Codling Moth, *Cydia pomonella* (Lepidoptera: Tortricidae) – Major Pest in Apple Production: an Overview of its Biology, Resistance, Genetic Structure and Control Strategies

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Summary

The codling moth *Cydia pomonella* (CM) (Linnaeus) is a key pest in pome fruit production with a preference for apple. The pest is very adaptable to different climatic conditions and is known for developing resistance to several chemical groups of insecticides. Because of these reasons, the populations of codling moth are differentiated in many ecotypes of various biological and physiological development requirements. The article provides a bibliographic review of investigation about: morphology, biology, dispersal, damages, resistance to insecticides, population genetic structure and genetic control of this pest.

Key words

Cydia pomonella; apple; insecticide resistance; population genetic structure; genetic control; Tortricidae

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Introduction

The codling moth (CM) (*Cydia pomonella* L.) is the major pest infecting the apple, both in Croatia and abroad. Besides apple this pest attacks pear, walnut, quince and some stone fruits causing economic losses in fruit production (Ciglar, 1998).

The pest was originally present in Eurasia, but during the last two centuries it dispersed around the world with the spread of the cultivation of apples and pears (Franck et al., 2007). It has achieved a nearly global distribution, being one of the most successful pest insect species known today (Thaler et al., 2008). Currently, CM is also present in North America, South America, South Africa, Australia and New Zealand (Franck et al., 2007) (Fig 1).

Frequent insecticide applications are harmful to human health, the environment and beneficial organisms. As a consequence of intensive control, CM developed resistance to several chemical groups of insecticides (Sauphanor et al., 2000; Boivin et al., 2001; Bouvier et al., 2001; Brun-Barale et al., 2005). Cross-resistance between chitin inhibitors, moult activating compounds such as tebufenozide and juvenile hormone analogues were detected in CM populations in South-Eastern France by Sauphanor and Bouvier (1995) and Sauphanor et al. (2000). Also, resistance to different classes of insecticides has been documented in CM populations from Italy (Ioriatti et al., 2000, 2005).

In order to reduce the amount of chemical pesticides in the environment and their residues on food, alternatives to broad
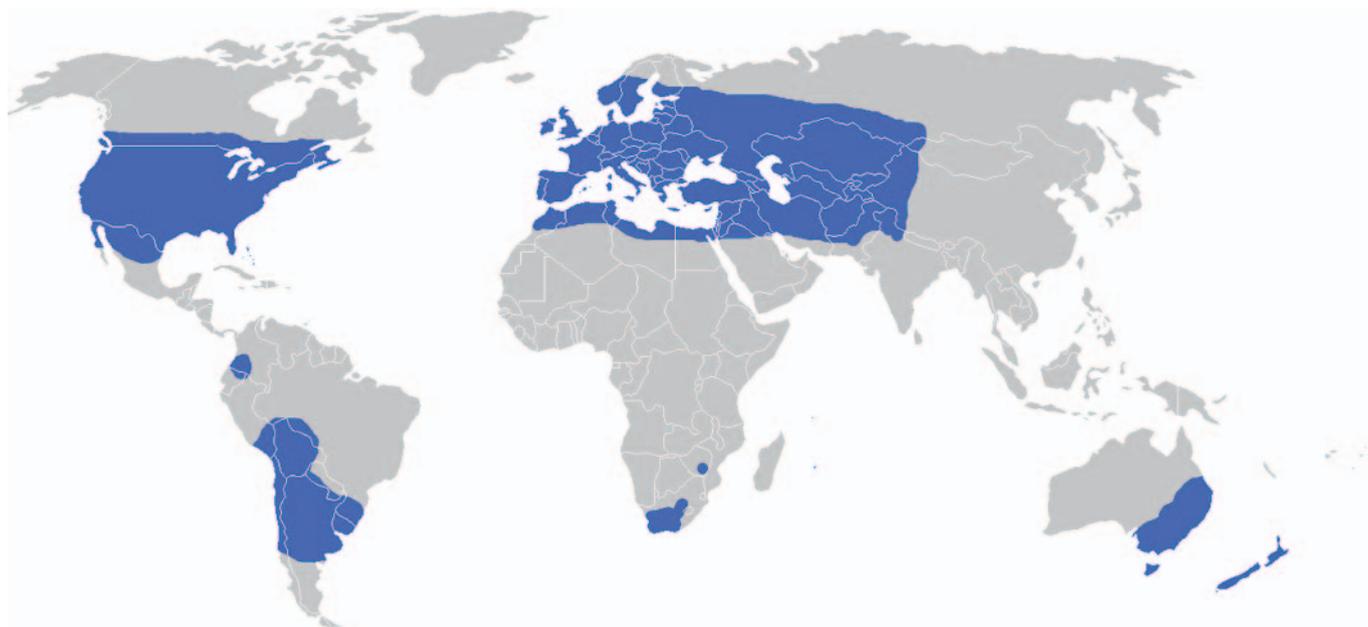

Figure 1. Worldwide distribution of *Cydia pomonella* L.

It has adapted successfully to different habitats by forming various ecotypes and populations, often designated with a term *strains*, which differ among each other in several morphological, developmental and physiological features (Meraner et al., 2008).

The first mention of CM as well as the information about its origin and description of the damages it causes on fruit stretches dates back to distant past. Theophrastus described it 371 years before Christ (cit. Balachowsky and Mesnil, 1935).

Depending on the cultivation area and climatic conditions, the pest develops one to four generations per year. In fruit production, the main market demand is the production of high quality fruits with no signs of damage by this pest. Despite a large number of chemical control treatments, damage to apple fruit remains greater than 1%, which is an unacceptable level of damage according to the guidelines of apple production.

Most growers use broad spectrum insecticides to control the CM and these chemical treatments must be applied multiple times in a season because of the pest biology (several generations in one year) (Lacey et al., 2008).

spectrum pesticides are being developed. Recently more attention is given to familiar and recognized principles of integrated pest management (IPM strategy). The IPM is based on application of environmentally and toxicologically acceptable treatments with an emphasis on application of bio-control methods such as using pheromones (attract-and-kill method and mating disruption) (Ciglar, 1998; Maceljski, 2002).

Mating disruption by synthetic pheromones is a promising and powerful tool for environmentally safe control of codling moth. The most important disadvantage of this technique, however, is that female behaviors are not affected (Yan et al., 1999).

Natural enemies (entomopathogens, predators and parasitoids) and their use as biological control agents play key roles in IPM (Lacey and Unruh, 2005).

A multitude of entomopathogens have been reported from codling moth, including virus (granulovirus), bacteria (*Bacillus thuringiensis*), fungi (*Beauveria basiana*), protozoa, microsporida (*Nosema carpocapsae*), and nematodes (*Steinernema carpocapsae, Steinernema feltiae, Heterorhabditis* spp.). Out of these,

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virus, and nematodes have been developed as microbial agents for augmentative biological control of codling moth (Lacey and Unruh, 2005).

Furthermore, large and mostly unexplored area for biological control of CM is the use of its numerous natural predators such as spiders, mites, birds, insects (true bugs, ground beetles, ants, thrips, earwigs) and parasitoids (i.e. parasitic wasps from the families Braconidae and Ichneumonidae) (Lacely et al., 2003; Lacey and Unruh, 2005). In recent studies, special attention is given to determining the mechanisms of resistance of CM to certain chemical groups of insecticides and studies of the genetic structure and control strategies of CM populations.

Classification

Order: Lepidoptera Linnaeus, 1758

Suborder: Microlepidoptera

Family: Tortricidae Latreille, 1803

Sub-family: Olethreutinae

Tribe: Grapholitini

Genus: *Cydia* Hübner, 1825

Species: *Cydia pomonella* (Linnaeus, 1758)

Morphology

CM adults are ashy gray, with a wingspan of 15-22 mm. They can be distinguished from other moths associated with fruit trees by their dark brown wing tips with shiny, coppery markings. The eggs are about 1 mm in size, disc-shaped and transparent white when first laid. As they mature, eggs become opaque white and develop a red ring.

Caterpillars are white to pink with a mottled brown head and shield at the top of the first segment behind the head. Anal shield is pale and without anal comb. They have small dark warts with light brown hairs on their sides. Adult caterpillars can grow up to 18-20 mm. A cocoon is 8-10 mm long, of yellow-brown to dark-brown color (Kovačević, 1947; Kovačević, 1952; Alford, 1984; Ciglar, 1998; Maceljski, 2002).

Life cycle and dispersal

The pest overwinters as a fullgrown larva within a thick, silken cocoon that can be found under loose scales of bark and in soil or debris around the tree base.

The larvae pupate inside their cocoons in early spring, usually in March when spring temperatures exceed 10°C. Depending on temperature pupae development takes 7-30 days. For the development of adults the sum of Day Degrees (DD) of 100 is required (Wildbolz, 1965 cit Ciglar, 1998) that is usually at the end of April. The appearance of moths is associated with climatic conditions (temperature and humidity) as well as with fruit development period. The flight of the first generation of CM is much more intense from the middle or the end of May and lasts until the end of June. Moths are most active at sunset and before sunrise. In this period they mate. Female deposits 30 to 70 eggs singly on fruit or nearby leaves. After the eggs hatch, young larvae seek out and bore into a fruit. They feed on the interior of the fruit and reach full growth in four weeks. After completing their development they leave the fruit and drop from the trees to search out sites for pupation. The sum of Day Degrees of 610 is required for the development of a generation from the egg stage until the appearance of moths (Wildbolz, 1965 cit Ciglar, 1998).

The second generation appears after ten days and its flight lasts from mid-July to mid-August. In this period they lay eggs again and so the development cycle is repeated. In Croatia there are two generations of this pest per year (Kovačević, 1952; Alford, 1984; Ciglar, 1998; Maceljski, 2002).

Dispersal of CM is principally due to flight of adults, as the larval dispersal is restricted mainly within a few trees (Schumacher et al., 1997a). The codling moth is considered largely to be a 'sedentary insect' (Mani and Wildbolz, 1977 cit. Keil et al., 2001), however studies on the flight capacity of both sexes in the laboratory have demonstrated the existence of individuals with a capacity for both short and long flights. Dispersal capacity by flight is highly variable with approximately 10% of the individuals in a population being long-flyers (mobile) and the rest being short-flyers (sedentary) (Schumacher et al., 1997a; Schumacher et al., 1997b; Dorn et al., 1999; Gu et al., 2006). In the field some individuals are able to disperse over several kilometers, and distances of up to 11 km have been reported (Mani and Wildbolz, 1977 cit. Schumacher et al., 1997a). The occurrence of individuals with the ability to fly over long distances is considered ecologically significant for the colonisation of new habitats in response to deteriorating environmental conditions (Keil et al., 2001).

Damage

At first, an invading larva (typically one per infested fruit) forms a small cavity just below the fruit skin and after feeding for a few days burrows down to the core, leaving a prominent, red-ringed entry-hole on the side or near the eye, characteristically blocked by dry frass. Within the fruit, the larva eats away a large proportion of the flesh and also attacks the pips, so the cavity becomes filled with brown frass. The entry-point at the surface is greatly enlarged as tissue is eaten away and the larva eventually escapes leaving a small, unplugged exit hole. Sometimes a larva attacks another fruit in the same cluster before a full-grown stage, so damaged fruits tend to ripen and drop prematurely. Attacks can be serious, especially following the appearance of a second generation of larvae, and are often most severe close to stores and packhouses and on trees near piles of empty boxes which held the previous season's crop (Alford, 1984). If chemical treatment is not used in fruit production, CM can cause a decrease of product from 30% up to 50%. In certain years it can be as high as 80%. Intensive production tolerates 1% of affected fruit although producers try to lower that number below 0.5% with various methods of fruit protection (Kovačević, 1952; Ciglar, 1998).

Resistance to insecticides

Over 70% of the insecticide treatments in apple orchards are currently applied to control CM populations. As a consequence of these treatments, CM developed resistances to various groups of synthetic insecticides in the USA and Europe (Franck et al., 2007).

During the 1980s and 1990s CM control has been achieved by using broad-spectrum insecticides as pyrethroid and organ-

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ophosphate (OP) insecticides. Efficacy of these insecticides was reduced relatively quickly by the evolution of pesticide resistance (Sauphanor et al. 1997; Sauphanor et al., 2000; Bouvier et al., 2001; Stara et al., 2006). Since then, new cases of resistance have been reported for other groups of insecticides like the insect growth inhibitors (IGIs) (Sauphanor et al., 2000; Ioriatti et al., 2007).

Currently, the resistance spectrum of some CM populations has increased dramatically, including neonicotinoids and environmentally favorable biological insecticides neonicotinoids (avermectins) (Reyes et al., 2007).

An additional problem appeared with the development of cross-resistance due to the pest becoming resistant to several chemical groups of insecticides simultaneously.

Phenomenon of cross-resistance made the protection even more complicated and difficult (Sauphanor et al. 1998; Dunley et al., 2000; Reuveny and Cohen, 2004). Resistance mechanisms are multiple, and their lone or cumulative effects in a single population are not completely understood (Reyes et al., 2007).

Franck et al. (2007) found that the mechanisms involved in such forms of resistance include both increases in the activity of several metabolic enzymes, such as cytochrome P450 oxidases or glutathione-S-trensferases that confer nonspecific insecticide resistences, and modifications related to the targets of some insecticides groups, notably the pirethroids (Franck et al., 2007). Brun-Barale et al. (2005) have also studied the development of CM resistance on pyrethroids. Based on the findings that knockdown resistance (*kdr*) to pyrethroid insecticides has been associated with point mutations in the genetic structure of a great variety of insects, it has been developed a diagnostic test based on PCR amplification of specific allele (PASA) in order to determine the presence or the absence of the *kdr* allele in pyrethroid susceptible or resistant strains of CM. Franck et al. (2007) used the same test to assess the variability of *kdr* alleles in CM populations sampled in treated and untreated apple orchards in Armenia, Chile, France and Italy.

Although the highest proportions of *kdr* alleles was found in CM populations sampled from orchards that have been extensively treated with pyrethroids, a similar proportion of *kdr* alleles was found in CM populations sampled from orchards that have been in the system of organic production for several years.

Boivin et al. (2001) have conducted tests to compare the fitness of sensitive and resistant CM strains. Comparing the mating rate, fecundity, fertility, developmental time, fifth instar weight and adult longevity, it was found that the resistant strains were less fecund and fertile, developed more slowly, weighed less, and had shorter life-spans than the susceptible strain. With the development of resistance to insecticides, many experts have become engaged in testing the effectiveness of insecticides on different developmental stages of CM. These tests can determine the correct dosage of a particular chemical group of insecticide related to developing resistance by CM (Sauphanor et al., 1998, 1999, 2000; Boivin et al., 2003, 2004, 2005; Bouvier et al., 2001; Pasquier et al., 2003; Reuveny and Cohen, 2004; Ioriatti et al., 2007).

Genetic structure of CM populations

In spite of its economic importance, little is known about the genetic differentiation and gene flow of CM (Franck et al.,

2007). It is assumed that due to climate change and frequent insecticide treatments CM populations differentiate into many ecotypes with different biological and physiological requirements related to their development (Thaler et al., 2008).

The genetic structure of CM populations was studied using allozyme markers, but low genetic differentiation between sampled populations was observed (Buès et al., 1995).

However, recent studies have shown a relative low level of isoenzyme polymorphism as a molecular marker, so this finding should be taken with prudence.

Also, Timm et al. (2006) used AFLP markers and successfully established differences among sampled CM populations even at small geographic distances. Timm's et al. (2006) study was corroborated by Thaler et al. (2008) who also used AFLP markers to study the molecular phylogeny and genetic structure of CM.

The application of mitochondrial genetic markers has led to identification of recent evolutionary history of CM from the Pleistocenic splitting of the CM into two refugial clades, to the interbreeding of mitochondrial haplotypes in the Holocene, and finally to human-aided complete intermixing and splitting of populations into many locally adapted populations (Thaler et al., 2008). Recently, Franck et al. (2005) and Zhou et al. (2005) isolated more applicable co-dominant microsatellite markers from CM. Franck et al. (2007) used these microsatellites to estimate the level of genetic structure found among CM populations from France. Surprisingly, despite the high polymorphism of microsatellite loci, the results showed low genetic differentiation among populations and a marginal impact of insecticide treatments (selection) on the allelic richness of CM. Similarly, low genetic variation ($F_{ST} = 0.002$) was found among populations sampled in abandoned orchards (without insecticide treatments) and production orchards (organic and conventional production orchards) in Chile (Fuentes-Contreras et al., 2008). Franck and Timm (2010) used only males for genetic structure analyses, sampled by pheromone traps from two apple orchards (one organic and the other treated using chemical insecticides) situated 30 km apart in France and also found low genetic variation among sampled populations.

Franck and Timm's (2010) study was corroborated by Pajač et al. (2011) who also used microsatellite markers to study the genetic structure and gene flow among three populations of males in Croatia. Although they found low genetic variation among sampled populations, there was significant partitioning of genetic variation within individuals (70 - 96%).

Conversely, Chen and Dorn (2009) reported significant genetic differentiation among CM populations sampled from different host plants with the ability to distinguish local populations sampled on the same host within a distance of 10 km using the same microsatellite markers as Franck et al. (2005) and Zhou et al. (2005).

Genetic control

The genetic research on the CM is also moving in the direction of genetic transformation by using biotechnological methods. During the past 40 years, a number of pest insects including CM, have been sterilized by irradiation or chemicals used in genetic control programs (Hoy, 2003). This approach to pest manage-

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ment has been called the sterile insect release method (SIRM) or the sterile insect technique (SIT).

It involves the colonization and mass rearing of the target pest species, sterilization through the use of gamma radiation and releasing them into the field on a sustained basis and in sufficient numbers to achieve appropriate sterile to wild insect over flooding ratios. Here the sterile males find and mate with fertile females, transferring sterile sperm (Hoy, 2003). It results in no offspring, thereby causing a reduction in the natural pest population.

Unlike non-selective insecticide-based control, SIT represents a biologically-based tool for pest control in view of the species specificity involved. As a result of its species-specificity, SIT can be effectively used to replace insecticides for control of insect pests.

The SIT is the only environment-friendly technology available to eradicate insect pests if applied consistently on an area-wide basis. It's compatible with other pest control methods, and can therefore be effectively integrated with other methods including biological methods, such as parasitoids, predators and insect pathogens.

To avoid heavy fruit losses caused by codling moth, intensive insecticide treatments are routinely required producing worm-free fruit. The resulting damage to non-target beneficial organisms, disruption of biologically based controls of other orchard pests, residues on fruit and general contamination of the environment, are driving the need for more environment-friendly methods such as SIT to control codling moth (Thistlewood and Judd, 2003).

Currently, in the world several area-wide programmes for CM have been implemented (Dyck and Gardiner, 1992; Judd and Gardiner, 2005).

Genetic control of pest insects represents an attractive alternative to chemical control in terms of safety, specificity, and its limited negative environmental impact (Hoy, 2003).

Conclusion

CM has been present in Europe for centuries and it is probably the major pest on apple, pear, quince, walnut and chestnut. The ways of CM control have been changing throughout the history of fruit production in accordance with the development of chemical insecticides from chlorinated hydrocarbons, organophosphates, carbamates, pyrethroids to avermectins. After the period of using only chemical control measures, the emergence of resistance increased the use of biotechnical and biological means of protection. These approaches are environmentally necessary but are not yet economically viable for the control of CM. In recent years, evident changes associated with the increase of pathogenicity, viability and pace of reproduction of CM population have been observed. These changes are probably related to climate changes (i.e. global warming) and frequent application of certain groups of insecticides. New approach to CM control problem is focused on the study of CM genome, genetic structure and differentiation of its populations. Unfortunately, this has not yet given explanations for changes mentioned previously. It seems that the mechanisms of survival and rapid expansion of CM are more associated with maintaining a large genetic variability of its populations rather than increase of frequency or fixation of certain alleles of resistant genotypes. For better understanding of mechanisms of CM adaptation to different ways of control the experimental approach requires the analysis of the genetic structure of susceptible and resistant strains as described by Boivin et al. (2001).

Attractive alternative to chemical control in terms of safety, specificity, and limited negative environmental impact is application of genetic control (the sterile insect technique or SIT) (Hoy, 2003).

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