

BIOLOGICAL CONTROL OF CODLING MOTH (*CYDIA POMONELLA*, LEPIDOPTERA: TORTRICIDAE) AND ITS ROLE IN INTEGRATED PEST MANAGEMENT, WITH EMPHASIS ON ENTOMOPATHOGENS

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ABSTRACT Codling moth, *Cydia pomonella*, is a worldwide pest of apple and pear. Traditional control methods have been based predominantly on broad spectrum insecticides. Concerns over the safety, environmental impact, and sustainability of synthetic pesticides have stimulated development and use of softer control methods within the integrated pest management (IPM) strategy. Natural enemies (entomopathogens, predators and parasitoids) and their use as biological control agents play key roles in IPM. In this review we summarize the literature on biological control of codling moth and discuss its integration with other control options in orchard IPM. A variety of entomopathogens have been reported from codling moth, but only the codling moth granulovirus (CpGV) and entomopathogenic nematodes (EPNs) have been developed as microbial control agents. CpGV is highly virulent and selective for neonate codling moth larvae, but may require frequent reapplication due to solar inactivation, especially when population densities are high. The EPNs *Steinernema feltiae* and *S. carpocapsae* have good potential for control of overwintering cocooned larvae when temperatures are above 10 and 15°C, respectively and adequate moisture is maintained in the orchard for several hours after EPN application. Parasitism by *Mastrus ridibundus* (Ichneumonidae) in some Washington State orchards can exceed 40% in the year following releases which can further supplement parasitism by *Ascogaster quadridentata* (Braconidae) that sporadically approaches 25%. Together, these parasitoids and many predators could provide significant biological control of codling moth when the use of broad spectrum pesticides is minimized. Several aspects regarding the role of biological control in IPM in the orchard agroecosystem are discussed including the combination of chemical and biological interventions; interaction of natural enemies (antagonistic, synergistic); and ecological engineering of orchards to increase or conserve natural enemy populations.

KEYWORDS: Codling moth, *Cydia pomonella*, granulovirus, entomopathogenic nematodes, *Steinernema carpocapsae*, *Steinernema feltiae*, *Heterorhabditis* spp., *Beauveria bassiana*, *Bacillus thuringiensis*, *Nosema carpocapsae*, predatory insects, parasitoids, conservation biological control, habitat manipulation, ground covers, mulches.

RESUMEN La palomilla de la manzana, *Cydia pomonella*, es una plaga mundial de manzanas y peras. Los métodos de control tradicionales se han basado principalmente en insecticidas de amplio espectro. Preocupaciones sobre la seguridad, impacto ambiental, y sustentabilidad del uso de los insecticidas sintéticos han estimulado el desarrollo y uso de métodos de control más suaves dentro de la estrategia de manejo integrado de plagas (MIP). Los enemigos naturales (entomopatógenos, depredadores y parasitoides) y su uso como agentes de control biológico juegan un papel clave en el MIP. En esta revisión se resume la literatura sobre control biológico de la palomilla de la manzana y se discute su integración con otras alternativas de control en el MIP en las huertas. Se ha descrito una variedad de entomopatógenos de la palomilla de la manzana, pero sólo el granulovirus de *Cydia pomonella* (CpGV) y los nematodos entomopatógenos (NEPs) se han desarrollado como agentes de control microbiano. El CpGV es altamente virulento y selectivo contra larvas neonatas de la palomilla de la manzana, pero puede requerir aplicaciones frecuentes debido a la inactivación solar, especialmente cuando la densidad de las poblaciones es alta. Los NEPs *Steinernema feltiae* y *S. carpocapsae* tienen buen potencial para controlar

las larvas invernantes en cocones cuando las temperaturas sobrepasan los 10 y 15°C, respectivamente, y se mantiene una humedad adecuada en las huertas por varias horas después de su aplicación. El parasitismo por *Mastrus ridibundus* (Ichneumonidae) en algunas huertas del Estado de Washington puede superar el 40% en el año siguiente a su liberación, lo cual puede complementarse con el parasitismo por *Ascogaster quadridentata* (Braconidae) que esporádicamente alcanza un 25%. Juntos, estos parasitoides y muchos depredadores pueden proveer de un control biológico significativo de la palomilla de la manzana cuando se minimiza el uso de plaguicidas de amplio espectro. Se discuten varios aspectos relativos al papel del control biológico en el MIP en el agroecosistema de las huertas, incluyendo la combinación de intervenciones químicas y biológicas; la interacción de los enemigos naturales (antagonismo, synergismo); y la ingeniería ecológica de las huertas para incrementar o conservar a las poblaciones de los enemigos naturales.

DESCRIPTORES: Palomilla de la manzana, *Cydia pomonella*, granulovirus, nematodos entomopatógenos, *Steinernema carpocapsae*, *Steinernema feltiae*, *Heterorhabditis* spp., *Beauveria bassiana*, *Bacillus thuringiensis*, *Nosema carpocapsae*, insectos depredadores, parasitoides, control biológico por conservación, manipulación del habitat, coberturas del suelo, mulches.

INTRODUCTION

Codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), is a major pest of apple, pear and walnuts in most countries where cultivars of these species are grown (Barnes 1991). It entered North America by 1750 (Slingerland 1898) and has been a serious pest since that time. Control methods have been based predominantly on the use of broad spectrum insecticides, such as Guthion® (azinphos-methyl). Concerns over the safety, environmental impact, and sustainability of synthetic pesticides have engendered development and use of softer control methods within the integrated pest management strategy. Another concern regarding the use of azinphos-methyl and some other pesticides is the development of insecticide resistance in codling moth (Croft & Hull 1991; Varela et al. 1993; Knight et al. 1994; Dunley & Welter 2000; Sauphanor et al. 2000; Boivin et al. 2001). One of the softer methods that is increasingly being employed for codling moth control is mating disruption employing the female codling moth sex attractant (Vickers & Rothschild 1991; Howell et al. 1992; Gut & Brunner 1998; Brunner et al. 2001; Calkins & Faust 2003). In order for mating disruption to be effective, codling moth population density

must be sufficiently lowered, usually through the use of chemical cover sprays early in the growing season. A concern of growers is that the elimination of broader spectrum pesticides used for conventional control allows some secondary pests, such as leafrollers (Tortricidae), to increase in numbers and cause economically unacceptable levels of damage to fruit (Gut & Brunner 1998).

When the use of broad-spectrum pesticides is minimized or eliminated, natural enemy populations increase and become more diverse (DeBach 1964; van den Bosch et al. 1982), including those in apple orchards (Blommers et al. 1987; Knight 1994; Knight et al. 1997; Epstein et al. 2000). Natural enemies play a key role in the integrated pest management strategy. A variety of natural enemies, including entomopathogens, predators and parasitoids, have been evaluated and utilized for codling moth control in all three of the biological control strategies: classical, augmentative and conservation biological control. The literature on biological control of codling moth is voluminous hence we will only highlight research conducted on each of the groups of codling moth natural enemies and their potential roles in integrated management.

Codling moth eggs are laid singly on leaves

near fruit and on the fruit, the latter more commonly in the late summer period when fruit are large. Eggs hatch after 3-7 days and neonate larvae wander to find a fruit, occasionally feeding on foliage if the search is prolonged. They penetrate the fruit skin and feed near its surface for a day or two and then, as second instars, move toward the center of the fruit. They develop through 5 larval instars and exit the fruit after 18-40 days to find a hidden and dry site in which to spin their cocoon. These cryptic habitats include sites under loose bark, in litter at the base of trees, in nearby woodpiles, and fruit bins. The search for a cryptic site may be brief or prolonged. In early summer, cocooned larvae develop through pupae to adult in 1-2 weeks. In the shortening days of late summer, larvae are destined to diapause and pass the winter as mature larvae and prepupae in cocoons. Pupation begins in March in temperate climates. Males emerge slightly before females and mating typically occurs within the first few days of the female's life. In the Pacific Northwest of the United States, there may be two to three generations per growing season depending upon weather (Beers et al. 1993).

ENTOMOPATHOGENS

A multitude of entomopathogens have been reported from codling moth including, virus, bacteria, fungi, protozoa, microsporidia, and nematodes (Falcon & Huber 1991; Poinar 1991; Zimmermann & Weiser 1991; Lacey et al. 2000; Lacey & Shapiro-Ilan 2003). Of these, virus, and nematodes have been developed as microbial agents for augmentative biological control of codling moth.

Bacteria. *Bacillus thuringiensis* (*Bt*) is the most widely used biopesticide (Lacey et al. 2001). Although codling moth larvae are susceptible to Cry 1 and some of the other *Bt* toxins (Andermatt et al. 1988; Falcon & Huber 1991; Cross et al. 1999; Rang et al. 2000), its

value as a control agent of codling moth is very limited by the improbability of ingesting a lethal dose of *Bt* toxin during entry of the fruit by neonate larvae. The use of *Bt* against other orchard pest Lepidoptera, such as leafrollers is well documented (De Reede et al. 1985; Nicoli et al. 1990; Blommers 1994; Knight 1994; Li et al. 1995; Knight et al. 1998; Cross et al. 1999; Lacey et al. 2000). In addition to its efficacy for control of leafrollers, *Bt* is safe for orchard workers and the human food supply, and is compatible with natural enemies of codling moth and other orchard pests (Melin & Cozzi 1990; Lacey & Siegel 2000).

Fungi. Several fungal species have been reported from overwintering codling moth (Jaques & MacLellan 1968; Hagley 1971, Labanowski 1981; Glen 1982; Subinprasert 1987; Zimmermann & Weiser 1991). Of these, *Beauveria bassiana* has received the most attention as a potential microbial control agent (Ferron & Vincent 1978; Falcon & Huber 1991; Cross et al. 1999, Garcia-Gutierrez et al. 2004). Ferron & Vincent (1978) applied the elevated dosage of 6×10^9 conidia/tree against mature larvae as they exited fruit and observed up to 50% mortality. Garcia-Gutierrez et al. (2004) reported effective control of neonate codling moth larvae using a native strain (BbP1) and two commercial formulations (Mycotrol[®] and Meta-Sin[®]) of *B. bassiana* at 1.2×10^{12} conidia/ha. However, fruit damage was significantly higher for the *B. bassiana* treatments (2.4, 2.0 and 4.0%, respectively) than for azinphos-methyl treatment (0.95% using 250 g/ha).

Ferron (1978) and Falcon & Huber (1991) reviewed work on *B. bassiana* for codling moth control in the former Soviet Union with *Paecilomyces farinosus* and *B. bassiana* being most successful when combined with chemical pesticides. Attempts to develop *B. bassiana* as a microbial control agent of several insects have been somewhat successful (Goettel et al.

2005), but it has not been commonly used in North America or Western Europe for codling moth control.

Microsporida¹. The microsporidian, *Nosema carpocapsae*, has been reported from codling moth in North America, Europe, and Australia (Paillot 1938; Malone & Wigley 1981; Siegel et al. 2001). The effect of this pathogen on natural populations of codling moth has not yet been assessed, but it is not thought to be an important element in the regulation of this pest (Falcon & Huber 1991). Most other Microsporida have debilitating effects on natural insect populations expressed as reduced fecundity and longevity (Maddox 1987; Brooks 1988). *Nosema carpocapsae* is most devastating in laboratory colonies of codling moth where horizontal and vertical transmission is facilitated by confined and crowded populations (Siegel et al. 2001). The need to produce the organism *in vivo* and the lack of immediate population reduction decrease the attractiveness of *N. carpocapsae* for commercial development and widespread use as a biopesticide.

Virus. One of the most efficacious and highly selective pathogens of codling moth is a granulovirus (Baculoviridae). The *C. pomonella* granulovirus (CpGV) was originally isolated from infected codling moth larvae collected near Valle de Allende, Chihuahua, Mexico (Tanada 1964). CpGV and other granuloviruses derive their name from the granular appearance of the protein (granulin) occlusions that each contain a single enveloped viral rod. Its specificity for codling moth and a few closely related species and its safety to nontarget organisms are well documented (Falcon et al. 1968; Gröner 1986;

1990; Lacey et al. 2005a) and contributes to the conservation of other natural enemies in the orchard agroecosystem. It is one of the most virulent baculoviruses known; the LD₅₀ for neonate larvae has been estimated at 1.2 to 17 granules/larva (Laing & Jaques 1980; Huber 1986). CpGV must be ingested to infect and kill susceptible species. While virus is often acquired as larvae enter fruit, larvae may also become contaminated by walking or browsing on CpGV-sprayed leaf surfaces in as little time as 3.5 min. (Ballard et al. 2000b). Neonates may also become infected via virus-contaminated eggs at the time of hatching (L. A. Lacey & S. P. Arthurs, unpublished). Like other baculoviruses, the occlusion bodies are dissolved in the alkaline midgut of the target insect. Virus rods then pass through the cell membranes of the midgut epithelium and ultimately invade a multitude of other tissues, including the fat body, tracheal matrix and epidermal cells where production of virus rods and occlusion bodies takes place in the nuclei of infected cells (Tanada & Leutenegger 1968; Hess & Falcon 1987; Federici 1997). Etzel & Falcon (1976) found no evidence for transovariole transmission of CpGV, but observed transstadial transmission (larva to pupa and pupa to adult) and found virus on the surface of eggs originating from an infected colony. Biache et al. (1998) substantiated transstadial transmission by noting a 25% reduction in the rate of emergence of larvae that survived treatment with CpGV. Although horizontal transmission has been reported (Steineke & Jehle 2004), or suspected (Sheppard & Stairs 1976), acceptable levels of control have only been observed after inundative applications of the virus (10¹²-10¹³ granules/ha). Several surveys, most recently employing molecular methods for detection of the virus, indicate that CpGV is widespread wherever codling moth is found (Falcon & Huber 1991; Cross et al. 1999; Eastwell et al. 1999; Rezapanah et al. 2002; Kundu et al. 2003).

¹ Until recently, the Microsporida have been included in the Protozoa. Evidence presented by Hirt et al. (1999) and van de Peer et al. (2000) and others places the group with the fungi.

Falcon et al. (1968) first demonstrated the potential of CpGV for codling moth control and laid the groundwork for its registration and production in the United States (Falcon & Huber 1991). Unfortunately commercial production in the United States was only short lived. Many field trials have demonstrated good efficacy in a variety of settings across Europe, South Africa, Australia, New Zealand, South America, and North America (Keller 1973; Huber & Dickler 1977; Charmillot et al. 1984; Jaques et al. 1981; Glen & Payne 1984; Jaques 1990; Falcon & Huber 1991; Vail et al. 1991; Helsen et al. 1992; Wearing 1993; Guillon & Biache 1995; Cross et al. 1999; Arthurs & Lacey 2004; Lacey et al. 2004). The virus has been commercially produced and used by growers in Europe since the early 1990s (Cross et al. 1999). More recently, three commercial CpGV products based on the original Mexican isolate have been registered for use in North America (Arthurs & Lacey 2004): two of these are produced in Europe (France and Switzerland) and the other in Quebec, Canada. Their efficacy under a variety of orchard conditions in the Pacific Northwest of the United States and in Western Canada has been demonstrated by Arthurs and Lacey (2004), Lacey et al. (2004), Arthurs et al. (2005), and Cossentine & Jensen (2004).

The dosage of virus and spray interval required for good control depends on the product, number of codling moth generations, population pressure, and climatic factors. As little as two applications of virus have provided good codling moth control in orchards where there is one generation per year and population densities are low (Jaques et al. 1994). However, in areas where there are two or more generations per year and high codling moth population pressure, applications of virus every 7-10 days for as long as female moths are ovipositing may be required (Arthurs et al. 2005). Field trials of CpGV in Germany have shown that weekly applications of only 1/10 of the normal virus concentration

provides the same, or even better efficacy as spraying at two week intervals with the normal concentration (Dickler & Huber 1986; Helsen et al. 1992). The dissemination of low amounts of CpGV (10^8 - 10^9 granules/tree) during the second generation of codling moth in an Ohio apple orchard resulted in 34-42% reduction in populations (Sheppard & Stairs 1976).

Although CpGV is very effective in controlling codling moth populations, some of the concerns expressed by researchers and growers are: the potential for many shallow entries in the fruit; short residual activity of the virus and the need for multiple applications; slow speed of kill; lower efficacy against high codling moth densities; and cost of the virus (Glen & Clark 1985; Jaques et al. 1987; Arthurs et al. 2005). Glen & Clark (1985) observed that virus-infected larvae usually died as first instars soon after entering treated fruit. Despite blemishing due to shallow entries, CpGV-treated fruit can be used for processing. However, the major benefit of CpGV treatment is the reduction in population density of the moth.

A key disadvantage of CpGV is its sensitivity to solar radiation (Keller 1973; Krieg et al. 1981; Fritsch & Huber 1985; Jaques et al. 1987; Kienzle et al. 2003b; Arthurs & Lacey 2004; Lacey et al. 2004; Lacey & Arthurs 2005), necessitating frequent reapplication. The ultraviolet wavelengths of sunlight, particularly UV-B (280-320 nm) are the most damaging for entomopathogens and other biological systems (Diffey 1991; Ignoffo 1992). The addition of UV protectants to CpGV have improved activity (Keller 1973; Krieg et al. 1981; Wearing 1993; Burges & Jones 1998; Charmillot et al. 1998; Ballard et al. 2000a; Asano 2005), but further improvements are warranted. Method of application, formulation (sticker-spreaders), rainfall and overhead irrigation, cloud cover, and position of CpGV granules in the canopy can also influence the persistence of virus on foliage and fruit.

Previous studies have estimated CpGV half lives on foliage at between 2 and 3 days (Glen & Payne 1984; Huber 1980; Jaques et al. 1987). Persistence of CpGV under orchard conditions in British Columbia and Washington State range from three to eight days (Cossentine & Jensen 2004; Arthurs & Lacey 2004; Lacey et al. 2004). Some virus activity is detectable 14 days after application (Arthurs & Lacey 2004), although most virus is inactivated by sunlight within four days of application (Arthurs & Lacey 2004; Lacey et al. 2004). Much longer persistence in orchards in the UK was reported by Glen & Payne (1984) ostensibly due to greater cloud cover. Although CpGV infectivity was reduced by half in three days, Glen & Payne (1984) demonstrated that some activity persisted at least four-eight weeks after application.

Increased feeding on virus, especially before larvae enter fruit (i.e. from leaf surfaces) could decrease fruit damage by accelerating the onset of mortality. Ideally, a formulation that protected virus and stimulated feeding of codling moth neonates could not only extend the activity of the virus on sprayed surfaces that are exposed to UV radiation, but could also result in ingestion of greater quantities of virus from leaf surfaces before coming into contact with fruit. Laboratory studies by Ballard et al. (2000a), demonstrated that 15% cane molasses incorporated within a formulation of purified CpGV significantly reduced the average lethal exposure time to CpGV for codling moth neonates, but field trials revealed no significant improvement of CpGV persistence on apple foliage using 10 or 15% molasses formulations. Another field trial by Ballard et al. (2002a) demonstrated that 10% molasses, 10% sorbitol or 0.08% α -farnesene significantly reduced codling moth deep entry damage to fruit when these ingredients were added to formulations of pure CpGV, but substantial sooty-mold growth was observed on apple foliage treated with formulations containing molasses. Continued

research on phagostimulants to enhance virus uptake is warranted to reduce the number of shallow entries that are observed even when high mortality is attained with CpGV treatment (Arthurs & Lacey, 2004). Recent studies on monosodium glutamate as a codling moth phagostimulant are encouraging (Pszczolkowski et al. 2002).

Another avenue of research that could speed the rate of kill and potentially reduce the number of shallow entries was reported by Winstanley et al. (1998). Their genetic recombinant construct of CpGV does not express the ecdysteroid-UDP glucosyl transferase gene (*egt*). This recombinant CpGV kills faster and reduces feeding in infected larvae relative to the wild type (Cross et al. 1999).

An important issue that has been recently raised is the development of resistance to CpGV. Although use of the virus against the vast majority of codling moth populations is regarded as effective, Fritsch et al. (2005) and Sauphanor et al. (2006) reported development of resistance to CpGV in Germany and France in certain codling moth populations that have received regular virus applications for several years. Sauphanor et al. (2006) noted that the resistance appears to be highly dominant and not related to resistance to chemical insecticides. However, management of resistance along the same lines as for chemical insecticides has been recommended to prevent its extension.

The benefits of utilizing virus compared to that of broad spectrum insecticides such as azinphos-methyl are less apparent when simply comparing efficacy and labor costs. While comparable control of codling moth by CpGV and azinphos-methyl and other organophosphate insecticides has been reported by Huber & Dickler (1977), Glen & Payne (1984), Jaques et al. (1994) and Lacey et al. (2004) for CpGV, labor may be significantly reduced due the lower number of applications and a broader spectrum of tree

fruit pests insects that are controlled by azinphos-methyl. However, the absence of nontarget impacts, safety for applicators, and no re-entry or preharvest interval of the virus grow in importance when a sustainable IPM system is considered. Another potential benefit is the use of CpGV as a tool for resistance management (Kienzle et al. 2003a).

Entomopathogenic nematodes. Nematodes in the families Mermithidae and Steinernematidae have been reported from natural populations of codling moth (Poinar 1991). However, only the entomopathogenic nematode (EPN) species in the families Steinernematidae and Heterorhabditidae have shown promise as microbial control agents of codling moth. Several studies over the past 50 years have demonstrated their potential as biological control agents of a wide variety of insect pests (Koppenhöfer 2000; Grewal et al. 2005; Georgis et al. 2006) including orchard pests (Shapiro-Ilan et al. 2005). Steinernematids and heterorhabditids are obligately associated with symbiotic bacteria (*Xenorhabdis* spp. and *Photorhabdis* spp., respectively) which are responsible for rapidly killing host insects. The generalized life cycle of EPNs is depicted in Figure 1. After entering a host insect, the infective juvenile (IJ) stage of EPNs, also referred to as the Dauer stage, releases its symbiotic bacteria. In addition to killing the host, the bacteria digest host tissues and produce antibiotics to protect the host cadaver from saprophytes and scavengers. Steinernematids require the presence of males and females in order to reproduce whereas heterorhabditids are hermaphroditic and able to reproduce in the absence of conspecifics. After two to three reproductive cycles, when host nutrients are depleted, Dauer stage infective juveniles are produced and begin leaving the host insect. This stage is capable of immediately infecting a new host or may persist for months in the absence of a host. The safety of EPNs for nontarget organisms was

reviewed by Akhurst (1990) and Akhurst & Smith (2002). Materials and methods for the isolation, propagation and quantification of EPNs are presented by Kaya & Stock (1997).

Steinernema carpocapsae, one of the first EPN species to be commercialized, was originally isolated from cocooned codling moth larvae (Dutky & Hough 1955; Weiser 1955). The stage of codling moth that is most practical to control is the cocooned overwintering larva. In the fall, winter, and early spring in temperate zones, cocooned diapausing larvae represent the entire codling moth population. Their elimination or significant reduction at this stage would provide complete or substantial protection to fruit early in the following growing season. Cryptic habitats, such as those used by codling moth for their overwintering sites, are also favorable environmental sites for EPNs. Their potential for control of cocooned codling moth larvae and environmental factors that limit or enhance their activity in orchards have been elucidated by Kaya et al. (1984), Sledzevskaya (1987), Nachtigall & Dickler (1992), Unruh & Lacey (2001) and Lacey et al. (2006a, b). Most of the research thus far conducted on EPNs for codling moth control has been with *S. carpocapsae* and *Steinernema feltiae* although other *Steinernema* species and *Heterorhabditis bacteriophora* have shown promise in laboratory studies (Lacey & Unruh 1998).

The main obstacles for successful codling moth control with EPNs are low temperatures and desiccation of IJs before they have penetrated the host's cocoon. Applications will be ineffective if made late in the fall or early in the spring when prevailing temperatures remain below the threshold of activity of the EPN species (Lacey et al. 2006a). Codling moth pupae are less susceptible to infection than larvae (Lacey et al. 2005b), emphasizing the need to target spring applications before larvae pupate. Use of an EPN species that is both cold hardy and sufficiently efficacious against codling moth larvae will allow

applications to be made later in the fall which may be desirable after the harvest of late-ripening varieties or earlier in the spring before overwintering larvae pupate. The infectivity of *S. carpocapsae* for codling moth larvae and a variety of other insects decreases considerably at temperatures below 15°C and ceases altogether at 10°C (Lacey & Unruh 1998; Vega et al. 2000). *Steinernema feltiae* on the other hand, is active at 10°C and lower temperatures (Grewal et al. 1994b, 1996).

Selection of an EPN species with good activity against codling moth larvae that has an active host searching strategy could reduce the time that moisture must be maintained in the orchard. *Steinernema carpocapsae* is regarded as an ambusher species i.e. one with limited host searching behavior (Lewis et al. 1995; Campbell & Gaugler 1997). However, it provides good control of cocooned codling moth larvae under optimal temperature and moisture conditions. *Steinernema feltiae* is regarded as an intermediate search strategist with greater search capacity than *S. carpocapsae* (Grewal et al. 1994a; Lewis et al. 1995; Campbell & Gaugler 1997). Use of a cold hardy EPN with active search behavior, such as exhibited by some of the *Heterorhabditis* species (Griffin & Downes 1991; Wright 1992), warrants further attention for control of cocooned codling moth larvae.

Webster (1973) proposed manipulation of habitats where EPNs will be applied to favor IJ survival and infectivity. Environmental manipulation of the orchard agroecosystem by combining irrigation and mulches has the potential to extend the survival of IJs by maintaining the moisture necessary for their activity (Lacey et al. 2006b). Mulches such as wood chips can also provide an attractive habitat for overwintering larvae, especially in orchards where smooth-barked trees provide few alternative sites for hibernacula. Newer, high density, trellised orchards will be ideal sites for using mulches and EPNs for control of overwintering codling moth. The combin-

ation of providing easily treated sites that are attractive for codling moth hibernacula, and well suited to irrigation that could maintain adequate post-application moisture, will facilitate IJ infection of cocooned codling moth larvae. Under operational conditions, the exposure of cocooned codling moth larvae to viable IJs in mulch would not only be longer than that reported for experimental conditions, but the potential for recycling of IJs produced in infected larvae and subsequent infection of adjacent larvae could also enhance the level of control.

Manipulation of irrigation systems to provide needed moisture in a pear orchard was demonstrated by Lacey et al. (2006a). In this case, the combination of overhead irrigation for several hours after application of IJs and water retention in the bark of the trees provided sufficient moisture for successful penetration of cocooned codling moth larvae in the tree bark. Further improvement in efficacy is expected with the addition of adjuvants to EPN suspensions at the time of application. Formulation with surfactants and humectants improve penetration of host habitats and cocoons and help to maintain moisture around IJs until host larvae can be infected (Lacey et al. 2006a). In addition to their use in orchards, EPNs can control larvae in fruit bins (Lacey & Chauvin 1999; Cossentine et al. 2002; Lacey et al. 2005b). Bins infested with diapausing codling moth larvae are a potential source of reinfestation of orchards and may jeopardize the success of mating disruption programs and other control strategies (Higbee et al. 2001). Immersing bins in suspensions of IJs at the time fruit is floated could provide acceptable levels of control provided that the bins are stacked and stored to maintain moisture and kept at a temperature that is above the threshold of activity of the EPN (Lacey et al. 2005b). The combination of a wetting agent (Silwet L77) and humectant (Stockosorb[®]) with 10 *S. feltiae* IJs/ml in low

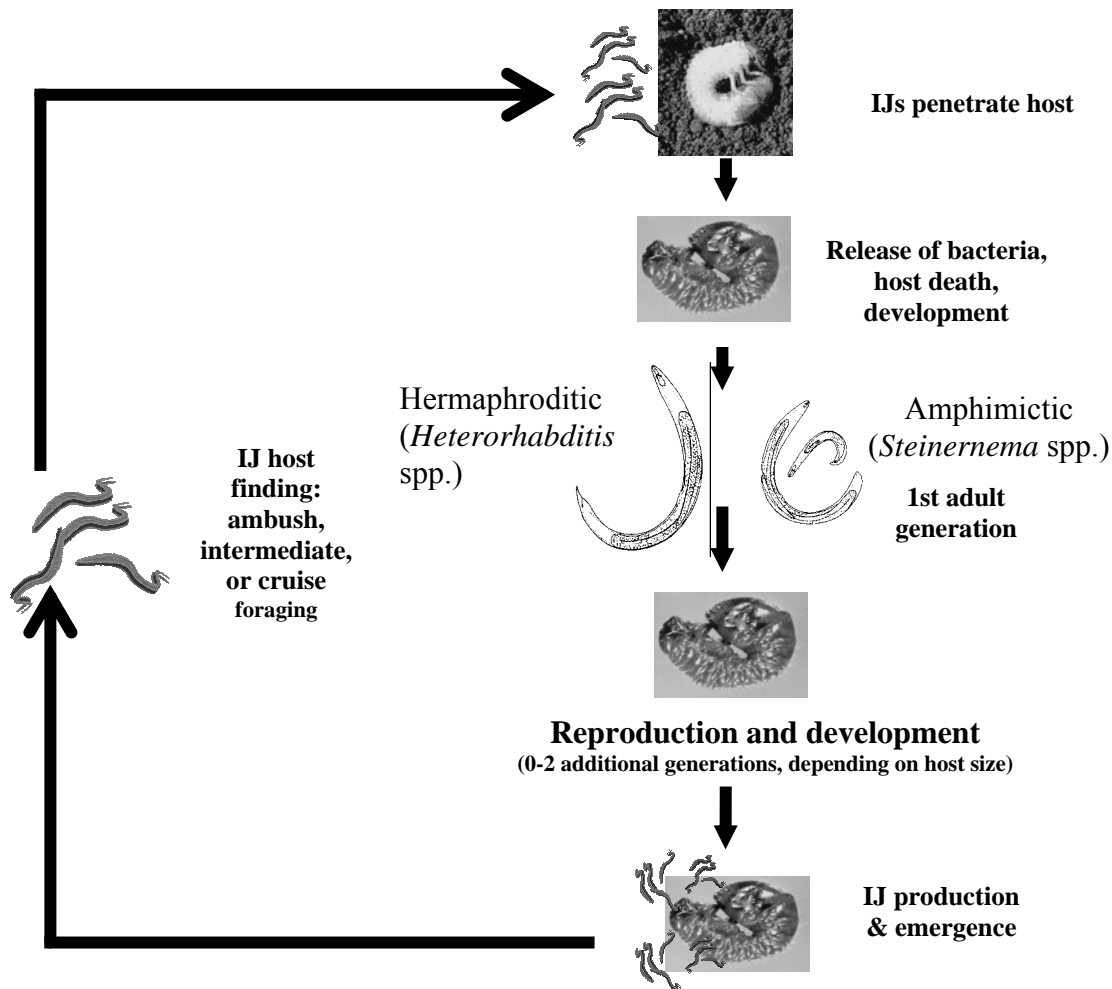


Fig. 1. Life Cycle of Entomopathogenic Nematodes. Host larva is *Popillia japonica* (courtesy of Patricia Stock; modified from Hazir et al. 2003). (IJ=infective juvenile)

and high humidity resulted in 92-95% mortality of cocooned codling moth larvae, versus 46-57% mortality at the same IJ concentration without adjuvants (Lacey et al. 2005b).

PREDATORS

Codling moth predators are the least studied guild of all its biological antagonists. In organically managed and research orchards that receive few or no disruptive insecticides, sentinel codling moth larvae deployed to measure parasitism or disease states often

disappear rapidly as a result of predator activity. Unlike death caused by disease and parasitoids, unwitnessed predation cannot be measured with confidence; the predator eats the evidence. Furthermore, important codling moth predators may often be nocturnal, such as spiders (Boyga & Mols 1996), bats (Hogan 2000), and earwigs. The difficulties in acquiring evidence for the activity of such predators have stifled quantitative work. Studies of codling moth predation have substantially focused on the highly visible groups such as birds (Solomon & Glen 1979),

and those that can be easily trapped, such as carabid beetles (Riddick & Mills 1994).

Birds are the most apparent predator guild. Their large size and interesting behavior have spawned observational, semi-quantitative and quantitative studies (McAtee 1911; LeRoux 1961; MacLellan 1971; Solomon et al. 1976; Wearing 1979). Small species, such as nuthatches (Sittidae), and larger birds, such as woodpeckers (Picidae) will attack large larvae, either walking to or already in their cocooning sites. Tits (*Parus* spp.: Paridae) in England and woodpeckers in Nova Scotia have been implicated as significant mortality factors of codling moth (LeRoux 1961; Solomon et al. 1976). Birds can severely disturb experimental studies of predation and parasitism because they appear to learn quickly that their prey may be found in the cardboard trap bands placed around tree trunks. Wearing (1979) demonstrated that predation by the silver eye, *Zosterops lateralis*, in New Zealand was density dependent, which suggests that bird predation may be slight at low pest densities. In contrast, MacLellan (1971) considered birds as important predators even during periods of low host density. Seasonally migratory birds appeared to be the most common predators (Glen & Milson 1978; Wearing 1979; in contrast see MacLellan 1971). In these studies, predation of codling moth by birds in unsprayed orchards ranged from 50% to 95%.

Other vertebrates may play a minor role in codling moth control. Some organic growers considered predation by bats to be important and have installed bat shelters to enhance their presence in their orchards. Some omnivorous rodents may also prey on cocooned larvae, but their secretive, nocturnal habits render study difficult.

Spiders and predacious mites are also poorly studied as predators of codling moth possibly because of their predominantly nocturnal habits or small size, respectively. Fifteen families of spiders are known from apple orchards (Bogya & Mols 1996) and

actively searching species are most likely to find cocooned larvae. Multiple spider species have been observed feeding on codling moth (Dondale 1956; Monsour et al. 1980) and have been implicated as important predators of leafrollers (Miliczky & Calkins 2002). In contrast, Acari, notably species of *Anystis* (MacLellan 1972) and *Belaustium* (T.R.U. unpublished) are likely predators of eggs and perhaps small larvae. No significant quantitative studies of spider or mite predation have been conducted.

The insects represent the largest group of codling moth predators and may account for the majority of predation in most settings. Predation of eggs and neonate larvae by small heteropterans including Anthocoridae such as the minute pirate bug, *Orius insidiosus*, *Anthocoris musculus* and various Miridae, such as *Hyaliodes harti*, *Blepharidopterus angulatus*, *Phytocoris* sp., *Diaphnidia* sp., and *Deraeocoris* spp. may numerically represent the highest level of predation of codling moth in undisturbed habitats (MacLellan 1962; 1977; Glen 1975). These predatory bugs, together with larger heteropterans in the Reduviidae and Nabidae, can consume large larvae as they transit from fruit to seek cocooning sites, or the predators may also find larvae in their cocoons (MacLellan 1962).

Carabidae are the best known beetle predators of codling moth; they dominate the epigeal zone around the tree base where codling moth cocoons are likely to be found (Riddick & Mills 1994). Using feeding trials, Jaynes & Marucci (1947) showed that over 20 species of carabids, and other beetle species in the families Trogossitidae, Malachiidae, Staphylinidae, Cleridae, Cantharidae, and even wireworms (Elateridae) fed on cocooned codling moth larvae. Studies by Hagley & Allen (1988) and Riddick & Mills (1994) found 5 dominant species of carabids feeding on codling moth. Most of the 44 species of carabids recorded in organic apple orchards in British Columbia probably feed on codling

moth (Smith et al. 2004). Members of the Trogossitidae, notably *Tenebroides* spp., also can be important predators on the tree trunk, especially in wetter climates (Woodside 1942). Species of Cleridae may be active on or around the tree trunk in some orchards.

An extensive series of observations and field studies have implicated ants (Formicidae) as important predators of mature larvae of codling moth (Jaynes & Marucci 1947). These authors found 6 ant species which were regularly associated with apple orchards and would prey on small and large larvae when they were encountered. Ants were the key predator guild producing up to 60% mortality in experimental studies (Jaynes & Marucci 1947). Ants may also be active predators of eggs in some orchards (T.R.U unpublished).

Two other groups are noteworthy as predators of codling moth: the predacious thrips and earwigs. *Haplothrips faurei* and *Leptothrips mali* are predators of various taxa including codling moth eggs (MacLellan 1962). Finally, the European earwig, *Forficula auricularia* can be a significant predator of eggs (Glen 1975) and cocooned larvae (T.R.U. unpublished). However, this species can cause fruit damage especially in soft fruit like peaches and clear skin pear varieties (Hilton et al. 1998).

PARASITOIDS

Over 100 parasitoid species have been recorded from codling moth (Lloyd 1958). However, only a few species are specialists that predominantly attack codling moth and fewer still are known to produce significant levels of parasitism. The majority of these originate from Western Europe and North America. Host specialization and the potential for impact should be considered in selecting species for introduction (Mills 2005). Until recently, only one species of specialized codling moth parasitoid existed in North America, the solitary koinobiont, endo-

parasitoid *Ascogaster quadridentata* (Hymenoptera: Braconidae), which attacks the egg and emerges from the penultimate larval stage (Brown & Kainoh 1992). *A. quadridentata* was presumed to be unintentionally imported into eastern North America and subsequently has been broadly distributed along with its host (Clausen 1978). Several unsuccessful attempts to introduce parasitoids of codling moth and the Oriental fruit moth, *Grapholita molesta*, were made at the turn of the century and in the 1940s and 1950s in the United States and Canada (Clausen 1978).

Field studies of the parasitoid complex throughout Europe often have demonstrated low total parasitism ranging from 5 to 20% (Rosenberg 1934; Geier 1957; Coutin 1974; Labanowski 1981; Mills 2005) while parasitism in Central Asia often exceeded 20% (Makarov 1982; Mills 2005; in contrast see Simmonds 1944, who observed higher parasitism in Europe). Higher parasitism in Asia is driven by the high abundance of *Mastrus ridibundus* (Hymenoptera: Ichneumonidae) which was not previously recorded from the West, and by *Microdes rufipes* (Hymenoptera: Braconidae) which is more abundant in Central Asia than in Europe (Mills 2005). These species are part of the larger complex of specialists which also includes *Trichomma enecator* and *Pristomerus vulnerator* (Hymenoptera: Ichneumonidae) and *Elodia tragica* and *E. morio* (Diptera: Tachinidae); all are koinobiont parasitoids of early-mid stage larvae, killing and emerging from the cocooned prepupae (Mills 2005).

Among the many generalist species that also attack codling moth are nine or more *Trichogramma* species (Lloyd 1958; Pinto et al. 2002). There are hundreds of studies spanning 70 years on the inundative release of *Trichogramma* species against codling moth, but consistently low efficacy suggests significant problems in their utilization for biological control of this pest. The most recent summary of work in California by Mills

(2003) suggests that releases of *Trichogramma* spp. can reduce codling moth damage by 50% in walnuts and pears (less in apples). This limited success may be improved by many point sources per hectare to overcome poor dispersal (Yu et al. 1984; McDougall & Mills 1997a), suitable pre and post-release feeding to enhance longevity and closely spaced or programmed releases to produce a pool of *Trichogramma* active throughout the season, and the use of a locally adapted species (McDougall & Mills 1997b; Mills 2003).

Recently, three hymenopterous codling moth parasitoids were introduced from Eurasia including a reintroduction of *Liotryphon caudatus* (Ichneumonidae) from southern Russia, and *M. rufipes* and *M. ridibundus* from Kazakstan (Unruh 1998; Kuhlmann & Mills 1999; Mills 2005). Both *L. caudatus* and *M. ridibundus* are idiobiont ectoparasitoids which attack, kill, and develop on the cadaver of the cocooned larvae (Unruh 1998; Mills 2005). *L. caudatus* is solitary and *M. ridibundus* is gregarious with an average of about 3 offspring per host (Smith & Vosler 1914; Makarov 1982; Bezemer & Mills 2001). Of the three introduced parasitoids, *M. ridibundus*, has the highest probability of becoming permanently established. It has been provided to several states in the United States and to Israel (T.R. Unruh & N. Mills, unpublished). *Mastrus ridibundus* displays excellent searching and dispersal ability in orchards (Bezemer & Mills 2001), locating codling moth from a kairomone in its silken cocoon (Jumean et al. 2005). Parasitism by *M. ridibundus* can exceed 40% in the year following releases (Unruh 1998; Mills 1999) which can further supplement parasitism by *A. quadridentata* that sporadically approaches 25%. Together these parasitoids and many predators could provide significant biological control of codling moth. Because of relatively high levels of codling moth damage, even in orchards with significant parasitism, there has been little effort to integrate parasitoids and

predators of codling moth into the pest management system of pome fruits over the last 50 years.

ROLE OF BIOLOGICAL CONTROL IN INTEGRATED PEST MANAGEMENT IN THE ORCHARD AGROECOSYSTEM

Codling moth biology and the horticulture of apple define the parameters in which its natural enemies act. During the large proportion of the insect's life history that is spent inside the fruit, the larvae are substantially protected from most pathogens, predators and parasitoids, especially in the large-fruited apple varieties that are commercially produced. The activity and abundance of parasitoids and predators may be further diminished by the relatively simple agroecosystem of apples, compared to the highly diverse plant community associated with wild apples, the setting where codling moth and many of its specialist natural enemies presumably evolved (Unruh 1998; Mills 2005). The last factor working against natural enemies in this system is the high value of apple fruit which requires that codling moth be kept at very low levels, usually through multiple applications of highly toxic synthetic insecticides. Thus, the benefits of predation and parasitism in pome fruit production have been minimal in our modern agricultural system, which protects fruit from both direct and cosmetic damage. The development of mating disruption and availability of CpGV provide the opportunities to develop new control strategies that maximize the effect of biological control agents.

Control of pest insects solely using chemical pesticides has generated myriad problems including: insecticide resistance; outbreaks of secondary pests normally held in check by natural enemies; safety risks for humans and both wild and domestic animals; contamination of ground water and riparian habitats; and decrease in biodiversity and other

environmental concerns. These problems and the lack of sustainability of programs based predominantly on conventional insecticides have stimulated increased and renewed interest in the Integrated Pest Management (IPM) of orchard pest species. A bio-intensive IPM strategy, in which natural enemies of pest arthropods and other alternative measures play significant roles in crop protection, is one aspect of sustainable agriculture that attempts to minimize the negative environmental impact and other deleterious effects due to insecticide usage (van den Bosch et al. 1982). Components of IPM including mechanical, physical and cultural control, host plant resistance, biological control, autocidal control, biorational chemical agents, biochemicals, conventional pesticides are often evaluated as stand alone tactics without consideration of their interactions with other components of the agroecosystem (Gurr et al. 2004a). An integrated approach for the implementation of IPM components in orchard agroecosystems that is based on pest densities and their relation to economic injury thresholds will ultimately be required before agriculture will be truly sustainable. Some of the combinations of interventions, alternative strategies and considerations for their use follow.

Combination of chemical and biological interventions. IPM may employ the judicious use of insecticides when needed. When selective insecticides, such as some of the insect growth regulators, are used for control of codling moth and other orchard pest insects the negative impact on beneficial insects is reduced (Croft 1990; Blommers 1994). An attract and kill strategy that selectively lures targeted insect pests to killing stations is another method that could employ synthetic insecticides with minimal effect on insect natural enemies. Sublethal dosages of certain insecticides, such as imidacloprid, may act synergistically in combination with entomopathogens by compromising the targeted

insect's immune response (Quintela & McCoy 1997; Koppenhöfer et al. 2000). Alternation of CpGV with an organically approved formulation of spinosad (Entrust[®]) was reported by Arthurs & Lacey (2004) as a strategy used by orchardists for control of codling moth as well as other pest insects. However, there have been several reports regarding the negative impact of spinosad on parasitoids and some other natural enemies of pest insects (Tillman & Mulrooney 2000; Williams et al. 2003, and others). The combination of mating disruption using the codling moth female sex attractant and CpGV to control resistant strains of codling moth has been successfully utilized in Europe (Trematerra et al. 1996; Miñarro & Dapena 2000; Charmillot & Pasquier 2002). The larval aggregation pheromone reported by Duthie et al. (2003) and Jumeau et al. (2004) could have potential in combination of EPNs for control of overwintering cocooned codling moth larvae.

Interaction of natural enemies (antagonistic, synergistic). Entomopathogens and parasitoids. Competition between microorganisms and multicellular animals for insect hosts is pervasive throughout nature (Hochberg & Lawton 1990). Premature death of the host due to infection is one of the main antagonistic interactions between entomopathogens and parasitoids (Brooks 1993). There is, however, mounting evidence for behavioral and biochemical mechanisms that minimize the negative interactions between entomopathogens and insect parasitoids (Harper 1986; Brooks 1993; Begon et al. 1999; Roy & Pell 2000; Lacey & Mesquita 2002). Although there are several reports on the innocuous nature of CpGV and *Bt* toward beneficial insects and other nontarget organisms (Falcon et al. 1968; Gröner 1986, 1990; Melin & Cozzi 1990; Lacey & Siegel 2000; Rodrigo-Simon et al. 2006), there are few studies on the specific interactions

between entomopathogens and arthropod natural enemies of codling moth.

Studies by Lacey et al. (2003) have revealed both antagonism and complementary activity between *S. carpocapsae* and two ichneumonid idiobiont parasitoids of codling moth. Exposure of *M. ridibundus* and *L. caudatus* developing larvae to infective nematodes within codling moth cocoons resulted in parasitoid mortality that was comparable to that of codling moth larvae. However, over-wintering full grown parasitoid larvae are almost completely protected from nematode penetration within their own tightly woven cocoons. This research also demonstrated the ability of *M. ridibundus* and *L. caudatus* females to detect and avoid laying eggs on nematode-infected cocooned codling moth larvae as early as 12 hours after treatment of the host with *S. carpocapsae* IJs. The compatibility of the two groups of biological control agents for codling moth control could be facilitated by careful timing of applications. The ability of parasitoids to avoid EPN-treated larvae and to actively seek out and kill cocooned codling larvae that survived nematode treatments enhances their complementarity. On the other hand, in one field study presented by Unruh & Lacey (2001), parasitism of cocooned codling moth larvae by *M. ridibundus* was negatively correlated with EPN infection of codling moth larvae. Dissections showed that ca. 10% of larvae infected by nematodes had been attacked by the wasp. Anecdotal evidence presented by Arthurs & Lacey (2004) indicated that CpGV applications in orchards were compatible with survival and parasitic activity of *M. ridibundus*.

Based on the models of Begon et al. (1999), coexistence and enhanced biological control are favored by complementarity between parasitoid and pathogens in terms of their extrinsic and intrinsic qualities. For example, environmental conditions and biological characteristics that favor parasitoids

or entomopathogens will influence the type of interaction and compatibility or antagonism of these two groups. Parasitoids are better suited for exploiting uninfected hosts, particularly in cryptic habitats, because of their abilities of search, whereas most pathogens, such as CpGV, must wait for chance encounters, proper environmental conditions (EPNs), or well-timed application by humans. According to Begon et al. (1999), one of the most important aspects to consider in the integration of pathogens and parasitoids is the stage of the host that is attacked. The fact that CpGV normally infects neonate larvae before or during entry into fruit, while *M. ridibundus* searches for and attacks cocooned larvae in cryptic habitats, would eliminate direct competition between virus and parasitoid and enhance combined control. On the other hand, pathogens with broader host ranges (most EPNs and fungi in the Hypocreales) could infect both codling moth and parasitoids competing for the same host resulting in interference competition (Begon et al. 1999). In addition to parasitoid avoidance of infected hosts, endoparasitic species that invade the host before or soon after the pathogen may produce protective substances that inhibit development of certain pathogens and enable parasitoids to complete their development (Brooks 1993; Lacey & Mesquita 2002; Furlong & Pell 2005). Parasitoids that attack infected hosts could facilitate the transmission of pathogens to uninfected hosts (Harper 1986; Brooks 1993; Begon et al. 1999; Lacey & Mesquita 2002; Furlong & Pell 2005).

Compatibilities and antagonism between other groups of codling moth natural enemies. Interactions are also likely between predators and parasitoids. The polyphagous nature of many predator groups suggest that they will also feed indiscriminately on parasitized hosts, such as cocooned larvae in the trunk or parasitized eggs or young larvae. However, parasitoids control of the behavior

and physiology of codling moth larvae may reduce this interaction and may reveal the selective forces which shaped these traits (Horton & Moore 1993). Notably, *A. quadridentata*-parasitized codling moth larvae spin significantly smaller cocoons, and select smaller crevices in which to do so, and are more likely to be in the tree canopy, making them less likely to be attacked by birds, carabid beetles and ants (Jaynes & Marucci 1947). A similar phenomenon is likely to apply to species attacked by *T. enecator* and *M. rufipes*. Intraguild predation by predators may be the norm (Rosenheim 1998) and may have significant negative consequences on specific predators or parasitoids (Snyder & Ives 2003; Rosenheim et al. 1999) resulting in reduced biological control (Rosenheim 2005).

Ecological engineering to increase or conserve natural enemies. Ecological engineering in the context of biological control and IPM is the manipulation of farm habitats to be less favorable for arthropod pests and more attractive to beneficial insects (Gurr et al. 2004a). The use of environmental modification with mulches and irrigation to enhance the activity of EPNs was covered earlier. In addition to improvement of nematode persistence and larvicidal activity, mulching can also have a variety of other beneficial effects. In orchard agroecosystems, surface mulches have been used for weed control, improvement in tree vigor, soil nutrient status and biological activity, and have buffered trees against moisture stress resulting from inadequate irrigation (Mathews et al. 2002; Forge et al. 2003; Neilsen et al. 2003a, b, 2004). Mulches have also resulted in enhanced biodiversity in orchards, including an increase in the numbers of ground dwelling predators (Kienzle & Zebitz 1997; Forge et al. 2003; Miñarro & Dapena 2003; Brown & Tworowski 2004; Mathews et al. 2004). Certain kinds of mulches, such as bark chips or walnut husks and shells, may be attractive to codling moth

seeking cocooning sites. This in turn may increase predation by ground dwelling predators such as carabid beetles (Riddick & Mills 1994). However, there may be negative consequences of habitat manipulations; some mulches may increase intraguild predation (Mathews et al. 2004) or increase pest problems from other species, including rodents and root diseases.

Living mulches, ground covers and weedy strips are often used to provide floral sources of carbohydrate and pollen that can enhance the longevity, fecundity, and biological control produced by parasitoids (Jervis et al. 1996; Baggen & Gurr 1998). They also may provide alternate hosts and habitats that support carabid beetles (=beetle banks). Recent studies show that not only the ground cover, but the frequency with which it is mowed may affect beneficial species abundance (Horton et al. 2003), demonstrating that there is a seasonal dynamic in the impact of these habitat modifications. Lewis et al. (1998) suggested that ground covers providing floral nectaries will retain insects and increase host foraging efficiency by satiating carbohydrate needs and freeing parasitoids to search for hosts. Unfortunately, studies to test these hypotheses in the field often do not demonstrate increased biological control despite measurable increased in nectar feeding (Lee & Heimpel 2003; Keller & Baker 2003). The density of beneficial insects may increase, but biological control of the target pest is not realized (Andow 1991; Landis et al. 2000), or pest densities are reduced for other reasons. In studies using intercropping or vegetation strips in vineyards, Costello & Daane (2003) showed reduced pest leafhopper densities on grape vines was due to competition between vines and the weedy strip crop, not due to the increased spider abundance which was also observed. This reveals a problem persistent in the literature of using biodiversity as an indirect measure for the level of biological control (Landis et al. 2000). Increased

biodiversity may reduce, have no effect, or enhance biological control (Gurr et al. 2004b; Snyder et al. 2005). The successful use of ground covers, weedy strips and other cultural controls and habitat manipulations require a clear vision of the mechanisms by which they enhance targeted natural enemies (Landis et al. 2000; Gurr et al. 2004b).

In recent studies, habitat modifications near orchards were shown to provide a required resource, specifically an overwintering host for a leafroller parasitoid, thereby increasing biological control of leafrollers in adjacent apple and cherry orchards (Unruh et al. 2001; Pfannenstiel & Unruh 2003). It was shown that *Colpoclypeus florus* (Eulophidae) needed to leave the orchard in autumn to find hosts which are large enough to attack and on which they can overwinter because the pest leafrollers overwintered as small larvae and eggs. An alternate host leafroller, *Ancylis comptana* (Tortricidae) was found feeding on multiflora rose in riparian habitats in Central Washington. Experimental gardens of the rose were planted near orchards and infested with *A. comptana* in 2000; parasitism of pest leafroller increased in adjacent orchards in 2001 and has continued to be much higher through 2005 (T.R.U. unpublished). This conservation biological control approach is similar to the use of prune trees to provide overwintering hosts for *Anagryus* spp., egg parasitoids of grape leafhopper (Flaherty & Wilson 1999). This approach ultimately failed because the blackberry or prune leafhopper eggs were parasitized too heavily by wasps from the grapes to provide a stable resource for the vineyards from year to year (Flaherty & Wilson 1999; Mills & Daane 2005). Studies by Miliczky & Horton (2005) demonstrated that beneficial species are more abundant on orchard edges and in habitats surrounding orchards. This suggests the possibility of new opportunities to enhance biological control through habitat manipulations, but only

carefully engineered modifications are likely to be successful.

CONCLUSIONS

Sustainable agriculture will rely increasingly on alternatives to conventional chemical insecticides for pest management that are environmentally friendly and reduce the amount of human contact with pesticides. Biological control agents of codling moth, in conjunction with other IPM components, can provide effective control of the moth and other orchard pests. The challenge we face is to find successful combinations of entomopathogens, predators, and parasitoids with new and old insecticide chemistries, semiochemicals, and habitat modifications to produce a profitable and sustainable orchard pest management system. Cost-effective suppression of codling moth populations with granulovirus, the use of EPNs to control cocooned larvae to reduce overwintering populations, and the establishment of codling moth parasitoids represent biological solutions that are compatible with mating disruption and may form the foundation of apple production without neurotoxic or disruptive insecticides. A substantial amount of basic and operational research remains to be done. For example, study is warranted on: testing the compatibility of biological control agents with other non-toxic controls such as particle films (Unruh et al. 2000; Knight et al. 2001); developing adjuvants to further improve granulovirus and EPN delivery and stability; discovery of improved habitat modifications; and the development of biocompatible interventions for control of the suite of secondary pests, including leafrollers, aphids, mites and other pests that occur in orchards with codling moth.

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