais*. *Entomologia Experimentalis Et Applicata*, 2003, 109: 21 – 29
- [37] Georghiou, G. P. Management of resistance in arthropods. *Pest Resistance to Pesticides*. G. P. Georghiou and T. Saito. New York, Plenum Press, 1983: 769 – 792
- [38] Georghiou, G. P. Overview of Insecticide Resistance. *Acs Symposium Series*, 1990, 421: 18 – 41
- [39] Giles, P. H. Bean storage problems in Nicaragua. *Tropical Stored Products Information*,

- 1977, 34:63 – 67
- [40] Grant, D. F. , Matsumura, F. Glutathione S – Transferase 1 and 2 in Susceptible and Insecticide Resistant *Aedes – Aegypti*. *Pesticide Biochemistry and Physiology*, 1989, 33:132 – 143
- [41] Guedes, R. N. C. , Kambhampati, S. , Dover, B. A. , Zhu, K. Y. Biochemical mechanisms of organophosphate resistance in *Rhyzopertha dominica* (Coleoptera: Bostrichidae) from the United States and Brazil. *Bulletin of Entomological Research*, 1997, 87:581 – 586
- [42] Guedes, R. N. C. , Lima, J. G. , Santos, J. P. , Cruz, C. D. Resistance to DDT and pyrethroids in Brazilian populations of *Sitophilus zeamais* Motsch. (Coleoptera: Curculionidae). *Journal of Stored Products Research*, 1995, 31:145 – 150
- [43] Guedes, R. N. C. , Lima, J. O. G. , Santos, J. P. , Cruz, C. D. Inheritance of Deltamethrin Resistance in a Brazilian Strain of Maize Weevil (*Sitophilus – Zeamais* Mots). *International Journal of Pest Management*, 1994, 40:103 – 106
- [44] Guedes, R. N. C. , Oliveira, E. E. , Guedes, N. M. P. , Ribeiro, B. , Serrao, J. E. Cost and mitigation of insecticide resistance in the maize weevil, *Sitophilus zeamais*. *Physiological Entomology*, 2006, 31:30 – 38
- [45] Guedes, R. N. C. , Zhu, K. Y. Characterization of malathion resistance in a Mexican population of *Rhyzopertha dominica*. *Pesticide Science*, 1998, 53:15 – 20
- [46] Guerrero, F. D. , Pruetz, J. H. , Kunz, S. E. , Kammalah, D. M. Esterase profiles of diazinon – susceptible and – resistant horn flies (Diptera : Muscidae). *Journal of Economic Entomology*, 1999, 92:286 – 292
- [47] Gunderson, C. A. , Samuelian, J. H. , Evans, C. K. , Brattsten, L. B. Effects of the mint monoterpene pulegone on *Spodoptera eridania* (Lepidoptera: Noctuidae). *Environmental Entomology*, 1985, 14:859 – 863
- [48] Gunning, R. V. , Moores, G. D. , Devonshire, A. L. Esterase inhibitors synergise the toxicity of pyrethroids in Australian *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae). *Pesticide Biochemistry and Physiology*, 1999, 63:50 – 62
- [49] Halliday, D. , Harris, A. H. , Taylor, R. W. D. Recent Developments in the Use of Phosphine as a Fumigant for Grains and Other Durable Agricultural Produce. *Chemistry , Industry*, 1983, 468 – 471
- [50] Harein, P. K. , Davis, R. Control of stored – grain insects. *Storage of Cereal Grains and their Products*. D. B. Sauer. American Association of Cereal Chemists, Inc. St. Paul, MN, USA, 1992: 492 – 534
- [51] Harwood, S. H. , Moldenke, A. F. , Berry, R. E. Toxicity of monoterpenes to the variegated cutworm (Lepidoptera: Noctuidae). *Journal of Economic Entomology*, 1990, 83:1761 – 1767
- [52] Haubruge, E. , Arnaud, L. , Mignon, J. The impact of sperm precedence in malathion resistance transmission in populations of the red flour beetle *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae). *Journal of Stored Products Research*, 1997, 33:143 – 146
- [53] Hemingway, J. , Karunaratne, S. H. P. P. , Claridge, M. F. Insecticide resistance spectrum and underlying resistance mechanisms in tropical populations of the brown planthopper (*Nilaparvata lugens*) collected from rice and the wild grass *Leersia hexandra*. *International Journal of Pest Management*, 1999a, 45:215 – 223
- [54] Hemingway, J. , Miller, J. , Mumcuoglu, K. Y. Pyrethroid resistance mechanisms in the head louse *Pediculus capitis* from Israel: implications for control. *Medical and Veterinary Entomology*, 1999b, 13:89 – 96
- [55] Hemingway, J. , Ranson, H. Insecticide resistance in insect vectors of human disease. *Annual Review of Entomology*, 2000, 45:371 – 391
- [56] Hillesheim, E. , Ritter, W. , Bassand, D. First data on resistance mechanisms of *Varroa jacobsoni* (OUD) against tau – fluvalinate. *Experimental , Applied Acarology*, 1996, 20:283 – 296
- [57] Hiroi, T. , Miyazaki, Y. , Kobayashi, Y. , Imaoka, S. , Funae, Y. Induction of Hepatic P450s in Rat by Essential Wood and Leaf Oils. *Xenobiotica*, 1995, 25: 457 – 467
- [58] Ho, S. H. , Winks, R. G. The Response of *Liposcelis – Bostrychophila* Badonnel and *Liposcelis – Entomophila* (Enderlein) (Psocoptera) to Phosphine. *Journal of Stored Products Research*, 1995, 31:191 – 197.
- [59] Hodges, R. J. , Dunstan, W. R. , Magazini, I. , Golob, P. An outbreak of *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae) in East Africa. *Protection Entomology*, 1983, 5:183 – 194
- [60] Ishaaya, I. , Ed. . Biochemical sites of insecticide action and resistance. Berlin Heidelberg New York, Springer – Verlag, 2001
- [61] Kljajic, P. , Peric, I. Susceptibility to contact insecticides of granary weevil *Sitophilus granarius* (L.) (Coleoptera: Curculionidae) originating from different locations in the former Yugoslavia. *Journal of Stored Products Research*, 2006, 42: 149 – 161
- [62] Kljajic, P. , Peric, I. Altered susceptibility of granary weevil *Sitophilus granarius* (L.) (Coleoptera: Curculionidae) populations to insecticides after selection with pirimiphos – methyl and deltamethrin. *Journal of Stored Products Research*, 2007, 43:134 – 141
- [63] Korytko, P. J. , Scott, J. G. CYP6D1 protects thoracic ganglia of houseflies from the neurotoxic insecticide cypermethrin. *Archives of Insect Biochemistry and Physiology*, 1998, 37:57 – 63
- [64] Kostaropoulos, I. , Papadopoulos, A. I. , Metaxakis, A. , Boukouvala, E. , Papadopoulou – Mourkidou, E. Glutathione S – transferase in the defence against pyrethroids in insects. *Insect Biochemistry and Molecular Biology*, 2001, 31:313 – 319
- [65] Kranthi, K. R. , Armes, N. J. , Rao, N. G. V. , Raj, S. , Sundaramurthy, V. T. Seasonal dynamics of metabolic mechanisms mediating pyrethroid resistance in *Helicoverpa armigera* in

- central India. *Pesticide Science*, 1997, 50
- [66] Kumar, H. Resistance in maize to the Larger Grain Borer, *Prostephanus truncatus* (Horn) (Coleoptera: Bostrichidae). *Journal of Stored Products Research*, 2002, 38: 267 – 280
- [67] Lale, N. E. S., Mustapha, A. Potential of combining neem (*Azadirachta indica* A. Juss) seed oil with varietal resistance for the management of the cowpea bruchid, *Callosobruchus maculatus* (F.). *Journal of Stored Products Research*, 2000, 36: 215 – 222.
- [68] Lee, S. – E. Biochemical mechanisms conferring cross-resistance to fumigant toxicities of essential oils in a chlorpyrifos-methyl resistant strain of *Oryzaephilus surinamensis* L. (Coleoptera: Silvanidae). *Journal of Stored Products Research*, 2002, 38: 157 – 166
- [69] Lee, S., Clark, J. M. Tissue distribution and biochemical characterization of carboxylesterases associated with permethrin resistance in a near isogenic strain of Colorado potato beetle. *Pesticide Biochemistry and Physiology*, 1996, 56: 208 – 219
- [70] Lee, S. E., Choi, W. S., Lee, H. S., Park, B. S. Cross-resistance of a chlorpyrifos – methyl resistant strain of *Oryzaephilus surinamensis* (Coleoptera: Cucujidae) to fumigant toxicity of essential oil extracted from *Eucalyptus globulus* and its major monoterpene, 1, 8 – cineole. *Journal of Stored Products Research*, 2000, 36: 383 – 389
- [71] Lee, S. H., Clark, J. M. Permethrin carboxylesterase functions as nonspecific sequestration proteins in the hemolymph of Colorado potato beetle. *Pesticide Biochemistry and Physiology*, 1998, 62: 51 – 63
- [72] Leong, E. C. W., Ho, S. H. Relative tolerance of *Liposcelis bostrychophila* (Bad) and *L-entomophila* (End) to some organophosphorus and carbamate insecticides. *Insect Science and Its Application*, 1994, 15: 343 – 349
- [73] Leong, E. C. W., Ho, S. H. In – Vitro Inhibition of Esterase-Activity in *Liposcelis bostrychophila* Bad and *L-Entomophila* (End) (Psocoptera, Liposcelididae). *Comparative Biochemistry and Physiology B-Biochemistry, Molecular Biology*, 1995, 110: 121 – 130
- [74] Li, X. C., Schuler, M. A., Berenbaum, M. R. Molecular mechanisms of metabolic resistance to synthetic and natural xenobiotics. *Annual Review of Entomology*, 2007, 52: 231 – 253
- [75] Lorini, I., Galley, D. J. Deltamethrin resistance in *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae), a pest of stored grain in Brazil. *Journal of Stored Products Research*, 1999, 35: 37 – 45
- [76] Markham, R. H., Wright, V. F., Rios Ibarra, R. M. A selective review of research on *Prostephanus truncatus* (Coleoptera: Bostrichidae) with an annotated and updated bibliography. *Ceiba*, 1991, 32: 1 – 90
- [77] Mills, K. A. Resistance to the fumigant hydrogen phosphide in some stored-product species associated with repeated inadequate treatments. *Communications of the German Association of General and Applied Entomology Meeting*, 1983, 4: 96 – 101
- [78] Monro, H. A. U. Insect resistance to fumigants. *Pest Control*, 1964, 32: 1 – 4
- [79] Moores, G. D., Denholm, I., Devonshire, A. L. Association between biochemical markers and insecticide resistance in the cotton aphid, *Aphis gossypii* Glover. *Pesticide Biochemistry and Physiology*, 1998, 62: 164 – 171
- [80] Navarro, S., Carmi, Y., Kashanchi, Y., Shaaya, E. Malathion Resistance of Stored – Product Insects in Israel. *Phytoparasitica*, 1986, 14: 273 – 280
- [81] Pantenius, C. U. Storage losses in traditional maize granaries in Togo. *Insect Science and its Applications*, 1988, 9: 725 – 735
- [82] Papachristos, D. P., Stamopoulos, D. C. Selection of *Acanthoscelides obtectus* (Say) for resistance to lavender essential oil vapour. *Journal of Stored Products Research*, 2003, 39: 433 – 441
- [83] Park, N. J., Kamble, S. T. Comparison of esterases between life stages and sexes of resistant and susceptible strains of German cockroach (Diptera: Blattellidae). *Journal of Economic Entomology*, 1998, 91: 1051 – 1057
- [84] Perez-Mendoza, J. Survey of insecticide resistance in Mexican populations of maize weevil, *Sitophilus zeamais* Motschulsky (coleoptera: curculionidae). *Journal of Stored Products Research*, 1999, 35: 107 – 115
- [85] Powles, S. B., Preston, C., Bryan, I. B., Jutsum, A. R. Herbicide resistance: Impact and management. *Advances in Agronomy*, 1997, 58: 57 – 93.
- [86] Prabhakaran, S. K., Kamble, S. T. Biochemical characterization and purification of esterases from three strains of German cockroach, *Blattella germanica* (Diptera: Blattellidae). *Archives of Insect Biochemistry and Physiology*, 1996, 31: 73 – 86
- [87] Raffa, K. F., Priester, T. M. Synergists as research tools and control agents in agriculture. *Journal of Agricultural Entomology*, 1985, 2: 27 – 45
- [88] Rajendran, S., Muralidharan, N. Performance of phosphine in fumigation of bagged paddy rice in indoor and outdoor stores. *Journal of Stored Products Research*, 2001, 37: 351 – 358
- [89] Rapa. Paddy Rice Storage in China. RAPA Publications. FAO, Bangkok, Regional Office for Asia and the Pacific, 1986
- [90] Ribeiro, B. M., Guedes, R. N. C., Oliveira, E. E., Santos, J. P. Insecticide resistance and synergism in Brazilian populations of *Sitophilus zeamais* (Coleoptera: Curculionidae). *Journal of Stored Products Research*, 2003, 39: 21 – 31
- [91] Ryan, M. F., Byrne, O. Plant – insect coevolution and inhibition of acetylcholinesterase. *Journal of Chemical Ecology*, 1988, 14: 1965 – 1975
- [92] Saim, N., Meloan, C. E. Compounds from leaves of bay (*Laurus nobilis* L.) as repellents for Tri-

- bolium castaneum (Herbst) when added to wheat flour. *Journal of Stored Products Research*, 1986, 22:141 – 144
- [93] Sawicki, R. M., Denholm, I. Adaptation of Insects to Insecticides. *Ciba Foundation Symposium*, 1984, 102:152 – 162
- [94] Saxena, R. C., Dixit, D. P., Harshan, V. Insecticidal action of *Lantana camara* against *Callosobruchus chinensis* (Coleoptera: Bruchidae). *Journal of Stored Products Research*, 1992, 28:279 – 281
- [95] Scharf, M. E., Hemingway, J., Reid, B. L., Small, G. J., Bennett, G. W. Toxicological and biochemical characterization of insecticide resistance in a field-collected strain of *Blattella germanica* (Dictyoptera: Blattellidae). *Journal of Economic Entomology*, 1996, 89:322 – 331
- [96] Scharf, M. E., Hemingway, J., Small, G. J., Bennett, G. W. Examination of esterases from insecticide resistant and susceptible strains of the German cockroach, *Blattella germanica* (L.). *Insect Biochemistry and Molecular Biology*, 1997, 27:489 – 497
- [97] Schlipalius, D. I., Cheng, Q., Reilly, P. E. B., Collins, P. J., Ebert, P. R. Genetic linkage analysis of the lesser grain borer *Rhyzopertha dominica* identifies two loci that confer high – level resistance to the fumigant phosphine. *Genetics*, 2002, 161:773 – 782
- [98] Schmale, I., Wackers, F. L., Cardona, C., Dorn, S. Combining parasitoids and plant resistance for the control of the bruchid *Acanthoscelides obtectus* in stored beans. *Journal of Stored Products Research*, 2003, 39:401 – 411
- [99] Semple, R. L., Hicks, P. A., Lozare, J. V., Castermans, A. Grain storage systems in selected asian countries, REAPASIA; 1988
- [100] Shaaya, E., Ravid, U., Paster, N., Juven, B., Zisman, U., Pissarev, V. Fumigant Toxicity of Essential Oils against 4 Major Stored-Product Insects. *Journal of Chemical Ecology*, 1991, 17:499 – 504
- [101] Silim Nahdy, M., Silim, S. N., Ellis, R. H. Some aspects of pod characteristics predisposing *pigeonpea* (*Cajanus cajan* (L.) Millsp.) to infestation by *Callosobruchus chinensis* (L.). *Journal of Stored Products Research*, 1999, 35:47 – 55
- [102] Singh, S. R., Singh, B. B., Jackai, L. E. N., Ntare, B. R. Cowpea research at IITA. Ibadan, Nigeria; 1983
- [103] Soderland, D. M., Bloomquist, J. R. Molecular mechanisms of insecticide resistance. *Pesticide Resistance in Arthropods*. R. T. Rousch and B. E. Tabashnik. New York and London, Chapman, Hall, 1990:58 – 96
- [104] Somta, P., Talekar, N. S., Srinives, P. Characterization of *Callosobruchus chinensis* (L.) resistance in *Vigna umbellata* (Thunb.) Ohwi, Ohashi. *Journal of Stored Products Research*, 2006, 42:313 – 327
- [105] Southwell, I. A., Maddox, C. D. A., Zalucki, M. P. Metabolism of 1,8 – Cineole in Tea Tree (*Melaleuca – Alternifolia* and *Melaleuca – Linariifolia*) by Pyrgo Beetle (*Paropsisterna – Tigrina*). *Journal of Chemical Ecology*, 1995, 21:439 – 453
- [106] Sparks, T. C., Lockwood, J. A., Byford, R. L., Graves, J. B., Leonard, B. R. The role of behaviour in insecticide resistance. *Pesticide Science*, 1989, 26:383 – 399
- [107] Srivastava, J. L. Pesticide residue in food grains and pest resistance to pesticides. *Bulletin of Grain Technology*, 1980:18
- [108] Stamopoulos, D. C. Effects of four essential oil vapours on the oviposition and fecundity of *Acanthoscelides obtectus* (Say) (Coleoptera: Bruchidae): laboratory evaluation. *Journal of Stored Products Research*, 1991, 27:199 – 203
- [109] Subramanyam, B., Harein, P. K., Cutkomp, L. K. Organo – Phosphate Resistance in Adults of Red Flour Beetle (Coleoptera, Tenebrionidae) and Sawtoothed Grain Beetle (Coleoptera, Cucujidae) Infesting Barley Stored on Farms in Minnesota. *Journal of Economic Entomology*, 1989, 82:989 – 995
- [110] Tubiello, F. N., Soussana, J. F., Howden, S. M. Crop and pasture response to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 2007, 104:19686 – 19690
- [111] Turner, B. D., Maude – Roxby, H., Pike, V. Control of the domestic insect pest *Liposcelis bostrychophila* (Badonnel) (Psocoptera): an experimental evaluation of the efficiency of some insecticides. *International Pest Control*, 1991, 33:153 – 157
- [112] Tyler, P. S., Taylor, R. W. D., Rees, D. P. Insect resistance to phosphine fumigation in food warehouses in Bangladesh. *International Pest Control*, 1983, 25:10 – 13
- [113] Uptis, R., Monro, H. A. U., Bond, E. J. Some aspects of inheritance of tolerance to methyl bromide by *Sitophilus granarius* (L.). *Journal of Stored Products Research*, 1973, 9:13 – 17
- [114] Vontas, J. G., Small, G. J., Hemingway, J. Glutathione S – transferases as antioxidant defence agents confer pyrethroid resistance in *Nilaparvata lugens*. *Biochemical Journal*, 2001, 357:65 – 72
- [115] Wang, J. – J., Zhao, Z. – M., Tsai, J. H. Resistance and some enzyme activities in *Liposcelis bostrychophila* *Badonnel* (Psocoptera: Liposcelididae) in relation to carbon dioxide enriched atmospheres. *Journal of Stored Products Research*, 2000, 36:297 – 308
- [116] Watson, E., Barson, G. 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. *Journal of Stored Products Research*, 1996, 32, 59 – 67
- [117] Welling, W., De Vries, J. W. Synergism of organophosphorus insecticides by diethylmaleate and related compounds in house flies. *Pesticide*

- Biochemistry and Physiology, 1985, 23: 358 – 369
- [118] White, N. D. G. , Bell, R. J. Inheritance of Malathion Resistance in a Strain of *Tribolium-Castaneum* (Coleoptera, Tenebrionidae) and Effects of Resistance Genotypes on Fecundity and Larval Survival in Malathion-Treated Wheat. Journal of Economic Entomology, 1988, 81: 381 – 386
- [119] White, N. D. G. , Bell, R. J. Relative Fitness of a Malathion – Resistant Strain of *Cryptolestes-Ferrugineus* (Coleoptera, Cucujidae) When Development and Oviposition Occur in Malathion – Treated and Untreated Wheat Kernels. Journal of Stored Products Research, 1990, 26: 23 – 37
- [120] Wildey, K. B. Repellency of insecticide formulations to Rust – red flour beetle (*Tribolium castaneum*). Stored Products Pest Control, BCPC Monograph No. 37. T. J. Lawson, 1987: 187 – 196
- [121] Wmo. Scientific Assessment of Ozone Depletion: 1991. World Meteorological Organization Report No. 25. World Meteorological Organization of the United Nations, Geneva, 1991
- [122] Wu, D. X. , Scharf, M. E. , Neal, J. J. , Suiter, D. R. , Bennett, G. W. Mechanisms of fenvalerate resistance in the German cockroach, *Blattella germanica* (L.). Pesticide Biochemistry and Physiology, 1998, 61: 53 – 62
- [123] Yu, S. J. Insect glutathione S – transferases. Zoological Studies, 1996, 35: 9 – 19
- [124] Yu, S. J. Substrate specificity of glutathione S – transferases from the fall armyworm. Pesticide Biochemistry and Physiology, 2002, 74: 41 – 51
- [125] Yu, S. J. , Nguyen, S. N. Insecticide susceptibility and detoxication enzyme activities in permethrin-selected diamondback moths. Pesticide Biochemistry and Physiology, 1996, 56: 69 – 77
- [126] Zettler, J. L. Phosphine resistance in stored product insects in the United States. Proceedings of the 5th International Working Conference on Stored – Product Protection Bordeaux, France, 1990