

Control of Aphids on Greenhouse Vegetable Crops

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Abstract

This thesis consists of two parts. In the first part, I review published information on the chemical, biological, and integrated control of aphids on greenhouse vegetable crops, primarily in Europe and Canada. Chemicals used to control aphids, problems of insecticide resistance, and ways in which resistant populations of aphids may be managed are described. The natural enemies of aphids which have been investigated for biological control are reviewed, and integrated control of aphids on greenhouse vegetable crops is discussed. I make recommendations and suggest topics that need further research.

In the second part, I describe my experience with setting up a 'banker plant' system for the potential biological control of the melon aphid, *Aphis gossypii* Glover, on greenhouse cucumbers in British Columbia. The goal of a 'banker plant' system is the rearing and sustained production of a parasite or predator of a crop pest on a non-pest host in the greenhouse; the non-pest host is reared on a plant other than the crop. However, two attempts to set up a working 'banker plant' system with the parasitoid, *Aphidius matricariae* Haliday, failed. Problems encountered with this system are discussed. The 'banker plant' system needs further study before it can be recommended to greenhouse vegetable growers in British Columbia.

Observations of natural enemies found on cucumbers in the 'banker plant' experiment indicated that spiders were abundant. The

role of spiders in the natural biological control of mite and insect pests on greenhouse vegetable crops needs further investigation.

Melon aphids collected from commercial lily, but not from commercial tomato and sweet pepper, could be successfully reared on cucumber. This suggests that several strains of the melon aphid with diverse impact on greenhouse vegetable crops may exist in British Columbia.

The rearing of a different parasitoid, *Aphelinus asychis* Walker, from melon aphid was successful. Further research is needed to determine if *A. asychis* would be a suitable biological control agent of melon aphid on greenhouse cucumbers in British Columbia.

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1. Introduction

The total area in the world covered by greenhouses is approximately 150,000 hectares (van Lenteren & Woets, 1988). Until 1968, more than fifty percent of the world's greenhouses were located in the Netherlands and the United Kingdom (van Lenteren & Woets, 1988). Today, greenhouses are used in many countries to produce a variety of crops, including vegetables. The major vegetable crops grown under greenhouse conditions are cucumber, sweet pepper, and tomato.

Although greenhouse production of vegetables is a small enterprise worldwide, it is an important business in some countries, e.g. the Netherlands, Belgium, and the United Kingdom. The Netherlands has 4,570 hectares of greenhouses devoted to growing vegetables and is the world leader in greenhouse vegetable production (van Lenteren & Woets, 1988). In Canada, the production of greenhouse cucumbers and tomatoes was an \$89.5 million industry in 1992 (Anonymous, 1994). Production is concentrated in the Province of Ontario, followed by the Provinces of British Columbia, Quebec, and Alberta (Anonymous, 1994). The Provinces of Nova Scotia, New Brunswick, Prince Edward Island, and Saskatchewan are minor producers of greenhouse vegetable crops.

Table 1 gives a more detailed description of greenhouse vegetable production in the Province of British Columbia. Tomato is the most important commodity, followed by cucumber and sweet pepper. Lettuce is a relatively minor crop. The total value of greenhouse vegetable crops in British Columbia was \$35.3 million in 1991

Table 1. Greenhouse Vegetable Production in the Province of British Columbia in 1991.

<u>Crop</u>	<u>Value (\$ '000)</u>
Cucumbers	8,145
Lettuce	1,450
Sweet Peppers	10,359
Tomatoes	15,361
Total	35,315

Reference: Anonymous (1993)

(Anonymous, 1993). In comparison, and to illustrate the importance of the greenhouse vegetable industry in British Columbia, the total value of field-grown tomato, cucumber, sweet pepper, and lettuce in British Columbia in 1991 was \$7.3 million (Anonymous, 1993). The total value of all field-grown vegetables in British Columbia in 1991 was \$62.9 million (Anonymous, 1993). One important market for the greenhouse vegetable industry in British Columbia is export to the U.S.A.

Many different insect pests attack greenhouse vegetable crops. These include aphids, mites, thrips, whiteflies, caterpillars, and fungus gnats. Along with spider mites and whiteflies, aphids are one of the more common insect pests on greenhouse vegetable crops (Rabasse & Wyatt, 1985; van Steenis, 1993).

This thesis reviews the control of aphids on greenhouse vegetable crops, primarily in Europe and Canada. I make recommendations and suggest topics which need further research. In the Appendix, my experience with a 'banker plant' system for the biological control of the melon aphid, *Aphis gossypii* Glover, on greenhouse cucumbers in the Province of British Columbia is described.

2. Aphid Biology and Pest Status on Greenhouse Vegetable Crops

2.1 Introduction

Aphids are insect parasites of plants, worldwide in distribution. Footitt and Richards (1993) classified aphids into several families belonging to the superfamily Aphidoidea. The Aphididae is the largest family of aphids and members are abundant in temperate climates. Aphid species in the Aphididae are common agricultural pests and include the genera *Aphis*, *Macrosiphum*, and *Myzus*.

The literature on aphids is extensive. General references on aphid biology were provided by Blackman and Eastop (1984). Eastop (1974) gave a list of references on more detailed aspects of aphid biology. Recent reviews include topics on aphid biology (Minks & Harrewijn, 1988), aphid ecology (Dixon, 1985a), aphid-plant relationships (Campbell & Eikenbary, 1990), chemical ecology of aphids (Pickett *et al.*, 1992), evolution of aphid life cycles (Moran, 1992), and the structure of aphid populations (Dixon, 1985b).

All Aphidoidea in the sense of Footitt and Richards (1993) are parthenogenetic and viviparous. Aphids have complex life histories and many species have intimate associations with their host plants. Both winged and wingless forms of aphids may occur. A winged aphid is termed an alate and, without wings, an aptera. The apterous form of aphids is usually most often seen. The alate form appears to be produced in response to environmental conditions, deterioration of host plant quality, and/or crowding of aphids on plants.

Aphids are small, soft-bodied insects that are pearlike in shape, with generally long antennae and legs. They have piercing and sucking mouthparts, and feed on plant sap. Aphids are usually distinguished by a pair of siphunculi, also known as cornicles, at the posterior end of the abdomen; the siphunculi secrete a defensive fluid.

Aphids excrete honeydew from the anus. The honeydew consists of excess plant sap and waste material from the aphid. Honeydew is attractive to many insects, particularly ants, and is a growth medium for various sooty mold fungi. Many species of aphids form large colonies, which may produce copious amounts of 'sticky' honeydew.

2.2 General Life Cycle of Aphids

Aphids generally overwinter in the egg stage on a primary host plant in temperate climates. The primary host plant usually is a winter-hardy, perennial, woody plant. In spring, the eggs hatch into apterous, parthenogenetic, viviparous females called fundatrices. The fundatrices remain on the primary host plant and produce exclusively female offspring. Several generations may be produced this way. Immature aphids are called nymphs and molt several times before becoming an adult. Later in the spring, alate, parthenogenetic, viviparous females are produced, which migrate to a secondary host plant.

The secondary host plant is usually restricted to a narrow range of different plant species. However, some species of aphids have a wide range of hosts. Secondary host plants are usually herbaceous or other woody plants. In the summer, both alate and apterous,

parthenogenetic, viviparous females are produced. The alates may fly to other plants of the same secondary host, or to a new secondary host plant of a different species. Later in the summer, alate females, termed sexuparae, migrate back to the primary host plant and continue to produce more females. In the autumn, sexually reproductive males and females, or sexuales, are produced by the sexuparae. Sexual females are called oviparae and almost always lack wings. Sexual males may, or may not, have wings. Males and females mate, and the females lay very small, shiny, black eggs, which overwinter on the primary host plant.

Some aphid species do not change host plants in the spring and reproduce continually on the same plant species. In this case, sexuales are produced in the autumn and eggs overwinter on the same host plant. In warmer climates, such as the southern United States, most aphid species do not reproduce sexually. The term for this lack of sexual reproduction is anholocycly.

2.3 Damage to Crops Caused by Aphids

The majority of aphid species are monophagous and are not agricultural pests (Dixon, 1977). The relatively few aphids which infest and damage crop plants are primarily host-alternating or polyphagous non-host alternating species (Dixon, 1977). Aphids may damage crop plants directly by sucking plant sap, particularly when the population of aphids is high, or indirectly by excreting honeydew. Honeydew serves as a food source for sooty mold fungi. Both the honeydew and sooty mold fungi may physically contaminate the

harvestable portion of the crop. Sooty mold fungi may also decrease photosynthesis on contaminated leaves of plants.

Aphids may also indirectly damage crop plants through the transmission of plant viruses. The most important vectors of plant viruses are aphids (Matthews, 1991). Plant viruses transmitted by aphids can cause many plant diseases (Matthews, 1991), resulting in damage to the crop, or a reduction in crop yield (Agrios, 1990). The general subject of aphids as vectors of plant viruses has been reviewed by Harris (1981, 1990), Harris and Maramorosch (1977), Pirone and Harris (1977), Rochow (1972), and Swenson (1968). McLean *et al.* (1986) and Plumb and Thresh (1983) have reviewed the epidemiology of plant viruses.

Aphids as a group are vectors of about 170 plant viruses (Agrios, 1988). The majority of plant viruses cause symptoms in plants which may include mottling, mosaic or yellowing of leaves, bushiness or stunting of plants, and distortion of leaves, flowers, and fruit (Agrios, 1988). Agrios (1990) has reviewed the economic aspects and consequences of viral diseases infecting crop plants.

Several plant viruses transmitted by aphids may cause economically important diseases affecting vegetable crops. Cucumber mosaic virus (CMV) occurs worldwide and is one of the most common and economically important viruses of plants, including greenhouse vegetable crops (Agrios, 1988, 1990). The host range of CMV includes cucumber, sweet pepper, and tomato (Agrios, 1988). Another common, destructive plant virus worldwide in occurrence is potato virus Y (PVY), which infects sweet pepper and tomato (Agrios, 1988, 1990). Transmission and disease caused by tobacco etch virus (TEV)

is limited to North and South America, but TEV is also an important virus of sweet pepper and tomato (Agrios, 1988, 1990).

2.4 Aphids as Pests on Greenhouse Vegetable Crops

The most important aphids that occur as economic pests on greenhouse vegetable crops are *Myzus persicae* (Sulzer), *Aphis gossypii* Glover, and *Macrosiphum euphorbiae* (Thomas) (van Lenteren & Woets, 1988; van Steenis, 1993). The general biology of all three species has been described by Blackman and Eastop (1984). All three aphid species may become serious pests in Europe (van Steenis, 1993), while *A. gossypii* and *M. persicae* are most troublesome for growers in British Columbia (Anonymous, 1992). All three aphid species, *M. persicae*, *A. gossypii*, and *M. euphorbiae*, are vectors of many plant viruses, including CMV, PVY, and TEV (Kennedy, Day, & Eastop, 1962).

2.4.1 *Myzus persicae* (Sulzer)

M. persicae is also known as the green peach or peach-potato aphid, and is the vector of about 120 plant viruses (Eastop, 1983). The biology and population dynamics of *M. persicae* have been reviewed by Mackauer and Way (1976). van Emden *et al.* (1968) have reviewed the ecology of *M. persicae*.

M. persicae is one of the most important aphid pests in the world (Mackauer & Way, 1976). Adults are 1.2-2.3 mm in length and are generally light green or yellow in color. The primary host plants include *Prunus* spp., particularly peach. Over 50 plant families serve

as secondary hosts (Blackman & Eastop, 1984). The secondary host list includes tobacco and many vegetable crops such as potato, crucifers, tomato, and cucumber.

M. persicae is made up of many lines ranging from holocycly to anholocycly. Anholocyclic lines are very common. *M. persicae* is considered to be a low-density pest of crops (Mackauer & Way, 1976) and causes damage primarily as a vector of plant virus diseases (Mackauer, 1968). *M. persicae* is a very dispersive aphid species and is particularly sensitive to the physiological condition of the host plant (Mackauer & Way, 1976). In western Europe, *M. persicae* is the most important aphid pest on sweet pepper (van Steenis, 1993), but it may also infest and become a pest on cucumber (van Lenteren & Woets, 1988) and tomato (Woets, 1985).

2.4.2 *Aphis gossypii* Glover

A. gossypii is also known as the cotton or melon aphid, and transmits over 50 plant viruses (Eastop, 1983). The biology and taxonomy of *A. gossypii* is still poorly understood (Furk & Hines, 1993; van Steenis, 1992). *A. gossypii* occurs worldwide and is commonly found in tropical countries (van Steenis, 1992). This aphid species appears to consist of many anholocyclic lines, often having intimate relationships with their host plants (Blackman & Eastop, 1984).

A. gossypii may also undergo sexual reproduction. Females have been observed to sometimes lay eggs in the autumn on primary host plants, which include *Hibiscus syriacus* (Inuazumi & Takahashi, 1988; Kring, 1959), *Catalpa bignoniodea* (Kring, 1959), and citrus (Komazaki

et al., 1979). More than 25 families of plants serve as secondary hosts for *A. gossypii* (Blackman & Eastop, 1984), and include cotton, cucurbits, and other vegetable crops.

A. gossypii can exhibit a high degree of polymorphism. Adults measure 0.9-1.8 mm in length and the body color may be light yellow, yellow, dark brown, or black. The yellow forms are small and appear to be produced under unfavorable environmental conditions (Kring, 1959). Distinguishing features of the melon aphid are short antennae, red eyes, and black siphunculi regardless of the body color.

Reproduction by virginoparous females lasts 5-10 days at 20-25°C (van Steenis, 1992). One female may produce up to 40 nymphs during this time (van Steenis, 1992). *A. gossypii* can multiply each week as much as 23-times under laboratory conditions, and 12-times on cucumbers in the greenhouse (Rabasse & Wyatt, 1985).

A. gossypii is a pest on greenhouse vegetable crops, primarily on cucumbers, in western Europe (van Letteren & Woets, 1985; van Steenis, 1992). However, *A. gossypii* is becoming more of a problem on sweet peppers in the Netherlands (van Steenis, 1992), and on cucumber and sweet pepper in British Columbia. The primary reasons for *A. gossypii* as a pest on greenhouse vegetable crops in western Europe are (1) rapid rate of increase (Wyatt & Brown, 1977), (2) resistance to the selective insecticide pirimicarb (Furk & Hines, 1993; Furk *et al.*, 1980; van Schelt *et al.*, 1990), (3) the use of broad spectrum insecticides would interfere with the biological control practices of other greenhouse pests (van Schelt *et al.*, 1990; van Steenis, 1990), and (4) lack of effective biological control agents (van Steenis, 1992).

2.4.3 *Macrosiphum euphorbiae* (Thomas)

The common name for this aphid is the potato aphid. *M. euphorbiae* is the vector of more than 50 plant viruses (Eastop, 1983). Adults measure 1.7-3.6 mm in length. Distinguishing features of this aphid are long legs and prominent siphunculi. Two color phases may occur; green or pink. The primary host plants are *Rosa* spp. and over 20 families of plants serve as secondary hosts. The secondary host plants for *M. euphorbiae* include sunflower, tomato, eggplant, and sweet pepper. In western Europe, *M. euphorbiae* is the most important aphid pest on greenhouse tomato (van Steenis, 1993), but it may also be a pest on greenhouse cucumber (van Letteren & Woets, 1988).

3. Chemical Control

3.1 Introduction

Many different chemicals are used to control aphids. Most of the chemicals belong to four classes of insecticides and include organophosphorous, organochlorine, carbamate, and pyrethroid compounds. All of these compounds are mainly contact or systemic insecticides. A contact insecticide works by acting directly on an insect. A systemic insecticide is applied to the seed, leaves, or roots of plants, and is translocated through the phloem or xylem to other plant tissues. The target organisms of systemic insecticides are a variety of phytophagous insect pests. Systemic insecticides are particularly useful against insect pests of plants with sucking mouthparts and are often good aphicides (Hassall, 1990).

Most of the organophosphorous insecticides are effective against aphids (Hassall, 1990). Organophosphorous insecticides commonly used to control aphids include demeton-S-methyl, diazinon, dimethoate, disulfoton, malathion, methamidophos, oxydemeton-methyl, and parathion (Anonymous, 1991; Hassall, 1990). Organophosphorous insecticides act by inhibiting acetylcholinesterase in the nervous system of insects (Ware, 1991). Many organophosphorous insecticides are registered in the Province of British Columbia for the control of aphids on field and greenhouse crops (Anonymous, 1991; Portree, 1993).

Demeton-S-methyl, dimethoate, disulfoton, methamidophos, and oxydemeton-methyl are all systemic insecticides (Anonymous, 1990).

Many systemic organophosphorous compounds need to undergo metabolic activation within the plant or insect in order to become active (Hassall, 1990). Systemic insecticides with this property are often weak contact insecticides (Hassall, 1990).

Aldicarb, carbofuran, methomyl, oxamyl, and pirimicarb are examples of some carbamate insecticides used to control aphids. Carbamate insecticides have the same mode of action as organophosphorous insecticides (Ware, 1991). Aldicarb, carbofuran, and methomyl are all systemic insecticides (Ware, 1991). Aldicarb and carbofuran are used in some states in the U.S.A. to control *A. gossypii* on cotton (Grafton-Cardwell, 1991; O'Brien *et al.*, 1992). Aldicarb and carbofuran are both registered in the Province of British Columbia to control aphids on potato (Anonymous, 1991). Methomyl and oxamyl are used to control *A. gossypii* on cucurbit crops, and cucurbit crops and eggplant, respectively in Hawaii (Hollingsworth *et al.*, 1994).

Pirimicarb is systemic if applied to the roots of plants and exhibits translaminar spread when sprayed on the leaves of plants (Martin & Worthing, 1977). Several sources have indicated that pirimicarb is useful against organophosphorous-resistant aphids (Hassall, 1990; Martin & Worthing, 1977; Seaman & Warrington, 1972). Pirimicarb is registered for control of aphids on many field vegetable crops in the Province of British Columbia (Anonymous, 1991), and has been used to control aphids on greenhouse vegetable crops in western Europe (Furk & Hines, 1993; van Schelt *et al.*, 1990).

The organochlorine insecticide, endosulfan, is used in some areas of the U.S.A. to control *A. gossypii* on cotton, watermelon, and eggplant (Grafton-Cardwell, 1991; Hollingsworth, 1994; O'Brien *et al.*, 1992).

Endosulfan and γ -benzenehexachloride, another organochlorine known by the trade name, Lindane, are used to control *A. gossypii* on cotton in the Sudan (Gubran *et al.*, 1992). Endosulfan and γ -benzenehexachloride have the same mode of action, which involves blocking γ -aminobutyric acid activated chloride channels in the nervous system of insects (Ware, 1991). Endosulfan is the only organochlorine insecticide registered for the control of aphids on field and greenhouse vegetable crops in the Province of British Columbia (Anonymous, 1991; Portree, 1993).

Bifenthrin, deltamethrin, and fenvalerate are examples of some pyrethroid insecticides used to control aphids. Bifenthrin and fenvalerate are used to control *A. gossypii* on cotton in some areas of the U.S.A. (O'Brien *et al.*, 1992), and on cucurbit crops in Hawaii (Hollingsworth *et al.*, 1994), respectively. Deltamethrin and fenvalerate are also used to control *A. gossypii* on cotton in the Sudan (Gubran *et al.*, 1992). No pyrethroids are registered to control aphids on field or greenhouse vegetable crops in the Province of British Columbia.

Some of the pyrethroids induce repetitive firing of neurons. This results in the knockdown of insects and eventual paralysis (Ware, 1991). Pyrethroids have a negative temperature coefficient, being more toxic to insects as the temperature declines (Ware, 1991). Deltamethrin appears to have also a repellency effect on aphids (Rice *et al.*, 1983).

3.2 Chemicals Used to Control Aphids on Greenhouse Vegetable Crops

The availability of insecticides to control aphids on greenhouse vegetable crops depends on the registration procedure of a particular country. Examples of insecticides used to control aphids on greenhouse vegetable crops can be taken from the Province of British Columbia. These are nicotine, insecticidal soap, endosulfan, diazinon, malathion, and parathion (Table 2). How does this differ from insecticides registered on the same crops but grown in the field?

A comparison of insecticides registered for the control of aphids on field- and greenhouse-grown cucumber, lettuce, pepper, and tomato in British Columbia can be seen in Table 2. More insecticides are registered for field-grown lettuce and pepper than greenhouse-grown lettuce and pepper. The reverse is true for cucumber and tomato. Systemic insecticides are registered only for use on field-grown lettuce. One major difference in the list of chemicals in Table 2 is the inclusion of insecticidal soap for greenhouse-grown cucumber and tomato, and nicotine for greenhouse-grown cucumber, lettuce, and tomato. Most of the chemicals listed in Table 2 for use on the greenhouse vegetables are contact insecticides. Nicotine and parathion are both registered and used as fumigants.

Another major difference among the list of chemicals in Table 2 is the lack of registration of pirimicarb for the greenhouse-grown vegetables. One possible reason is that because of concern over mammalian safety (Croft, 1990b), pirimicarb is not registered in the U.S.A., which is an important export market for greenhouse vegetables

Table 2. Insecticides registered for control of aphids on field- and greenhouse-grown cucumber, lettuce, pepper, and tomato in the Province of British Columbia.

<u>Class of insecticide</u>	<u>Common name</u>	<u>Crops</u>
Carbamate	Pirimicarb	Lettuce (F), pepper (F)
Botanical	Nicotine	Cucumber (G), lettuce (G), tomato (G)
Fatty Acid	Insecticidal soap	Cucumber (G), tomato (G)
Organochlorine	Endosulfan	Cucumber (F, G), pepper (F), tomato (F, G)
Organophosphorous	Diazinon	Pepper (F, G), tomato (F)
	Dimethoate	Lettuce (F)
	Disulfoton*	Lettuce (F)
	Malathion	Cucumber (G), lettuce (G), pepper (G), tomato (G)
	Methamidophos*	Lettuce (F)
	Parathion*	Cucumber (G), tomato (G)

References: Anonymous (1991); Portree (1993)

F= Field, G= Greenhouse

* Use restricted after 1992 January 01

produced in British Columbia. Pirimicarb has been used to control aphids on greenhouse vegetable crops in the United Kingdom and the Netherlands, but is not very effective anymore against *A. gossypii* because of resistance (Furk & Hines, 1993; van Schelt *et al.*, 1990). Heptenophos, an organophosphorous insecticide not registered in the Province of British Columbia, is used to control aphids on greenhouse-grown cucumber in the United Kingdom (Furk & Hines, 1993).

3.3 Insecticide Resistance

A common worldwide problem resulting from the use of chemicals to control arthropod pests is pesticide resistance. More than 500 species of arthropods are now resistant to one or several pesticides (Georghiou & Lagunes-Tejeda, 1991). Pesticide resistance in agriculturally and medically important arthropods has been the topic of much research. Georghiou and Saito (1983), Roush and Mckenzie (1987), and Roush and Tabashnik (1990) have all reviewed this important subject. Among the numerous insect pests reported to have developed insecticide resistance are two of the three common aphid pests of greenhouse vegetable crops, *M. persicae* (Devonshire, 1989) and *A. gossypii* (Furk & Hines, 1993). Insecticide resistance has not been reported for *M. euphorbiae* (Furk & Roberts, 1985).

The first published account of possible insecticide resistance in *M. persicae* was by Anthon (1955), who reported difficulty in controlling this aphid in peach orchards with organophosphorous insecticides in northcentral Washington in the United States. Since that time, insecticide resistance in *M. persicae* has developed throughout the

world (Devonshire, 1989). Wyatt (1965) reported insecticide resistance in *M. persicae* on greenhouse chrysanthemums in the United Kingdom. In the United Kingdom today, insecticide resistance is generally very high in greenhouse populations of *M. persicae* (Devonshire, 1989).

Sawicki and Rice (1978) reported cross-resistance in insecticide resistant *M. persicae* from the United Kingdom. Resistance was found to be generally greatest to pyrethroids, less so to organophosphorous insecticides, and least to carbamates. The mechanism of insecticide resistance in *M. persicae* from the United Kingdom was shown by Needham and Sawicki (1971) to be due to a more active carboxylesterase. This enhanced carboxylesterase activity, termed E4, was demonstrated by Devonshire (1977) to be the result of the production of more enzyme. Field *et al.* (1988) reported that the production of more esterase was caused by amplification of the esterase gene. Esterase E4 detoxifies insecticides by sequestration and metabolism (Devonshire & Moore, 1982).

The first indication of the potential of insecticide resistance in *A. gossypii* was from a study on insect resistance conducted by Boyce (1928). Boyce (1928) experimentally selected aphids apparently resistant to hydrocyanic acid. Many years later, Ghong *et al.* (1964) reported natural insecticide resistance in *A. gossypii* on cotton to demeton in China. Since 1964, insecticide resistance in *A. gossypii*, particularly to organophosphorous compounds, has been reported from various countries around the world (Furk & Hines, 1993).

Resistance in *A. gossypii* to all four major classes of insecticides used to control aphids has been reported. In the mid-southern United

States, O'Brien *et al.* (1992) found that *A. gossypii* infesting cotton was resistant to aldicarb (carbamate), endosulfan (organochlorine), chlorpyrifos (organophosphate), and bifenthrin (pyrethroid). Gubran *et al.* (1992) reported that *A. gossypii* infesting cotton in the Sudan was resistant to methomyl and pirimicarb (carbamates), γ -benzene-hexachloride and endosulfan (organochlorines), dimethoate and methidathion (organophosphorous compounds), and deltamethrin and fenvalerate (pyrethroids).

Furk *et al.* (1980) documented pirimicarb resistance in *A. gossypii* on greenhouse chrysanthemums. Prior to 1985, resistance in *A. gossypii* on this nursery crop was only to pirimicarb. After 1985, *A. gossypii* infesting greenhouse chrysanthemums in the United Kingdom also became resistant to diazinon (Furk & Vedhi, 1990).

In 1987, growers of greenhouse cucumbers in the United Kingdom began having difficulty controlling *A. gossypii* on cucumber with diazinon and pirimicarb (Furk & Hines, 1993). This resistance was later documented by Furk and Hines (1993). Pirimicarb resistance in *A. gossypii* on greenhouse cucumber has also been reported in the Netherlands (van Schelt *et al.*, 1990).

Multiple mechanisms appear to be responsible for insecticide resistance in *A. gossypii*. Many researchers have reported higher esterase activity in *A. gossypii* resistant to various organophosphorous compounds (O'Brien *et al.*, 1992; Sun *et al.*, 1987; Takada & Murakami, 1988). O'Brien *et al.* (1992) and Sun *et al.* (1987) also suggested insensitive acetylcholinesterase as a factor. Sun *et al.* (1987) also implicated higher mixed function oxidases. Silver (1984) and Gubran

et al. (1992) demonstrated that insensitive acetylcholinesterase is involved in resistance of *A. gossypii* to pirimicarb.

Gubran *et al.* (1992) did not find high esterase activity in organochlorine-, organophosphorous-, and pyrethroid-resistant *A. gossypii* in the Sudan, and could not explain the mechanism of resistance. Also, O'Brien *et al.* (1992) could not find evidence that organochlorine resistance in *A. gossypii* was also associated with higher esterase activity, and suggested that a different mechanism was responsible for resistance to endosulfan. Suzuki *et al.* (1993) stated that the role of esterases in organophosphorous resistance and other types of insecticide resistance in *A. gossypii* remained unclear. Their work demonstrated that carboxylesterase activity was closely correlated to organophosphorous insecticide resistance and acted as a sequestering protein in resistance to fenitrothion.

3.4 Chemical Selectivity

One disadvantage of using chemicals to control agricultural pests has been the negative impact on nontarget organisms, especially beneficial insects. The effect of chemicals on natural enemies of agricultural pests has been the subject of research by many workers, and has been extensively reviewed by Croft (1990b). Many chemicals, though, can be selective in their action towards beneficial insects.

Chemicals used to control pests may be classified as having physiological or ecological selectivity (Croft, 1990b). Physiological selectivity is a characteristic of a given chemical and involves a differential toxicity against individual pest and beneficial insects.

Ecological selectivity depends on the temporal and spatial use of a chemical, and operates on population and community levels of insects. Examples of ecological selectivity are systemic pesticides, or spot applications of a chemical, against an early infestation of a pest concentrated in a particular location within a crop. Broad physiological selectivity of chemicals to natural enemies is rare (Croft, 1990b). Many cases of selectivity are ecological, or ecological and physiological, although differentiating between the two can often be difficult (Croft, 1990b).

Much more is known about the effect of chemicals on pests than on beneficial insects (Croft & Brown, 1975). Modes of uptake of pesticides by predators and parasites may involve direct contact, residual contact, and food chain uptake and transfer of the pesticide (Croft, 1990b). Behavior may also influence pesticide uptake by beneficial insects. Adult parasitoids exhibit grooming and cleaning behavior, and during this process may contaminate their bodies with pesticides (Croft, 1990b). Effects of chemicals on natural enemies may be lethal or sublethal. Sublethal effects may include changes in fecundity, longevity, developmental rate, sex ratio, and behavior (Croft, 1990b).

In general, of the four common classes of insecticides used to control aphids, pyrethroids are the most toxic to natural enemies, followed as a group by organophosphorous compounds and the carbamates, and then the organochlorines (Croft, 1990b). Making generalizations about the selectivity of a particular class of insecticide is difficult because certain chemicals can be found in each class which exhibit some selectivity to natural enemies over their prey.

Croft (1990b) summarized the reports of pesticide selectivity to arthropod natural enemies. Chemicals in each of the four major classes of insecticides used to control aphids exist which have been reported to be selective towards at least one natural enemy of a greenhouse insect or mite pest. Several of these chemicals are commercially used to control aphids on greenhouse vegetable crops.

Pirimicarb (carbamate), endosulfan (organochlorine), and insecticidal soap have been reported to exhibit selectivity. All three chemicals are physiologically selective towards *Encarsia formosa* Gahan, a parasite of whiteflies, and to *Phytoseiulus persimilis* Athias-Henriot, a predator of the two-spotted mite (Croft, 1990b). Pirimicarb has been used to control aphids in an integrated control program of greenhouse vegetable pests in western Europe (Hussey, 1985; Woets, 1985). Endosulfan and insecticidal soap are registered for use to control aphids on greenhouse tomato and cucumber in the Province of British Columbia.

4. Biological Control

4.1 Introduction

Aphids have numerous natural enemies and the effect of predators, pathogens, and parasites on aphid populations has been reviewed by Hagen and van den Bosch (1968), Mackauer and Way (1976) and van Emden *et al.* (1969). Hodek (1966) and Niemczyk and Dixon (1988) have reviewed the ecology of aphidophagous insects, and several workers have discussed methods used to study the efficacy of natural enemies (DeBach & Huffaker, 1971; Hodek *et al.*, 1972; Luck *et al.*, 1988).

Some natural enemies have been investigated for the control of aphids on greenhouse vegetable crops, but only a few have met with commercial success. These select biological control agents, however, are important, and many growers in Europe and Canada use them. In this chapter, I review the natural enemies of aphids that have been studied for the control of aphids on greenhouse vegetable crops.

4.2 Predators

4.2.1 Introduction

Most studies measuring the impact of predators on aphid populations have been observational in nature. The effectiveness of predators has been based primarily on correlation of predator numbers with changes in the aphid population (Mackauer & Way,

1976). Mackauer and Way (1976) stated that experimental evidence demonstrating the role of predators in regulating aphid populations, and data on predator/prey relationships, was rare. Direct experimental evidence demonstrating the role of predators is valuable, but, unfortunately, this area of research has received little consideration until very recently. Many different predators have been found to play an important role in regulating natural aphid populations in certain situations (Chambers & Adams, 1986; Chambers *et al.*, 1983; Chiverton, 1986; DeBarro, 1992; Entwistle & Dixon, 1989; Kring *et al.*, 1985; Riechert & Bishop, 1990).

There are a large number of organisms that prey on aphids and these include insects, spiders, and birds (Fraser, 1988a). The most important predators of aphids in nature are insects and are found predominantly in the families Coccinellidae (ladybird beetles), Chrysopidae (common green lacewings), Syrphidae (syrphid, flower, or hover flies), Cecidomyiidae (gall midges), and Anthocoridae (minute pirate bugs) (Hagen & van den Bosch, 1968). Coccinellid beetles, lacewings, and syrphid flies, in addition to the midge, *Aphidoletes aphidimiza* (Rondani), have been evaluated for their potential to control aphids on greenhouse vegetable crops.

4.2.2 Coccinellidae

The biology of the Coccinellidae has been reviewed by Fraser (1988b), Hagen (1962), and Hodek (1967, 1973). The adults and larvae of most Coccinellidae are predators of aphids, scales, whiteflies, mealybugs, and mites. Some species of aphids are toxic to certain

coccinellids (Hodek, 1970). When prey is scarce, coccinellid beetles may feed on honeydew, nectar and pollen.

Coccinellid beetles have the greatest impact on aphids among all other aphidophagous insects (Hodek, 1970). However, few direct field studies have demonstrated the effectiveness of coccinellids in regulating the population of aphids (Hodek, 1970). Some of this important work has been conducted in Europe and the U.S.A. In Czechoslovakia, a research team using field cages demonstrated that coccinellids were important in regulating the population of *A. fabae* on sugar beet (Hodek, 1970). Kring *et al.* (1985) used exclusion techniques to show that *Hippodamia* spp. were effective at suppressing light to moderate infestations of *Schizaphis graminum* (Rondani) on high plains sorghum in Texas.

In western Europe, Gurney and Hussey (1970) compared four species of Coccinellidae as predators of aphids on greenhouse cucumber and chrysanthemum. The species of coccinellids tested were *Adalia bipunctata* (L.), *Coccinella septempunctata* L., *Coelomegilla maculata* de G., and *Cycloneda sanguinea* L. Since adult coccinellids tend to fly out of the unscreened vents in greenhouses (Gurney and Hussey, 1970), only larvae were considered in this study. The most voracious species in laboratory feeding tests was *C. maculata*, which at 21°C consumed a mean number of 486 *A. gossypii* and 272 *M. persicae* during the life of a larva.

Laboratory studies were conducted by Gurney and Hussey (1970) to determine the potential of coccinellid larvae for aphid control on cucumber and chrysanthemum plants. One species of coccinellid, *C. septempunctata*, was not included in this test, because sufficient

numbers could not be reared. Cucumber plants were infested with about 1000 *A. gossypii* and coccinellid larvae were released at a ratio of one larva to 50 aphids. Two species of coccinellids, *A. bipunctata* and *C. sanguinea*, reduced the melon aphid population by about one-third and one-half of the control, respectively. The most voracious coccinellid tested, *C. maculata*, had no effect on *A. gossypii*. The larvae of *C. maculata* became irritated by the hairs of the cucumber leaves and fell off the plants.

In a larger laboratory experiment, Gurney and Hussey (1970) determined the potential of *C. sanguinea* to control increasing numbers of melon aphid on cucumber plants. Cucumber plants were infested with aphids, and larvae of *C. sanguinea* were released on a proportion of plants on successive days. The ratio of one larvae to 20 aphids provided complete control, and only a few aphids remained at a ratio of one larvae to 40 aphids.

In similar experiments with *M. persicae* on chrysanthemum plants (Gurney & Hussey, 1970), all three coccinellid species provided control of aphids at a release rate of one larva to 100 aphids. Aphid populations were reduced about 30 to 200 times that of the control. Larvae of *C. sanguinea* were the most effective at reducing the aphid population. In a larger experiment, larvae of *C. sanguinea* were released at a ratio of one larva to 20 aphids when about 1000 aphids were infesting four chrysanthemum plants growing in the same pot. After two weeks about 20 aphids were left on the plants in each pot.

Gurney and Hussey (1970) concluded from this study that *C. sanguinea* was the most efficient coccinellid species tested. In anticipation of possible commercial use, the authors also tested the

fecundity of all four coccinellid species. They found that *C. sanguinea*, when fed on a diet of *A. gossypii* or *M. persicae*, produced about three times the number of eggs as the other two coccinellid species. A rearing technique was developed using a natural diet consisting of a mix of *A. gossypii* and *M. persicae*, on which an average of about 20 eggs were laid daily by *C. sanguinea*. Gurney and Hussey (1970) stated that mass-rearing of *M. persicae* was difficult, because this aphid does not produce dense colonies. Another aphid, *Acyrtosiphon pisum* (Harris), was used to rear *C. sanguinea*. Adult *C. sanguinea* lived for several months on *A. pisum*, but egg production ceased after about three weeks of continuous feeding on this aphid (Gurney & Hussey, 1970). Non-breeding adult *C. sanguinea* also survived for a month on a sugar and water diet. Oviposition of adults resumed after about a week of feeding on aphids.

In conclusion, Gurney and Hussey (1970) thought that the commercialization of *C. sanguinea* was hindered by the lack of an artificial diet to rear this potential biological control agent under factory conditions. The authors did not comment on the possibility or problems of rearing the coccinellid beetle solely on *A. gossypii*.

In the former Soviet Union, the coccinellid *Leis axyridis*, has been studied for the control of *A. gossypii* and *M. persicae* (Lipa, 1985). The larva and adult each killed 200-300 aphids. The larvae fed more on aphids at higher temperatures (22-30°C). A release ratio between one to 10 and one to 30, larvae to aphids, reduced the population of *A. gossypii* on cucumber plants over 8-9 days, but did not eliminate the aphids.

4.2.3 Chrysopidae

The biology of the Chrysopidae has been reviewed by Canard *et al.* (1984) and New (1988). Members of the Chrysopidae are known as common green lacewings. The prey includes aphids, mealybugs, mites, and other insects. Adults generally feed on the same prey as the larvae.

Another family resembling the Chrysopidae is the Hemerobiidae, or brown lacewings (New, 1988). Brown lacewings are similar to green lacewings, except that the former are brown in color, generally smaller in size, and eggs are not laid on a stalk, but directly on the surface of plants.

The green lacewing, *Chrysoperla* (= *Chrysopa*) *carnea* Stephens, is an important predator of many different insects, including aphids (New, 1988). The potential impact of this predator on aphid populations appeared high when compared to other predators of aphids (Sundby, 1966). Potential advantages of using *C. carnea* as a biological control agent in greenhouses are the recent development of cold storage for mass-reared insects (Tauber *et al.*, 1993) and resistance to many insecticides (Bartlett, 1964; Bigler, 1984; Grafton-Cardwell & Hoy, 1985; Pree *et al.*, 1989). One disadvantage of *C. carnea* is that the adults do not feed on aphids (Hagen, 1962). Pree *et al.* (1989) considered *C. carnea* a prime candidate for use in integrated pest management programs.

Most of the work using green lacewings to control aphid pests of greenhouse vegetable crops has been conducted in the former Soviet Union (Tulisalo, 1984). These studies have been reviewed by Lipa

(1985) and Tulisalo (1984). Several chrysopid species have been tested, but *C. carnea* has been the subject of most of the research, since the rearing of this species is the best developed (Tulisalo, 1984). Eggs or larvae have been transferred to greenhouse plants. More eggs than larvae were usually needed because cannibalism reduces egg hatch (Tulisalo, 1984). Larvae of *C. carnea* were found to each consume 200-300 *A. gossypii* or *M. persicae* (Lipa, 1985).

Lacewings have been used to control aphid pests on sweet peppers, cucumbers, celery, lettuce, eggplant and other vegetable crops (Tulisalo, 1984). Larvae are most effective on lower growing crops with dense foilage such as lettuce, and where the aphid pest is evenly distributed over the leaves of plants (Tulisalo, 1984). Lacewing larvae may fall off of the leaves of taller crops with an open canopy (Tulisalo, 1984).

Effective predator:prey ratios using *C. carnea* ranged from 1:1.3, if eggs are used, and between 1:5 and 1:50, if larvae are released (Tulisalo, 1984). Similar ratios were needed when other chrysopid species were tested (Tulisalo, 1984). Periodic releases throughout the growing season were needed to achieve effective control (Lipa, 1985; Tulisalo, 1984). Control of *M. persicae* on lettuce was possible for an entire season, with two releases at two week intervals of second instar larvae of *C. carnea* at a ratio of 1:50 (Lipa, 1985). The same procedure was also effective for *M. persicae* on celery at a lower rate of 1:25 (Lipa, 1985). Larvae of *Chrysopa septempunctata* are reported in the former Soviet Union to be more effective than *C. carnea* for control of *A. gossypii* on cucumber, but are also more difficult and time consuming to rear (Lipa, 1985).

High temperatures in the greenhouse have been found to have a negative impact on egg development and behavior of lacewings. Temperatures in greenhouses should not be allowed to rise above 30° C. (Tulisalo, 1984). Greenhouse aphid pests controlled using lacewings included *A. gossypii*, *M. euphorbiae*, and *M. persicae*. However, the degree of control is not clear from these studies, and Lipa (1985) has stated that lacewings do not provide permanent control of aphid pests on greenhouse vegetable crops.

Scopes (1969) investigated the potential of *C. carnea* as a biological control agent of *A. gossypii* on cucumber and *M. persicae* on chrysanthemum. Larval development was 13.4 days at 21.1°C, and was the same regardless of aphid species used. Larvae at 21.1°C consumed an average of 425 second instar *A. gossypii* and 385 second instar *M. persicae*. Development of larvae was 29.5 days at 15.5°C with second instar *M. persicae*, and consumption of aphids was slightly reduced. Other laboratory experiments suggested a relationship between aphid size and numbers of aphids consumed by larvae of *C. carnea*. When third instars of *M. persicae* were used, 40% fewer aphids were eaten by larvae.

Unfortunately, the potential of *C. carnea* to control *A. gossypii* on cucumber could not be further studied by Scopes (1969), because the hairs of cucumber leaves inhibited the movement of larvae. Larvae of the genus *Chrysoperla* use an adhesive anal secretion to adhere to, and to move over, leaf surfaces (Spiegler, 1962). The hairs of cucumber leaves appeared to have interfered with this process. This result conflicts with a report from the former Soviet Union, where *C. carnea*

has been used to achieve some measure of control of *A. gossypii* on cucumber (Lipa, 1985).

In laboratory and greenhouse experiments by Scopes (1969) with *M. persicae* on chrysanthemum, aphids were controlled by one day old larvae at a ratio up to one larva to 50 aphids. Third instar larvae controlled *M. persicae* at a ratio of one larva to 200 aphids. Larvae effectively searched as far as 15 cm away from the introduction site. When aphid densities were four or less per plant, the searching capacity of larvae did not increase, and control of aphids was less effective.

4.2.4 Syrphidae

Certain larvae of the Syrphidae are common and important predators of aphids (Chambers, 1988). The larvae of some species of syrphids have been shown to be important in controlling the population of cereal aphids (Chambers & Adams, 1986; Entwistle & Dixon, 1989). Adult syrphids feed on nectar and pollen, and are important pollinators (Schneider, 1969). Adult syrphids appear to be either generalist or selective foragers of flowers (Cowgill *et al.*, 1993; Haslett, 1989). Adult syrphids may also feed on the honeydew of aphids (Schneider, 1969). Members of the Syrphidae are also known as hover flies, because of the characteristic rapid movement of their wings and hovering habit, especially around flowers.

Adult female syrphid flies require pollen for normal egg production (Schneider, 1969). Barlow (1961) determined the average total egg production of individual adult female *Metasyrphus* (=

Syrphus) *corollae* to be about 400. Eggs are laid by most species of aphidophagous syrphids in response to the presence of aphids (Chandler, 1968b). In this case, most eggs are laid near or within an aphid colony (Schneider, 1969). Volk (1964) demonstrated that olfactory cues were important for oviposition of *M. corollae*. Honeydew alone, from the aphids, *Metopolophium dirhodum* Walker or *A. pisum*, but not *Microlophium carnosum* (Bukt.), has been shown to be an ovipositional stimulant for *E. balteatus* DeGeer (Budenberg & Powell, 1992). Cues from aphid host plants alone appear to stimulate oviposition by some species of aphidophagous syrphids (Chandler, 1968a).

Syrphid flies have three larval stages and consume the greatest amount of food during the third instar (Schneider, 1969). Larvae of *M. corollae* completed development in 10 days at 22°C and 55% relative humidity (Schneider, 1969). During this time, larvae consumed an average of 867 medium-sized individuals of *A. fabae* and *M. persicae* (Schneider, 1969). Other syrphid species consumed 100-200 aphids during larval development (Schneider, 1969). Scott and Barlow (1986) reported that larvae of *M. corollae* ate up to 115 aphids during larval development. However, they did not give details on the species of aphid used, nor environmental conditions at which their experiments were conducted.

The syrphid flies *M. corollae* (F.) and *E. balteatus* DeGeer have been found to control cereal aphid populations at low densities in winter wheat (Chambers *et al.*, 1985). Natural syrphid predation on chrysanthemums in greenhouses has been found in the United Kingdom (Chambers, 1986). These two observations, along with the

high fecundity of female syrphids and considerable voracity of the larvae, led Chambers (1986) to investigate the potential of *M. corollae* for the control of an aphid with a high rate of increase. The model aphid chosen by Chambers (1986) was *A. gossypii* on cucumber.

The study by Chambers (1986) indicated control of the melon aphid population on individually caged cucumber plants grown at 21° C, was achieved by larvae of *M. corollae* on days 2, 3, or 4, after hatching from eggs laid on the plants on day 0, if no more than 9 aphids per egg were present at the end of oviposition. Percent egg hatch of larvae was determined to be 45%. One, two, or three day old syrphid larvae prevented melon aphid population increase as long as there were no more than 15, 26, or 41 aphids per larva, respectively.

Continuous control of aphids on cucumbers was possible as long as one gravid female syrphid was present in the cage. Hairs on cucumber leaves were not found to be a major deterrent to the larvae of *M. corollae*. Some hindrance to locomotion of young larvae was observed. However, very small larvae were capable of movement between hairs. Two factors regarding syrphid flies and their potential use in greenhouses discussed by Chambers (1986) are that adults need a source of pollen, and the other is the tendency for pre-reproductive females to disperse. On sunny days they may fly out of any unscreened vents in the greenhouse.

4.2.5 Cecidomyiidae

Members of the Cecidomyiidae are also known as gall midges because most species cause galls on plants (Borror *et al.*, 1981). Three

species prey on aphids: *Aphidoletes aphidimyza* (Rondani), *Aphidoletes urticae* (Kieffer), and *Monobremia subterranea* (Kieffer) (Harris, 1973). Only *A. aphidimyza* has been studied as a biological control agent of aphids on greenhouse vegetable crops (Markkula & Tiittanen, 1985).

Harris (1973) and Nijveldt (1988) have reviewed the biology of the Cecidomyiidae. The potential of *A. aphidimyza* in the biological control of aphids on greenhouse vegetable crops has been reviewed by Markkula and Tiittanen (1985). Results have generally been successful and *A. aphidimyza* is commercially available, and used by greenhouse vegetable growers in Canada (Anonymous, 1992; Portree, 1993), Finland (Markkula and Tiittanen, 1985), and in eastern Europe and the former Soviet Union (Lipa, 1985). The use of this biological control agent, however, is still primarily in the experimental stages in western Europe (Hussey, 1985). Commercial use of *A. aphidimyza* is growing in western Europe, but only 81 hectares of greenhouses were treated in 1985 (van Lenteren and Woets, 1988). This compares with 2,361 and 5,176 hectares treated with the parasitoid, *E. formosa*, and the predatory mite, *P. persimilis*, for whitefly and spider mite control, respectively (van Lenteren and Woets, 1988).

4.2.5.1 *Aphidoletes aphidimyza* (Rondani)

A. aphidimyza is a holarctic species and is found in most European countries, Japan, Canada, and the U.S.A. (Markkula & Tiittanen, 1985). The adult is a slender insect with long legs and is about 2 mm long. Females undergo monogenic reproduction, where all

offspring are either males or females (Sell, 1976). Under greenhouse conditions, the life span of adults is about 2 weeks (Markkula & Tiitanen, 1985). Adult *A. aphidimyza* are active only at night and during dusk (Markkula & Tiitanen, 1985). The adults feed on honeydew and the larvae are aphidophagous predators. Gravid females usually oviposit under leaves, and only on plants infested with aphids. El Titi (1972) found that the presence of aphids, or their secretions, stimulated oviposition. The species and variety of plants can effect the oviposition of gravid females. Meisner (1975) reported that this effect was due to differences in leaf structure and hairiness of the leaf. Gravid females deposit more eggs near adult aphids than nymphs (Markkula & Tiitanen, 1985). Gilkeson and Hill (1986) and Gilkeson (1987) found that females laid about 155 eggs. Other workers have reported much lower fecundities (Gilkeson, 1987). Gilkeson (1987) observed that the presence of water influences egg production. When adult females were provided with access to water, females laid about 249 eggs. Some females laid over 300 eggs and one laid 444 eggs.

Eggs of *A. aphidimyza* are about .3 mm long and .1 mm wide, and are smooth, shiny, and orange in color. Eggs hatch after 2 days at 23°C (Bouchard *et al.*, 1981). Newly emerged larvae are about .3mm long and grow to a length of 2-3 mm. Larvae are orange to red in color and have four instars. The larvae have to feed on aphids in order to complete development. The host range is over 60 species of aphids and includes *A. gossypii*, *M. persicae*, and *M. euphorbiae* (Markkula & Tiitanen, 1985). The prey species does not appear to influence the oviposition behavior of females.

After hatching, larvae immediately start searching for aphids and find prey mainly by olfactory cues (Wilbert, 1974) though vision may also play a role (Markkula & Tiitanen, 1985). Larvae usually attack aphids by biting their leg joints and injecting a toxin, which paralyzes the aphid (Markkula & Tiitanen, 1985). Paralysis takes place within a few minutes. After this action, the larva usually bites into the thorax of the aphid and sucks the prey dry. Uygun (1971) reported that larval development takes 7 days at 15°C, 3.8 days at 21°C, and 3 days at 27°C. Bouchard *et al.* (1981) found larval development to take 5.5 days at 23°C. An advantage of the larvae of *A. aphidimyza* in biological control is the functional response of the larvae in the presence of high aphid densities. Larvae may kill and eat more aphids than they consume (Uygun, 1971), or that are required for development (Markkula & Tiitanen, 1985).

After the larvae are fully developed, they crawl down the stem of the plant or fall to the ground. The larvae burrow down to a depth of about 3 cm and build a cocoon. Pupation takes place 2-4 days after the cocoon has formed. The pupal stage lasts 10-14 days at room temperature. Shorter daylengths and lower temperatures induce diapause (Markkula & Tiitanen, 1985). Under natural conditions in Finland, *A. aphidimyza* diapauses in the cocoon in the fall, pupates in the spring, soon followed by emergence of adults (Markkula & Tiitanen, 1985). Under greenhouse conditions, diapause occurs later in the fall and finishes earlier in the spring (Markkula & Tiitanen, 1985).

The egg or larval stages of *A. aphidimyza* can be transferred to a crop in the greenhouse. However, this practice is not suitable for commercial production because both eggs and larvae can be killed

during transport as a result of desiccation and lack of food (Markkula & Tiitanen, 1985). There has not been much success in releasing the adult stage of *A. aphidimyza* (El Titi, 1974; Markkula, 1979). Better results have been obtained rearing adults in the greenhouse in an 'open' culture (El Titi, 1974). The best and easiest method for commercial use has been found to be the rearing and transfer of cocoons (Markkula & Tiitanen, 1985). Markkula & Tiitanen (1985) provided details on the mass production of cocoons.

Commercial production of *A. aphidimyza* first began in Finland in 1978 (Markkula & Tiitanen, 1985), where results have been good and consistent. The advantages of using *A. aphidimyza* as a biological control agent on greenhouse vegetable crops are (1) mass production is easy and economical, (2) cocoons can be transported and distributed, (3) *A. aphidimyza* can overwinter in the greenhouse if a suitable medium for pupation is available, and no harmful chemicals are used to clean the greenhouse, and (4) the functional response of larvae results in the effective control of aphids.

The cost of commercially producing *A. aphidimyza* may now be reduced due to the work of Gilkeson (1990). Gilkeson found that cold storage of *A. aphidimyza* was possible. Last instars in cocoons were induced to diapause at 1-11°C in total darkness. Less than 10% mortality and high adult emergence occurred at storage of 2 weeks at 10-11°C, up to 4 weeks at 5°C, and up to 2 months at 1°C after acclimation for 10 days at 5°C.

One disadvantage of using *A. aphidimyza* as a biological control agent is that the larvae undergo diapause in the greenhouse, and are not effective against aphids on greenhouse vegetable crops during late

Fall, Winter, and early Spring. However, Gilkeson and Hill (1986a) found that diapause in *A. aphidimyza* can be overcome by using artificial low light intensity in greenhouses. Gilkeson and Hill (1986a) found that a 1:10 predator:prey release ratio effectively controlled *M. persicae* in a small trial on greenhouse sweet peppers during winter greenhouse conditions, where the maximum daytime temperature was 21°C and supplemental light was provided. Gilkeson and Hill (1986b) were also able to select nondiapausing lines of *A. aphidimyza*. Morphology, sex ratio, and fecundity of nondiapausing lines were not affected. However, nondiapausing larvae developed faster than diapausing larvae from the same line. The possibility exists that a nondiapausing strain of *A. aphidimyza* could be exploited commercially in the future.

Gilkeson and Hill (1987) briefly reviewed the work with *A. aphidimyza* in the former Soviet Union. Release rates of 1:200 up to 1:1 (pupa to aphids) have successfully controlled *A. gossypii* on cucumber. van Schelt *et al.* (1990) found that *A. aphidimyza* did not provide control of *A. gossypii* on cucumbers, but this was possibly due to pesticides used in the trials to control spider mites and thrips. van Schelt *et al.* (1990) observed that ants protected aphids from the midge larvae. Chambers (1990) reported that weekly releases of 10 cocoons per square meter effectively controlled *A. gossypii* on chrysanthemums, but stated that commercial use at this rate would be uneconomical in the United Kingdom. Chambers (1990) also used *A. aphidimyza* against *A. gossypii* on greenhouse cucumber. While no release rates were mentioned, weekly releases of cocoons appeared promising in controlling this aphid.

Control of *M. persicae* was achieved on greenhouse peppers in Finland (Markkula & Tiitanen, 1977; Markkula, 1978), and on greenhouse peppers and tomatoes in the U.S.A. (Meadow *et al.*, 1986), with a release ratio of 1:3, or two to five pupae per meter square, respectively at 2 week intervals. van Schelt *et al.* (1990) also achieved good success controlling *M. persicae* on sweet peppers, but the importance of *A. aphidimyza* was difficult to assess, since natural parasitization of aphids with an *Aphidius* sp. also occurred.

4.3 Pathogens

4.3.1 Introduction

Fungi are the most important group of aphid pathogens (Latgé & Papierok, 1988) and commonly cause epizootics in natural populations of aphids (Hagen & van den Bosch, 1968; Mackauer & Way, 1976; van Emden *et al.*, 1969). The most prevalent fungi found infecting aphids belong to the order Entomophthorales (Latgé & Papierok, 1988). The species of Entomophthorales capable of causing disease in aphids are *Conidiobolus*, *Entomophthora*, *Erynia*, *Neozygites*, and *Zoopthora* (Latgé & Papierok, 1988). The Deuteromycete, *Verticillium lecanii* (Zimm.) Viegas, may cause significant disease, and a reduction in aphid populations, under tropical or greenhouse conditions (Latgé & Papierok, 1988). The development of epizootics, caused by entomopathogenic fungi, depends on many abiotic and biotic factors. Epizootics, though, usually occur when humidity and the population density of aphids are high (Latgé & Papierok, 1988).

The subject of fungal pathogens of aphids has been reviewed by Latgé & Papierok (1988). Hagen and van den Bosch (1968), Mackauer and Way (1976), and van Emden *et al.* (1969) have all discussed the impact of Entomophthorales species on aphids. Research has focussed on *V. lecanii* for the control of aphids on greenhouse vegetable crops (Samson & Rombach, 1985). In this section, I, too, will focus my review on *V. lecanii*. Readers desiring more information on the aphid-infecting Entomophthorales are referred to the above cited literature. Other works by Ferron (1978), Samson *et al.* (1988), and Tanada and Kaya (1993) are given for those interested in the general topic of entomopathogenic fungi.

4.3.2 *Verticillium lecanii* (Zimm.) Viegas

V. lecanii was first reported by Viegas in 1939 on the scale insect *Coccus viridis* (Green) (Samson & Rombach, 1985). The species is common and can be isolated from soil, decaying organic debris, and food stuffs (Domsch *et al.*, 1980; Samson *et al.*, 1980). *V. lecanii* is a facultative parasite and may infect various insects and arachnids, and is also hyperparasitic on other fungi (Samson & Rombach, 1985).

V. lecanii regularly causes natural epizootics of aphids in tropical climates (Latgé & Papierok, 1988) and has been found to naturally parasitize aphids under greenhouse conditions in western Europe (Samson & Rombach, 1985). No epizootics caused by *V. lecanii* have been reported in natural aphid populations from temperate climates (Samson & Rombach, 1985).

The biology of *V. lecanii* has been reviewed by Latgé and Papierok (1988) and Samson and Rombach (1985). Growth and multiplication of *V. lecanii* occurs at 15-20°C and relative humidities of 85-90% in the greenhouse (Hall, 1985). Epizootics of aphids can occur if high humidity is present for at least 10-12 hours per day (Hall, 1985).

V. lecanii produces two types of spores. Conidia are readily produced from phialides arranged in the typical whorl shape on conidiophores characteristic of the genus *Verticillium* (Samson & Rombach, 1985). Conidia are sensitive to dessication, but can survive a few months at cold temperatures and high humidity (Hall, 1981). Blastospores (yeast-like bodies) are sometimes produced by budding of the fungus (Latgé & Papierok, 1988) and are also formed in liquid culture (Hall & Burges, 1979; Samson & Rombach, 1985). Hall and Burges (1979) stated that conidia and blastospores were similar in their pathogenicities for aphids.

The infection process of aphids by *V. lecanii* is not well understood (Samson & Rombach, 1985). Unlike other entomopathogenic fungi, infection does not rely solely on the direct contact between a conidium and an aphid (Samson & Rombach, 1985). Conidia germinate and may initially grow as saprophytes on honeydew excreted by insects. Infection of aphids can occur by conidia or hyphae after the initial saprophytic growth phase.

After infection, the fungus grows throughout the aphid and sporulates. *V. lecanii* is visibly seen on the aphids as a whitish yellow, cottony colony. Conidia are most likely dispersed in water (Hall, 1981), not by air movement (Samson & Rombach, 1985), in the

greenhouse. Insects and mites may disperse conidia (Samson & Rombach, 1985). Predatory mites and parasitoids might be significant vectors of the fungus (Sanson & Rombach, 1985). Ekblom (1979) found that adult *E. formosa* were occasionally infected by *V. lecanii*.

Hall (1981, 1985) has discussed the control of aphids on greenhouse crops using *V. lecanii* as a microbial insecticide. Hall and Burges (1979) were the first to study the potential commercial use of *V. lecanii* to control aphids on greenhouse crops. Hall and Burges (1979) thought that a greenhouse, where temperature and humidity is favorable and can be manipulated, would provide a good environment for entomopathogenic fungi. Low densities of *M. persicae* on chrysanthemum were successfully controlled by Hall and Burgess (1979) after 2-3 weeks with one spray of a spore suspension of *V. lecanii*. However, poorer results were obtained for *Brachycaudus helichrysi* (Kltb.) and *Macrosiphoniella sanborni* (Gillette).

In a large greenhouse experiment with about 3000 cucumber plants, Khalil *et al.* (1985) used a spray with a blastospore suspension of *V. lecanii* against a mixed infestation of three aphid species on cucumber. Eradication of *M. persicae*, *M. sanborni*, and *Brachycaudus* sp. was achieved at $25 \pm 2^\circ\text{C}$ and 100% relative humidity (RH) in 25, 30, and 35 days, respectively.

Harper and Huang (1986) tested a native isolate of *V. lecanii* from Alberta, Canada against several aphid species, including *M. persicae*, and several other insects. Control of *M. persicae* on broadbean plants, which were maintained in a greenhouse at about 20°C with high humidity, ranged from 50-100%.

Hall (1981) reported that less mobile greenhouse pests, such as *A. gossypii*, were difficult to control with *V. lecanii*, and required repeated sprays. The addition of a substrate, which encourages germination, growth, and sporulation of the fungus on the leaf surface, to the spore suspension, was found useful against *A. gossypii*. Such a formulation of the fungus could effectively control this aphid pest on cucumber with only one spray (Hall, 1985).

Helyer and Wardlow (1987) used frequent, low dose, and ultra low volume applications to successfully control *A. gossypii* and *M. persicae* on chrysanthemum. More research is needed to determine if these methods are applicable on greenhouse vegetable crops.

The study by Hall and Burges (1979) led to the commercial production of *V. lecanii* as a microbial insecticide for the control of aphids on greenhouse vegetable crops. The trade name of this commercial product is 'Vertalec'. Another strain of *V. lecanii* has been commercially developed for use on whiteflies in greenhouses and is called 'Mycotal'. The major problem with both of these products is the requirement for prolonged periods of a consistently high RH for infection and transmission (Milner & Lutton, 1986). A period of 14 hours at 100% RH and 15-20°C is needed for high levels of infection of aphids (Hall, 1981).

Milner and Lutton (1986) were the first to report the effects of different humidity levels on the transmission and sporulation of *V. lecanii*. Maximum transmission of *V. lecanii* to *M. persicae* on sweet pepper at 20°C occurred with 100% RH and where free water was available. Transmission was delayed and inhibited at lower humidities. Little transmission was found at 93% and none at 80% RH.

Sporulation from dead aphids was also delayed and inhibited below 100% RH. Few spores were produced at 80% RH. The commercial product 'Vertalec' required at least 36 hours at 100% RH to become infectious. Infection of *M. persicae* reached 94.5% by 96 hours after spraying 'Vertalec'.

4.3.3 Other Pathogens

Pathogens other than fungi, such as bacteria, viruses, protozoans, and nematodes, have been reported by Gustafsson (1971), Hagen and van den Bosch (1968), and Mackauer and Way (1976) to rarely attack aphids. Since these reviews, two viruses have been discovered that naturally infect aphids, *R. padi* virus (RhPV) (D'Arcy *et al.*, 1981; Rybicki & van Wechman, 1982a), and aphid lethal paralysis virus (ALPV) (Williamson *et al.*, 1988). RhPV and ALPV are the only aphid viruses that have been described in any detail (Williamson, 1989). Because of these developments, I will briefly review the topic of aphid viruses.

Many researchers have reported observations of virus-like particles in the tissues of several aphid species (Allen & Ball, 1986; Kitajima, 1976; Kitajima *et al.*, 1978; Moericke, 1963; Parrish & Briggs, 1966; Peters, 1965), but few viruses have been isolated and characterized. Fraval and Lapierre (1970) described an isometric virus isolated from *R. padi*. Allen and Ball (1986) reported the partial characterization of an isometric virus isolated from *Sitobion avenae* (F.). Orlob *et al.* (1973) found that a granulosis virus isolated from *Pieris rapae* (L.) was toxic to *M. persicae* and *R. padi* when ingested or

injected into the aphids, but not when applied as a spray. The toxicity was nonspecific because the virus did not multiply within the aphid or cause any apparent infection.

D'Arcy *et al.* (1981a) and Rhybicki and van Wechmar (1982) independently characterized RhPV. Williamson *et al.* (1988) discovered and characterized ALPV, which is serologically distinct from RhPV. Both RhPV and ALPV have been found in natural cereal aphid populations, and have been reported to decrease longevity and fecundity of infected aphids (D'Arcy *et al.*, 1981b; Rybicki, 1984). von Wechmar *et al.* (1991) reported an association between ALPV and Entomophthorales fungi parasitizing cereal aphids in South Africa. The presence of both high fungal and viral infections of aphids were correlated with a sudden decrease in a natural cereal aphid population. Fungal spores and hyphae were found to carry ALPV, and may possibly act as a vector of the virus (von Wechman *et al.*, 1991). A specific viral disease alone has never been reported to cause an epizootic in aphids (Latge & Papierok, 1988).

The discovery of RhPV and ALPH suggests that viral infections of aphids may be more common than originally thought. The search for more aphid viruses should continue, and the testing of RhPV and ALPV on aphid pests should be explored. The possibility of fungi acting as a vector of ALPV (or other aphid viruses), and the possible role of ALPV (or other aphid viruses) in making aphids more susceptible to fungal infections, needs further investigation.

If it is true that fungi are important vectors of aphid viruses, aphid viruses might make aphids more susceptible to fungal infections. Or, viral infections might be present as an enzootic in

natural populations of aphids, and when certain environmental conditions are proper, perhaps, viral incidence among aphids increases, making more aphids susceptible to fungal infections. In either case, viral infections of aphids might be masked as secondary fungal infections. This may possibly be the reason for the low number of aphid viruses known to date.

4.4 Parasites

4.4.1 Introduction

Primary insect parasites of aphids belong to the families Aphidiidae and Encyrtidae (subfamily Aphelininae) of the order Hymenoptera, and Cecidomyiidae of the order Diptera (Mackauer & Chow, 1986). The cecidomyiid parasites of aphids are relatively rare and will not be considered here. Mackauer and Chow (1986) have reviewed the general biology of aphid parasites and their impact on aphid populations, as well as given references for host and distribution records for the Aphidiidae and Aphelininae.

All members of the Aphidiidae are primary solitary endoparasites of aphids. Some of the important genera are *Aphidius*, *Ephedrus*, and *Trioxys*. Most species of the Aphelininae are primary parasites of scale insects (Mackauer & Chow, 1986), but two genera are also primary solitary endoparasites of aphids, *Aphelinus* and *Protaphelinus*. Larvae of the Aphidiidae and Aphelininae are also subject to attack by insect parasites; these are called hyperparasites.

Most species of Aphidiidae and Aphelininae are arrhenotokous; males develop from unfertilized eggs and females from fertilized eggs. Adult females of the Aphidiidae and Aphelininae usually lay only one egg inside their host (Mackauer & Chow, 1986). The larva of the parasite feeds inside the aphid, eventually killing the host. The hardened empty shell of the aphid is termed a mummy. The parasite usually pupates inside the host and the adult parasite cuts a hole in the mummy to emerge. Adult Aphidiidae feed on honeydew, while adult Aphelininae engage in host-feeding, and may also feed on honeydew. This is done by wounding the host with their ovipositor.

Many aphid parasites have a narrow host range. Parasitism of aphids in the field may reach up to 80-90%, but is usually much lower. Successful parasitism depends on four processes; (1) location of the host habitat, (2) location of the host, (3) recognition of the host, and (4) attack of the host (Vinson, 1976). Semiochemicals appear to be important in these sequence of events. Honeydew has also been shown to attract, and increase the searching times of, parasitoids (Bouchard & Cloutier, 1984; Budenberg, 1990).

A. gossypii has several known insect parasites (van Steenis, 1993). Mackauer (1968) listed and described the insect parasites of *M. persicae*. An important parasite of *M. persicae* was found to be *Aphidius matricariae* Haliday (Schlinger & Mackauer, 1963). *A. matricariae* is the only aphid parasite that has been commercially developed as a biological control agent against aphid pests on greenhouse vegetable crops.

4.4.2 *Aphidius matricariae* Haliday

Mackauer (1968) has reviewed the biology of *A. matricariae*. The host range of *A. matricariae* consists of 40 different species of aphids in 20 genera (Schlinger & Mackauer, 1963). Schlinger & Mackauer (1963) reported that this parasite was probably accidentally introduced into North America. *A. matricariae* has been found in 19 countries around the world (Giri *et al.*, 1982).

Giri *et al.* (1982) studied various aspects of the biology of *A. matricariae* in detail using *M. persicae* as the host. They found that temperatures between 12.8°C and 21°C were optimal for production of offspring and survival of the parasites during the mummy stage. Emergence of adults from mummies was about 80% between 10° and 21°C, but declined significantly at 24°C and above. Longevity of both male and female adult parasites decreased as temperatures increased. Adult female parasites lived significantly shorter than males at 10°C and 15.6°C. The sex ratio was found to range from 2:3 (males:females) at 12.8°C to 1:3 at 26.7°C, the average being 1:2.

A. matricariae is used commercially in western Europe and Canada for the control of aphids on greenhouse vegetable crops, and is particularly effective against *M. persicae* on sweet pepper (Hussey, 1985; Woets, 1985). Hyperparasitism limits the effectiveness of *A. matricariae* during the summer in British Columbia (Portree, 1993).

4.5 Ways to Enhance Biological Control

Scopes (1970) used regular introductions of chrysanthemum cuttings infested with *M. persicae*, which had been heavily parasitized by *A. matricariae*, to control *M. persicae* on chrysanthemum. Stacey (1977) reported control of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westw.), on tomatoes in a commercial greenhouse by rearing the parasitoid, *E. formosa*, on 'banker plants'. The 'banker plants' were tomato plants infested with the pest, which had been parasitized by *E. formosa*. These were introduced into the greenhouse, and the presence of whiteflies and honeydew on the introduced tomato plants provided a source of food for the parasitoids during the early stages of the infestation. Hofsvang & Hågvar (1979) used a paprika 'banker plant' infested with *M. persicae*, which had been parasitized by *Ephedrus cerasicola* Stary, a parasitoid of *M. persicae*, to control *M. persicae* on paprika in a small greenhouse trial. Bennison & Corless (1993) have renewed interest in the use of 'banker plants' as a way to potentially increase the effectiveness of biological control agents of the melon aphid on greenhouse vegetable crops. The new goal of the recently revived 'old' concept of a 'banker plant' system is the rearing and sustained production of a parasite or predator of a crop pest on a non-pest host in the greenhouse; the non-pest host is reared on a plant other than the crop (Bennison & Corless, 1993).

5. Discussion

5.1 Managing Insecticide Resistance

Croft (1990a) discussed the framework for developing a pesticide resistance management program. According to Croft (1990a), the primary goals of managing pesticide resistance in pest populations are (1) avoid resistance development, (2) decrease the rate of resistance development, and (3) let resistant populations 'revert' to more susceptible levels and keeping resistance at a manageable level. This usually involves a change in pesticide use patterns or the use of biological or cultural controls (Croft, 1990a).

Some of the changes in pesticide use patterns include treating crops only when economic levels of pests are present, varying the dose and reducing the frequency of treatments, using less persistent pesticides, targeting pesticide applications on particular life stages of the pest, and alternating or rotating pesticides (Metcalf, 1980).

Metcalf (1989) has stated that changes in pesticide use patterns needed in resistance management are the basis for integrated pest management (IPM), and expressed concern that the developing field of 'Resistance Management' not be used to foster chemical control of pests. Metcalf (1989) thought resistance management should complement IPM, but pointed out that some workers in this field have encouraged the use of new pesticides with little consideration for biological control.

Understanding the basis for insecticide resistance is important in any pesticide resistance management program (Croft, 1990a). In the

case of *M. persicae*, which appears to have a single mechanism of resistance to a wide spectrum of chemicals, alternating classes of insecticides to control resistant aphids has no real value because each will select the same mechanism (Devonshire & Moore, 1982).

However, since resistance is least to carbamates, the use of this class of insecticide will pose the least selection pressure (Devonshire & Moore, 1982). In countries where carbamates are not registered for use on greenhouse vegetable crops, including the Province of British Columbia, the use of endosulfan, an organochlorine, would be an alternate choice. Insecticide resistance to endosulfan in natural populations of *M. persicae* has not been reported. However, heavy reliance on endosulfan would most likely cause resistance in the future.

Management of insecticide resistance in *A. gossypii* appears somewhat easier than for *M. persicae*. Multiple mechanisms of resistance in *A. gossypii* seem responsible for insecticide resistance to the four major classes of insecticides to control aphids. O'Brien *et al.* (1992) suggested alternating classes of insecticides throughout the growing season to manage resistant field populations of *A. gossypii*. This strategy could be applied to greenhouse conditions, but the problem in the Province of British Columbia is that pyrethroids and carbamates are not registered for use on greenhouse vegetable crops. This leaves only two classes of insecticides for growers in British Columbia to choose from, organochlorines and organophosphorous compounds. Resistance of *A. gossypii* infesting greenhouse vegetable crops in British Columbia to these chemicals is only a matter of time, since resistance to endosulfan and various organophosphorous

compounds has been reported in other parts of the world. These chemicals, though, could be rotated to slow the development of, and manage, resistant populations of *A. gossypii*.

No detailed study on the status of insecticide resistance of aphids infesting greenhouse vegetable crops in the Province of British Columbia has ever been published. However, insecticide resistant aphids have been observed (Anonymous, 1992). In the Province of British Columbia, nicotine and parathion are alternative chemicals to control aphids in general, including those that are resistant to insecticides. One disadvantage of using fumigant insecticides is the detrimental effect on beneficial insects. Systemic organophosphorous compounds might reduce this impact (Hassall, 1990), but none are registered on greenhouse vegetable crops in the Province of British Columbia. Spot applications of available registered contact insecticides (e.g. endosulfan, insecticidal soap) of early aphid infestations should reduce this problem. Rotations of spot applications between endosulfan and insecticidal soap would reduce the selection pressure on aphids, and would likely slow the development of resistance to endosulfan.

Life stages of *A. gossypii* from cotton in California appear to have a differential response to insecticides. Grafton-Cardwell (1991) reported that apterous adults were generally less tolerant than alate nymphs and adults to the organochlorine-, organophosphorous-, and pyrethroid-insecticides tested. Grafton-Cardwell suggested that chemical control should target the more susceptible apterous stage of *A. gossypii*. While this might be good advice for growers of field crops, this is not a good strategy for

greenhouse vegetable growers since initial infestations of aphids are usually alate adults which migrate into greenhouses from outside fields.

Greenhouse vegetable growers relying on chemical control of aphids should try to spray early aphid infestations with a rotation of registered insecticides of different classes as soon as possible after being observed. If the aphids are not resistant to the insecticide being sprayed, this procedure reduces the amount of insecticide used by allowing spot application of the insecticide, and has less of an impact on beneficial insects. Rotation of the chemicals would likely slow the development of resistant aphid populations.

Hollingsworth *et al.* (1994) demonstrated that significant intra-island variation in insecticide resistance existed in Hawaii among field populations of *A. gossypii*. Some of the variation in susceptibility was attributed to local pesticide use, and large differences were found in populations of aphids less than 1 km apart. If this is also true for greenhouse populations of *A. gossypii*, greenhouse vegetable growers may be able to slow resistance development themselves through the prudent, judicious, and reduced use of insecticides (Hollingsworth *et al.*, 1994). Regional management may be necessary if susceptibility varies primarily at the regional level (Hollingsworth *et al.*, 1994).

5.2 Integrated Control

Integrated control is the combination of biological, chemical, and cultural controls to manage a single pest or complex of pests in a particular crop. Until recently, an integrated control program specifically targeted at aphids on greenhouse vegetable crops was not practiced widely by commercial growers. Integrated control with aphids was in the larger context of managing the several pests of greenhouse vegetable crops.

Integrated control programs for greenhouse pests in western Europe have been reviewed by Woets (1985) for tomatoes, and by Hussey (1985) for cucumbers and sweet peppers. In general, insect pests other than aphids have been controlled by biological control agents. Fungal diseases have been managed with selective fungicides. Aphid infestations have usually been sprayed with the selective insecticide, pirimicarb, which has not significantly interfered with the biological control of other greenhouse pests, or natural parasitization of aphids.

On greenhouse tomato and sweet pepper in western Europe, pirimicarb and natural parasitization has kept *M. persicae* under control (Woets, 1985; Hussey, 1985). Recently, the commercial use of *A. aphidimyza* and *A. matricariae* as biological control agents have given good results for control of *M. persicae* on greenhouse tomato and sweet pepper in Denmark (Jensen, 1992). An integrated control program has been developed for aphids on sweet pepper in the Netherlands, which involves the use of *A. aphidimyza*, *Aphidius* spp., pirimicarb, and spot applications of the organophosphorous compound.

heptenophos (van Steekelenburg, 1992). The major problem now for greenhouse vegetable growers in western Europe is how to control pirimicarb-resistant populations of *A. gossypii* on cucumber.

A 'banker plant' system using *A. matricariae* has been suggested as a way to improve the chances of biological control of *A. gossypii* on greenhouse vegetable crops, particularly on cucumber (Bennison & Coorless, 1993). An important question regarding the 'banker plant' system: Is *A. matricariae* an effective biological control agent of the melon aphid? If so, why is the 'banker plant' system necessary? Traditional biological control agents have been successful in achieving seasonal control of other aphid pests. Why not for the melon aphid? In Europe, *Aphidius colemani* Viereck is now being used in the 'banker plant' system instead of *A. matricariae*. Researchers there now admit that initial work with the 'banker plant' system utilizing *A. matricariae* was actually a mixture of *A. matricariae* and *A. colemani* (Jacobson, 1993). After this confusion had been sorted out, van Steenis (1993a) reported success with using *A. colemani* as a biological control agent of the melon aphid on greenhouse cucumbers.

Recent research in western Europe suggests that repeated releases of *A. colemani* may be as effective as using a 'banker plant' system (Jacobson, 1993; van Steenis, 1993a). This would be expected for an effective parasitoid. The economics of each program would determine which control measure will be best for the grower. My personal experience with a 'banker plant' system indicated that this control strategy has several drawbacks (Appendix). Perhaps a better alternative for controlling the melon aphid in British Columbia would be to focus on finding a more effective parasitoid, one not requiring a

'banker plant' system. *A. colemani* is not native to Canada and has never been officially released in this country. If the search for another parasitoid was pursued, parasitoids which have been released previously in, or which are native to, North America should be explored.

The melon aphid has been reported to be a host for at least four parasitoids. These are *A. colemani*, *A. matricariae*, *Lysiphlebus testaceipes* (Cresson), and *Aphelinus asychis* Walker (Carver & Woolcock, 1985; van Steenis, 1993b). To my knowledge, no comparative study has ever been conducted under laboratory or greenhouse conditions to determine which of the four parasitoids may be the most effective biological control agent for the melon aphid. van Steenis tested three parasitoids of the melon aphid under laboratory conditions (van Steenis, 1993b) and came up with the following ranking: *A. colemani* followed by *L. testaceipes*; van Steenis did not consider *A. matricariae* to be an effective parasitoid of the melon aphid.

The parasitoid, *A. asychis*, is a candidate as a biological control agent of the melon aphid. I confirmed that *A. asychis* can be reared from *A. gossypii* (Appendix). Also, I was able to rear this parasitoid from *Rhopalosiphum padi* (L.).

A. asychis is an interesting parasitoid because the adult wasps may cause mortality among host aphids in two ways. One is by directly feeding on the aphids and the other is by parasitizing them. This double cause of mortality may be an important factor in controlling aphids with a rapid rate of increase like the melon aphid. *A. asychis* has been introduced into North America. This parasitoid

was imported into the United States in the late 1950's and 1960's from the Middle East for control of the aphids, *Therioaphis trifolii* (Monell), and *S. graminum*, which are pests of alfalfa (van den Bosch *et al.*, 1964) and small grain crops (Jackson & Eikenbary, 1971), respectively. However, *A. asychis* may not adapt well to the high temperatures in a greenhouse environment. van den Bosch *et al.* (1964) reported that *A. asychis* was relatively most active during the cooler, more humid times of the year in the field in California.

Finally, an important consideration of biological control is whether it is cost effective. How does biological control in greenhouses compare to chemical control in economic terms? van Lenteren (1992) recently reviewed the economics of biological control. The costs of developing a new pesticide is on average US\$50 million and for developing a biological control agent on average US\$2million (van Lenteren, 1992). Cost-benefit ratios of research are 1:30 for biological control compared to 1:5 for chemical control (DeBach, 1964; Tisdell, 1990).

Ramakers (1982) estimated that the cost of chemical control of whitefly in 1980 was twice as expensive as biological control with *E. formosa*. Presently, the cost of biological control of the two-spotted mite, *Tetranychus urticae* Koch, with predatory mites is about half that of chemical control (van Lenteren, 1990). The cost of chemical control of pests on greenhouse tomato and cucumber in the United Kingdom is 3- to 5-times that of biological control (Wardlow, 1992). A biological control program employing different biological control agents on the same greenhouse vegetable crop does not cost more than chemical control (Ramakers, 1992). The business of supplying natural enemies

to greenhouse growers can be significant, and was a US\$20 million industry in the Netherlands in 1990.

5.3 Recommendations and Further Studies

In the Province of British Columbia, greenhouse vegetable growers are in a more difficult position than their European counterparts when it comes to controlling *M. persicae*. Pirimicarb is not registered and endosulfan is only registered for use on tomato and cucumber. Spot applications of registered chemicals, such as diazinon or malathion might be helpful, but use of *A. aphidimyza* and *A. matricariae* would be my recommendation to control *M. persicae* on sweet pepper. Spot applications of endosulfan in rotation with insecticidal soap of early aphid infestations would be my recommendation for control of *M. persicae* on tomato and *A. gossypii* on cucumber. After plants are established, *A. aphidimyza* and *A. matricariae*, might prove useful in the control of *M. persicae* on tomato. At this time, biological control agents do not appear to be effective against *A. gossypii* on greenhouse cucumber, but I would recommend *A. aphidimyza* over *A. matricariae* for those wishing to try.

I think the following should be given consideration for future study on the control of aphids on greenhouse vegetable crops:

(1) Very little information is available on economic thresholds of aphids on greenhouse vegetable crops. Lipa (1985) reported that the economic threshold of *A. gossypii* on greenhouse cucumber in the former Soviet Union was 1000 aphids per plant. Hussey (1985) stated that greater than 7 aphids per square centimeter of leaf area would

result in a decline of yield in cucumber caused by *A. gossypii*. Quaglia *et al.* (1993) found in Italy that greenhouse tomato plants infested with *M. persicae*, which were not sprayed, did not differ significantly in fruit production as compared to the tomato plants which were sprayed. The aphid population on the unsprayed tomato plants reached a density of about 100 aphids per plant in one variety that was tested before declining on its own naturally.

The study by Quaglia *et al.* (1993) raises an interesting question. Do aphid infestations need to be automatically sprayed by growers? I think greenhouse vegetable growers would benefit from knowing the economic threshold of aphid pests on the commonly grown commercial cultivars at different stages of growth.

(2) Another important question which follows from (1) is whether the incidence of plant virus diseases differs under greenhouse conditions as compared to field situations. If the incidence or severity of virus diseases does not differ between greenhouse and field conditions, then a grower would not likely allow an infestation of aphids to increase out of fear that the aphids would transmit a virus disease to the crop.

(3) Future work should concentrate on finding a way to control *A. gossypii* on greenhouse cucumber. The search for effective biological control agents should continue. In western Europe, *A. colemani* appears promising (van Steenis, 1993b), but more research is necessary before commercial use can be recommended. In Canada, where *A. colemani* is not native and has never been officially released, *A. asychis* is a candidate biological control agent.

The promising results obtained by Chambers (1986) suggests that the use of syrphid flies as a potential biological control agent of the

melon aphid should be further explored. This potential biological control agent may be useful to control the melon aphid (or other aphids) on tomato or sweet pepper, but would probably not be useful for control of *A. gossypii* on cucumber because of the lack of pollen of cultivars used under greenhouse conditions (van Steekelenburg, 1992). (4) Breeding for plant resistance takes many years (Wardlow & O'Neil, 1992), but resistant greenhouse tomato cultivars are available against nematodes and *Fusarium*. This might be an avenue to pursue for cucumber and *A. gossypii*. Weathersbee and Hardee (1994) found that melon aphid densities in the field were lower on cotton cultivars having a smooth-leaf characteristic. However, other workers have obtained different results (Weathersbee & Hardee, 1994). Changing the leaf structure or hairiness of leaves might also affect beneficial insects, such as negatively (more hairs) (Price *et al.*, 1980) or positively (less hairs) (Li *et al.*, 1987) impacting the search efficiency for prey.

(5) Finally, in the general area of arthropod pest management on greenhouse vegetable crops, the relative abundance of spiders in greenhouse vegetable operations (Appendix) needs to be acknowledged. Further study is necessary to determine the role and importance spiders play in the natural biological control of arthropod pests on greenhouse vegetable crops.

Appendix

Experiment Using a 'Banker Plant' System for the Biological Control of *Aphis gossypii* Glover on Greenhouse Cucumbers in British Columbia

Introduction

The melon or cotton aphid, *Aphis gossypii* Glover, has recently become a pest on greenhouse vegetable crops in the Province of British Columbia. Serious crop damage has occurred on cucumbers and sweet peppers (*personal communication*, J. Portree). The melon aphid has also been found in British Columbia on a variety of ornamental horticulture, landscape, and floriculture crops (Forbes & Chan, 1989).

The melon aphid poses a problem for greenhouse vegetable growers in British Columbia. Firstly, the choice of insecticides to control this aphid is limited because few chemicals are registered in British Columbia for the control of aphids on greenhouse vegetable crops. Secondly, the melon aphid becoming resistant to the available, registered insecticides in British Columbia is a real possibility. Thirdly, broad spectrum pesticides are usually needed to control the melon aphid (van Schelt *et al.*, 1990). Many greenhouse vegetable growers in British Columbia have a biological control program already in place to manage other traditional greenhouse pests such as mites, whiteflies, thrips, caterpillars, fungus gnats, and another aphid pest, *Myzus persicae* (Sulzer). This practice would be upset by the use of such chemicals.

One answer to the problem of the melon aphid faced by greenhouse vegetable growers in British Columbia would be to find and use an effective biological control agent. The biological control agents, *Aphidius matricariae* Haliday and *Aphidoletes aphidimyza* Rondani, even when used together, have not been successful in the biological control of the melon aphid (Bennison & Corless, 1993). The use of 'banker plants' has received recent attention as an aid in the biological control of *A. gossypii* (Bennison & Corless, 1993). The purpose of this experiment was to evaluate the potential of 'banker plants' for the biological control of the melon aphid on greenhouse cucumbers in the Province of British Columbia.

Materials and Methods

Aphid colonies. The melon aphid used in this study was obtained from C. K. Chan, Agriculture Canada, Vancouver, B.C. This melon aphid was originally collected from greenhouse cucumber in B.C. and had been reared under laboratory conditions for 2-3 years. The cereal aphid, *Rhopalosiphum padi* (L.) clone 'C7', was supplied by Dr. M. Smith, University of Winnipeg, Winnipeg, M.B. This clone was collected from a field of canaryseed a few miles northwest of Winnipeg in July 1989, and had been continuously reared on barley. In this study, colonies of *A. gossypii* and *R. padi*, were reared in cages under laboratory conditions on cucumber and wheat, respectively, with 12 h supplemental light provided by four 40 w fluorescent light bulbs. The temperature and relative humidity ranged from 20-33°C and 20-44%, respectively, while rearing the aphids before use in this study.

Greenhouse Study

Greenhouse experiments were set up at the B.C. Ministry of Agriculture, Fisheries, and Food in Abbotsford, B.C. A 100 meter square greenhouse was divided into two sections by a fine-screen material. In each section, 56 Long English Cucumber plants at the 4- to 6-true leaf stage were transplanted into bags containing sawdust. The cucumber varieties 'Flamingo' and 'Mustang' were used in Trial 1, the variety 'Flamingo' in Trial 2. Standard commercial greenhouse hydroponic and cultural practices were followed (Portree, 1993). Once established, cucumber plants were pruned and trained 3- to 4-times per week.

Banker plant system. Powdery mildew-resistant wheat infested with the cereal aphid, *R. padi*, was chosen as the 'banker plant' system. The parasitoid used was *A. matricariae*. This parasitoid was chosen because of the difficulties in obtaining specimens of *Aphidius colemani* Viereck. Powdery mildew-resistant wheat variety 'AW 229' was obtained from Dr. D. Gillespie, Agriculture Canada, Agassis, B.C. and used throughout the course of this study. The parasitoid, *A. matricariae*, was supplied by the commercial biological supply company, Applied Bionomics, Sydney, B.C.

The banker plant system was set up two days prior to the introduction of the melon aphid. Wheat was grown in plastic pots (13 cm in diameter, 12 cm tall) with a garden mix soil. Wheat seedlings at the two to four leaf blade stage (approximately 14 days old) were infested with *R. padi*. Aphid density was estimated by counting the number of aphids from five randomly selected seedlings from each

pot. The pots of wheat were placed in a cage in an effort to reduce hyperparasitism. Initially, 30 female and three male *A. matricariae* were introduced into the cage with two pots of aphid infested wheat. After 24 h the cage was opened. The cage was closed 24 h later. The banker plant system was supplemented with fresh wheat plants or wheat plants infested with *R. padi*, or *A. matricariae*, as needed. The goal for the banker plants was to keep the system self-perpetuating without the need for supplementation of *R. padi* and *A. matricariae*.

Wheat plants were hand watered at least every other day with tap water. Aphid mummies were counted and either gently scraped off the blade of wheat, or the blade of wheat was cut around the mummy and transferred to a wax paper cup (9 cm in diameter, 6 cm tall) and placed into the cage. The sex ratio of the adult parasitoids was estimated by collecting a random sample of 20 mummies, placing them in a wax paper cup with plastic lid (9 cm in diameter), and allowing adult wasps to emerge.

Infestation of cucumber plants with melon aphid. Fourteen plants in each greenhouse section were artificially infested with melon aphid when plants were about 2 m tall and being trained along a horizontal steel wire. Plants to be infested were chosen by a random number generator produced by the computer program Minitab. Five third- to fourth-instar nymphs of the melon aphid were individually transferred to one cucumber leaf disc. Transfers were made with a camel hair brush dipped in distilled water. Before transfer, leaf discs were placed bottom side up on a small piece of glass wool covered with distilled water on the bottom of a 8.5 cm plastic petri dish. This

method confined aphids to the leaf disc before being transferred to cucumber plants in the greenhouse.

Five leaf discs were prepared, then one leaf disc was placed with a forceps on the fully expanded leaf nearest to the training wire on each plant. The leaf was then tagged with flag tape to indicate the leaf and plant infested. Time to prepare five leaf discs and transfer all of them to plants was approximately 30 minutes.

Estimation of aphid nymph survival after transfer was made by preparing leaf discs with aphids and transferring to caged cucumber plants potted in a garden mix soil. After transfer, plants were grown under laboratory conditions at room temperature. The number of live nymphs on each leaf were counted after 24 h.

Monitoring the population of melon aphid. The melon aphid population was monitored in two ways. All plants were inspected over time and the presence or absence of aphids noted. This was to determine the spread of aphids throughout the greenhouse. The number of leaves infested with aphids and the number of aphids per leaf were also counted on five selected artificially infested plants in each section.

Pest management. Visual inspection of plants and yellow sticky traps were used to monitor other greenhouse pests. Commercially available biological control agents were used for control where possible. These included *Encarsia formosa* Gahan for whitefly and the predatory mites *Amblyseius cucumeris* (Oudemans) for thrips, and *Hypoaspis miles* for fungus gnats. Spot applications of insecticidal soap (Safer's) were used occasionally to control an early aphid infestation in Trial 1 and a late two-spotted spider mite infestation in Trial 2. Endosulfan (Thiodan)

was applied as a spray to leaves of all plants in the first week of Trial 2 to control thrips. Physical control was used to manage lepidopteran pests; larvae were picked by hand and destroyed.

Natural enemy observations. Cucumber plants were inspected weekly during the day to observe the presence of natural enemies.

Observations were also made during routine maintenance of the cucumber plants.

Laboratory Study

Commercial infestations of melon aphid. Melon aphid was collected from commercial greenhouse tomato, sweet pepper, and lily at different times during this study. Identification of melon aphids was made by Dr. B. Costello, B.C. Ministry of Agriculture, Fisheries, and Food, Cloverdale, B.C. (tomato), J. Lee (sweet pepper), and C. K. Chan, Agriculture Canada, Vancouver, B.C. (lily). Plant samples infested with aphids were placed in plastic bags and brought back to the laboratory where the aphids were transferred to leaves of cucumber plants (variety 'Straight Eight'), which were potted in a garden mix soil. Plants were put in a cage and reared at room temperature.

Rearing of parasitoids. Combinations of aphid and parasitoid tried were *A. gossypii* and *R. padi* with *A. matricariae*, and *A. gossypii* with *Lysiphlebus testaceipes* (Cresson). Two to three hundred mixed instars of *A. gossypii* or *R. padi* were placed in a wax paper cup with a plastic lid with pieces of leaf tissue the aphids were reared on. Five female parasitoids were introduced into each cup and allowed access to the aphids for 3.5-4.5 h. Parasitoids were removed from the cup and aphids transferred to and reared on their respective host plants at

room temperature. Host plants were cucumber (variety 'Straight Eight') for *A. gossypii* and wheat for *R. padi*.

A different procedure was used for the parasitoid *Aphelinus asychis* Walker. A separate room, where *A. asychis* has been continuously reared on *Acyrtosiphon pisum* (Harris) for many years, was made available at Simon Fraser University, Burnaby, B.C. A pot of three cucumber plants or a pot of wheat infested with mixed instars of *A. gossypii* or *R. padi*, respectively, was placed in a cage, then 15 female parasitoids of *A. asychis* were introduced into the same cage. The room was supplied with continuous lighting and maintained at a temperature of $20^{\circ}\text{C}\pm 2^{\circ}\text{C}$.

Results

Greenhouse study

Both attempts at establishing a 'banker plant' system failed. Trial 1 resulted in a poor stand of cucumber plants. This was thought to be a result of a combination of several factors including high populations of thrips despite standard commercial biological control practices, boron deficiency in the hydroponic feeding solution, moderate to heavy powdery mildew infection of most plants, and heat stress caused by periods of several hot summer days. This trial was terminated at the end of August 1993. However, before pulling the plants, a trial run of the introduction of the melon aphid and setting up of the banker plant system was tried, and the logistics of both operations went well.

A new cucumber crop was planted on 30 August 1993. Estimation of aphid nymph survival in the laboratory after 24 h using the leaf disc transfer method ranged between 88% and 96%, the mean being 93% (n=5). Initial aphid density of the banker plant system before the addition of *A. matricariae* was a mean of 22.5 aphids/wheat seedling (n=10). A large number of *A. matricariae* can be produced with the banker plant system. In the first round of the banker plant system with approximately 1868 cereal aphids infesting 83 wheat seedlings, 30 female *A. matricariae* produced approximately 379 female offspring. The sex ratio was 7 females to 3 males. After addition of *A. matricariae* to the banker plant system, mummies formed about 10-12 days later. Problems encountered with self-perpetuation of the banker plant system included difficulty regulating cereal aphid densities on the wheat seedlings, large numbers of cereal aphids becoming alates and leaving the wheat plants, and later on lack of mummy formation in the cereal aphids even with *A. matricariae* present in the cage.

In the second trial, the melon aphid population increased over several weeks, before starting to decline. The melon aphid spread to only a few non-artificially infested plants in both sections. Soon after the decline of the melon aphid population, grayish black and swollen aphids were seen on the leaves of plants. However, this phenomenon also occurred in the control section of the greenhouse where the banker plant system was not present, and no release of *A. matricariae* had taken place. Few mummies of the melon aphid were observed in either section of the greenhouse. Of the mummies observed, most were 3rd-4th instars. A sample of aphids was collected, brought back

to the laboratory and dissected. No larva of any parasitoid was found. Squash mounts of aphids were made and looked at under a compound microscope to check for evidence of pathogens. No signs of a fungal pathogen were present. Samples of aphids were given to Dr. M. Goettel, insect pathologist at Agriculture Canada, Lethbridge, Alberta. He did not find any signs of a fungal pathogen.

Spiders were by far the most numerous predators observed in both trials. Many different species of spiders were seen and consisted of both web-builders and hunters. However, the assemblage of spiders present appeared dominated by only a few species and the complex seemed to change over time. Other predators included one syrphid and three coccinellid beetles. Many *Orius* sp. were seen toward the end of Trial 2 when the thrips population was very high.

Laboratory Study

Melon aphids collected from commercial lily, but not from commercial tomato and sweet pepper, were successfully reared on cucumber. All the melon aphids collected from tomato and lily were black, while all the melon aphids collected from sweet pepper were grey in colour.

A very small parasitoid, possibly an *Aphelinus* sp., emerged from the melon aphid collected from commercial lily. Unfortunately, sufficient numbers of the parasitoid could not be continuously reared for identification purposes.

The rearing of *L. testaceipes* from *A. gossypii* was not successful. The rearing of *A. asychis* from *A. gossypii* and *R. padi* was successful. *A. asychis* was reared on the melon aphid for several months.

Discussion

In trial 2 the decrease in the melon aphid population could not be attributed to the release of the parasitoid, *A. matricariae*. Thus, the impact of the banker plant system on the biological control of the melon aphid could not be assessed. There are at least four possibilities for the cause of the decline observed for the melon aphid in this study:

- 1) some type of pathogen
- 2) chronic toxicity to some type of chemical
- 3) host or nutritional effect
- 4) changes in environmental conditions (e.g. temperature, day length)

A large number of *A. matricariae* can potentially be produced in the banker plant system. Even so, results indicated that this parasitoid did not become established under the greenhouse conditions tested. The parasitoid may not have found established colonies of the melon aphid, the adult wasps may have died shortly after release, or may have escaped out of the unscreened vents in the ceiling of the greenhouse.

The longevity of wheat plants was short. There are several possible explanations. Wheat, in general, may not have grown well under the conditions of the study, or the particular variety of wheat

used was not adapted well to greenhouse conditions. This may possibly be overcome by using another variety of wheat or cereal such as barley, or another crop as the banker plant. The problem with the latter is in finding a suitable aphid species and parasitoid. Also, high aphid densities may have contributed to the short life-span of the wheat plants.

Self-perpetuation of the banker plant system was difficult. A continuous supply of new wheat plants already infested with cereal aphids appears necessary to keep the system going. Regulation of the cereal aphid population on the wheat seedlings was also difficult. A high aphid density appears stressful to the wheat plants. An aphid density of 10-15 aphids/seedling appears best. Supplemental lighting may prove useful in the reduction of cereal aphids leaving the wheat seedlings. One positive note about the wheat variety used in this study was the absence of powdery mildew, which can be a problem when growing cereals under greenhouse conditions.

While conducting this study, I found little information about the melon aphid in British Columbia. Simple, basic but important questions remain unanswered. What is the source of the melon aphid? Does the melon aphid migrate into the province by wind currents from the U.S.A.? or Is the melon aphid established in British Columbia? Does the melon aphid overwinter in the province? If so, how and where? Are there different strains of the melon aphid present in British Columbia? Preliminary results from this study suggest that different strains of *A. gossypii* exist in the province. Melon aphid collected from commercial tomato and sweet pepper did not reproduce

on cucumber, but aphids collected from commercial lily, identified as *A. gossypii*, were reared successfully on cucumber.

If confirmed, the presence of strains of the melon aphid in British Columbia may have important implications for greenhouse vegetable growers. Should the cucumber grower worry about the melon aphid infestation of greenhouse tomatoes of his neighbor down the road? Can commercial lily be an alternate host for the melon aphid infesting cucumber? Many growers live in close proximity to each other. How far can the melon aphid spread? Answers to the above questions are important. Basic knowledge about the melon aphid in British Columbia is lacking, and this information would be useful in efforts to control this pest.

In this study, *L. testaceipes* was not successfully reared from the melon aphid under laboratory conditions. However, *A. asychis* was successfully reared from *A. gossypii* and *R. padi*. Other reported aphid hosts successfully parasitized by *A. asychis* include *M. persicae* on pepper and *Macrosiphum euphorbiae* (Thomas) on apple (Carver & Woolcock, 1985).

Conclusions

In summary the following conclusions can be drawn from this study:

-- If conditions do not change, the melon aphid will continue to be a pest on greenhouse vegetable crops in the Province of British Columbia.

- Basic information about *A. gossypii* in the Province of British Columbia is lacking.
- The banker plant system for the control of the melon aphid needs further investigation before being recommended to commercial greenhouse cucumber growers in the Province of British Columbia.
- The parasitoid, *A. asychis*, appears to be a potential candidate as a biological control agent of the melon aphid.
- Further research is needed to determine if *A. asychis* would be effective as a biological control agent of the melon aphid on cucumbers under greenhouse conditions in the Province of British Columbia.
- The role of spiders in the regulation of arthropod pests on greenhouse vegetable crops needs further study.

Literature Cited

Agrios, G. N. 1988. *Plant Pathology*. 3rd Edition. Academic Press, San Diego. 803 pp.

Agrios, G. N. 1990. Economic considerations. In: *Plant Viruses* (C. L. Mandahar, ed.). Volume II. CRC Press, Boca Raton, Florida. pp. 1-22.

Allen, M. A. and B. V. Ball. 1986. Properties of a virus pathogenic in the aphid *Sitobion avenae*. In: *Proceedings of Applied Biology..... Pathways Forward*. Residential Meeting, Association of Applied Biologists, University of Warwick, 29 September - 1 October 1986.

Anthon, E. W. 1955. Evidence for green peach aphid resistance to organophosphorous insecticides. *J. Econ. Entomol.* 48: 56-57.

Anonymous. 1990. *Handbook for Pesticide Applicators and Dispensers*. 5th edition. Province of British Columbia, Ministry of Environment, Pesticide Control Branch. Victoria, British Columbia. 253 pp.

Anonymous. 1991. *Vegetable Production Guide for Commercial Growers*. Province of British Columbia, Ministry of Agriculture, Fisheries, and Food. Victoria, British Columbia. 134 pp.

Anonymous. 1992. *Integrated Control of Greenhouse Pests for Commercial Growers*. Province of British Columbia, Ministry of Agriculture, Fisheries, and Food. Victoria, British Columbia. 19 pp.

Anonymous. 1993. *Annual Statistics 1991*. Province of British Columbia, Ministry of Agriculture, Fisheries, and Food. Victoria, British Columbia. 131 tables.

Anonymous. 1994. *Fruit and Vegetable Production*. Catalogue 22-003, February 1994. Statistics Canada, Agriculture Division, Horticulture Crops Unit. Ottawa, Ontario. 28 pp.

Barlow, C. A. 1961. On the biology and reproductive capacity of *Syrphus corollae* Fab. in the laboratory. *Entomol. Exp. Appl.* 4: 91-100.

Bartlett, B. R. 1964. Toxicity of some pesticides to eggs, larvae and adults of the green lacewing *Chrysopa carnea*. *J. Econ. Entomol.* 57: 366-369.

Bennison, J. A. and S. P. Corless. 1993. Biological control of aphids on cucumbers: Further development of open rearing units or 'banker plants' to aid establishment of aphid natural enemies. *SROP/WPRS Bulletin XVI/2*: 5-8.

Bigler, F. 1984. Biological control by chrysopids: Integration with pesticides. In: *Biology of Chrysopidae* (M. Canard, Y. Séméria, and T. R. New, eds.). Dr. W. Junk, The Hague, The Netherlands. pp. 233-245.

Blackman, R. L., and V. F. Eastop. 1984. *Aphids on the World's Crops: An Identification and Information Guide*. John Wiley & Sons, New York. 466 pp.

Borror, D. J., D. M. DeLong, C. A. Triplehorn. 1981. *An Introduction to the Study of Insects*. 4th edition. Holt, Rhinehart, and Winston, New York. 827 pp.

Bouchard, Y. and C. Cloutier. 1984. Honeydew as a source of host-searching kairomones for the aphid parasitoid *Aphidius nigripes* (Hymenoptera: Aphidiidae). *Can. J. Zool.* 62: 1513-1520.

Bouchard, D., J. C. Tourner, R. O. Paradis. 1981. Bio-ecologie d'*Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) prédatens du puceron du pommier, *Aphis pomi* DeGeer (Homoptera; Aphididae). *Ann. Ent. Soc. Quebec* 26: 119-130.

Boyce, A. M. 1928. Studies on the resistance of certain insects to hydrocyanic acid. *J. Econ. Entomol.* 21: 715-720.

Budenberg, W. J. 1990. Honeydew as a contact kairomone for aphid parasitoids. *Entomol. Exp. Appl.* 55: 139-148.

Budenberg, W. J. and W. Powell. 1992. The role of honeydew as an ovipositional stimulant for two species of syrphids. *Entomol. Exp. Appl.* 64: 57-61.

Campbell, R. K. and R. D. Eikenbary (eds.). 1990. *Aphid - Plant Genotype Interactions*. Elsevier, Amsterdam. 378 pp.

- Canard, M., Y. Séméria, and T. R. New (eds.). 1984. *Biology of Chrysopidae*. Dr. W. Junk, The Hague, The Netherlands. 294 pp.
- Carver, M. and L. T. Woolcock. 1985. Interactions between *Acyrtosiphon kondoi* [Homoptera: Aphidoidea] and *Aphelinus asychis* [Hymenoptera: Chalcidoidea] and other parasites and hosts. *Entomophaga* 30: 193-198.
- Chambers, R. J. 1986. Preliminary experiments on the potential of hoverflies [Dipt.: Syrphidae] for the control of aphids under glass. *Entomophaga* 31: 197-204.
- Chambers, R. J. 1988. Syrphidae. In: *World Crop Pests - Aphids: Their Biology, Natural Enemies and Control* (A. K. Minks and P. Harrewijn, eds.). Volume 2B. Elsevier, The Netherlands. pp. 259-270.
- Chambers, R. J. and T. H. L. Adams. 1986. Quantification of the impact of hoverflies (Diptera: Syrphidae) on cereal aphids in winter wheat: Analysis of field populations. *J. Appl. Ecology* 23: 895-904.
- Chambers, R. J., K. D. Sunderland, I. J. Wyatt, and G. P. Vickerman. 1983. The effects of predator exclusion and caging on cereal aphids in winter wheat. *J. Appl. Ecol.* 20: 209-224.
- Chambers, R. J. 1990. The use of *Aphidoletes aphidimyza* for aphid control under glass. *SROP/WPRS Bulletin XIII/5*: 51-54.
- Chandler, A. E. F. 1968a. Some host-plant factors affecting oviposition by aphidophagous Syrphidae (Diptera). *Ann. Appl. Biol.* 61: 415-423.
- Chandler, A. E. F. 1968b. The relationship between aphid infestations and oviposition by aphidophagous Syrphidae (Diptera). *Ann. Appl. Biol.* 61: 425-434.
- Chiverton, P. A. 1986. Predator density manipulation and its effects on populations of *Rhopalosiphum padi* (Hom.: Aphididae) in spring barley. *Ann. Appl. Biol.* 109: 49-60.
- Cowgill, S. E., S. D. Wratten, and N. W. Sotherton. 1993. The selective use of floral resources by the hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) on farmland. *Ann. Appl. Biol.* 122: 223-231.

Croft, B. A. 1990a. Developing a philosophy and program of pesticide resistance management. In: *Pesticide Resistance in Arthropods* (R. T. Roush and B. E. Tabashnik, eds.). Chapman and Hall, London. pp. 277-296.

Croft, B. A. 1990b. *Arthropod Biological Control Agents and Pesticides*. John Wiley & Sons, New York. 723 pp.

D'Arcy, C. J., P. A. Burnett, A. D. Hewings, and R. M. Goodman. 1981a. Purification and characterization of a virus from the aphid *Rhopalosiphum padi*. *Virology* 112: 345-349.

D'Arcy, C. J., P. A. Burnett, and A.D. Hewings. 1981b. Detection, biological effects, and transmission of a virus of the aphid *Rhopalosiphum padi*. *Virology* 114: 268-272.

DeBach, P. (ed.). 1964. *Biological Control of Insect Pests and Weeds*. Chapman and Hall, London. 844 pp.

DeBach, P. 1974. *Biological Control by Natural Enemies*. Cambridge University Press, London. 323 pp.

DeBarro, P. J. 1992. The impact of spiders and high temperatures on cereal aphid (*Rhopalosiphum padi*) numbers in an irrigated perennial grass pasture in South Australia. *Ann. Appl. Biol.* 121: 19-26.

Devonshire, A. L. 1977. The properties of a carboxylesterase from the peach-potato aphid, *Myzus persicae* (Sulz.), and its role in conferring insecticide resistance. *Biochemical Journal* 167: 675-683.

Devonshire, A. L. 1989. Insecticide resistance in *Myzus persicae*: From field to gene and back again. *Pestic. Sci.* 26: 375-382.

Devonshire, A. L. and G. D. Moore. 1982. A carboxylesterase with broad substrate specificity causes organophosphorous, carbamate and pyrethroid resistance in peach-potato aphids (*Myzus persicae*). *Pestic. Biochem. Physiol.* 18: 235-246.

Dixon, A. F. G. 1985a. *Aphid Ecology*. Blackie, London. 157 pp.

Dixon, A. F. G. 1985b. Structure of aphid populations. *Ann. Rev. Entomol.* 30: 155-174.

- Domsch, K. H., W. Gams, and T. Anderson. 1980. *Compendium of Soil Fungi*. Volumes I and II. Academic Press, London. 859 and 405 pp.
- Eastop, V. F. 1983. The biology of the principal aphid virus vectors. In: *Plant Virus Epidemiology - The Spread and Control of Insect-Borne Viruses* (R. T. Plumb and J. M. Thresh, eds.). Blackwell Scientific Publications, London. pp. 115-132.
- Ekbom, B. S. 1979. Investigations on the potential of a parasitic fungus (*Verticillium lecanii*) for the control of greenhouse whitefly (*Trialeurodes vaporariorum*). Swed. J. Agri. Res. 9: 129-138.
- El Titi, A. 1972. Die Verteilung der Eier von *Aphidoletes aphidimyza* (Rond.) und ihre Bedeutung für den Einsatz unter Glas. Diss. Univ. Göttingen. 80 pp.
- El Titi, A. 1974. Zur Auslösung der Eiablage bei der aphidophagen Gallmücke *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). Entomol. Exp. Appl. 17: 9-21.
- Entwistle, J. C. and A. F. G. Dixon. 1989. The effect of augmenting grain aphid numbers in a field of winter wheat in spring on the aphid's abundance in summer and its relevance to the forecasting of outbreaks. Ann. Appl. Biol. 114: 397-408.
- Ferron, P. 1978. Biological control of insect pests by entomogenous fungi. Ann. Rev. Entomol. 23: 409-442.
- Field, L. M., A. L. Devonshire, and B. G. Forde. 1988. Molecular evidence that insecticide resistance in peach-potato aphids (*Myzus persicae* Sulz.) results from amplification of an esterase gene. Biochemical Journal 251: 309-312.
- Footitt, R. G. and W. R. Richards. 1993. *The Insects and Arachnids of Canada. Part 22 - The Genera of the Aphids of Canada: Homoptera: Aphidoidea and Phylloxeroidea*. Research Branch, Agriculture Canada, Publication 1885, Centre for Land and Biological Resources Research, Ottawa, Ontario, Canada. 766 pp.
- Fraser, B. D. 1988a. Predators. In: *World Crop Pests - Aphids: Their Biology, Natural Enemies and Control* (A. K. Minks and P. Harrewijn, eds.). Volume 2B. Elsevier, The Netherlands. pp. 217-230.

- Fraser, B. D. 1988b. Coccinellidae. In: *World Crop Pests - Aphids: Their Biology, Natural Enemies and Control* (A. K. Minks and P. Harrewijn, eds.). Volume 2B. Elsevier, The Netherlands. pp. 231-247.
- Fraival, A. and H. Lapierre. 1970. Isolément à partir de graminées et de pucerons (Homoptera: Aphididae) d'un virus à RNA. C. R. Acad. Sci. Paris 270: 890-893.
- Furk, C., D. F. Powell, and S. Heyd. 1980. Pirimicarb resistance in the melon and cotton aphid, *Aphis gossypii* Glover. Plant Pathology 29: 191-196.
- Furk, C., and H. Roberts. 1985. Baseline responses of United Kingdom field populations of *Macrosiphum euphorbiae* (Thomas) and *Brevicoryne brassicae* (L.) (Hemiptera: Aphididae) to demeton-S-methyl. Bull. Entomol. Res. 75: 65-71.
- Furk, C. and S. Vedhi. 1990. Organophosphorous resistance in *Aphis gossypii* (Hemiptera: Aphididae) on chrysanthemum in the UK. Ann. Appl. Biol. 116: 557-561.
- Furk, C. and C. M. Hines. 1993. Aspects of insecticide resistance in the melon and cotton aphid, *Aphis gossypii* (Hemiptera: Aphididae). Ann. Appl. Biol. 123: 9-17.
- Georghiou, G. P. and T. Saito (eds.). 1983. *Pest Resistance to Pesticides*. Plenum Press, New York. 809 pp.
- Georghiou, G. P. and A. Lagunes-Tejeda. 1991. *The Occurrence of Resistance to Pesticides in Arthropods*. FAO of United Nations, Rome. Publication PGPP/Misc/91-1. 318 pp.
- Ghong, K., G. Zhang, and G. Zhai. 1964. Resistance of cotton aphids to demeton. Journal of Entomology 13: 1.
- Gilkeson, L. A. 1987. A note on the fecundity of the aphid predator, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae). Can. Entomol. 118: 1145-1146.
- Gilkeson, L. A. and S. B. Hill. 1986a. Diapause prevention in *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) by low intensity light. Environ. Entomol. 15: 1067-1069.

- Gilkeson, L. A. and S. B. Hill. 1986b. Genetic selection for and evaluation of nondiapause lines of predatory midge, *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae). *Can. Entomol.* 118: 869-879.
- Gilkeson, L. A. and S. B. Hill. 1987. Release rates for control of green peach aphid (Homoptera: Aphididae) by the predatory midge *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae) under winter greenhouse conditions. *J. Econ. Entomol.* 80: 147-150.
- Gilkeson, L. A. 1990. Cold storage of the predatory midge *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae). *J. Econ. Entomol.* 83: 965-970.
- Giri, M. K., B. C. Pass, K. V. Yeagan, and J. C. Parr. 1982. Behavior, net reproduction, longevity, and mummy-stage survival of *Aphidius matricariae* [Hym. Aphidiidae]. *Entomophaga* 27: 147-153.
- Grafton-Cardwell, E. E. 1991. Geographical and temporal variation in response to insecticides in various life stages of *Aphis gossypii* (Homoptera: Aphididae) infesting cotton in California. *J. Econ. Entomol.* 84: 741-749.
- Grafton-Cardwell, E. E. and M. A. Hoy. 1985. Intraspecific variability in response to pesticides in the common green lacewing *Chrysoperla carnea* (Stephens). *Hilgardia* 53: 1-32.
- Gubran, E. M. E., R. Delorme, D. Auge, and J. P. Moreau. 1992. Insecticide resistance in cotton aphid *Aphis gossypii* (Glov.) in the Sudan Gezira. *Pestic. Sci.* 35: 101-107.
- Gurney, B. and N. W. Hussey. 1970. Evaluation of some coccinellid species for the biological control of aphids in protected cropping. *Ann. Appl. Biol.* 65: 451-458.
- Gustafsson, M. 1971. Microbial control of aphids and scale insects. In: *Microbial Control of Insects and Mites* (H. D. Burgess and N. W. Hussey, eds.). Academic Press, London. pp. 375-384.
- Hagen, K. S. 1962. Biology and ecology of predaceous Coccinellidae. *Ann. Rev. Entomol.* 7: 289-326.
- Hagen, K. S. and R. van den Bosch. 1968. Impact of pathogens, parasites, and predators on aphids. *Ann. Rev. Entomol.* 13: 325-384.

- Hall, R. A. 1981. The fungus *Verticillium lecanii*, as a microbial insecticide against aphids and scales. In: *Microbial Control of Pests and Plant Diseases 1970-1980* (H. D. Burges, ed.). Academic Press, London. pp. 483-498.
- Hall, R. A. 1985. Aphid control by fungi. In: *Biological Pest Control-The Glasshouse Experience* (N. W. Hussey and N. Scopes, eds.). Blandford Press, Dorset, U.K. pp. 138-141.
- Hall, R. A. and H. D. Burges. 1979. Control of aphids in glasshouses with the fungus, *Verticillium lecanii*. *Ann. Appl. Biol.* 93: 235-246.
- Harper, A. M. and H. C. Huang. 1986. Evaluation of the entomophagous fungus *Verticillium lecanii* (Moniliales: Moniliaceae) as a control agent for insects. *Environ. Entomol.* 15: 281-284.
- Harris, K. F. 1981. Arthropod and nematode vectors of plant viruses. *Ann. Rev. Phytopathol.* 19: 391-426.
- Harris, K. F. 1990. Aphid transmission of plant viruses. In: *Plant Viruses* (C. L. Mandahar, ed.). Volume II. CRC Press, Boca Raton, Florida. pp. 177-204.
- Harris, K. F. and K. Maramorosch (eds.). 1977. *Aphids as Virus Vectors*. Academic Press, New York. 559 pp.
- Harris, K. M. 1973. Aphidophagous Cecidomyiidae (Diptera): taxonomy, biology and assessments of field populations. *Bull. Entomol. Res.* 63: 305-325.
- Haslett, J. R. 1989. Interpreting patterns of resource utilisation: Randomness and selectivity in pollen feeding by adult hoverflies. *Oecologia* 78: 433-442.
- Hassall, K. A. 1990. *The Biochemistry and Uses of Pesticides*. 2nd edition. MacMillan Press, Ltd., London. 536 pp.
- Helyer, N. L. and L. R. Wardlow. 1987. Aphid control on chrysanthemum using frequent, low dose applications of *Verticillium lecanii*. *SROP/WPRS Bulletin X/2*: 62-65.

- Hodek, I (ed.). 1966. *Ecology of Aphidophagous Insects*. Dr. W. Junk, The Hague and Academia Press, Czechoslovakia. 360 pp.
- Hodek, I. 1967. Bionomics and ecology of predaceous Coccinellidae. *Ann. Rev. Entomol.* 12: 79-104.
- Hodek, I. 1970. Coccinellids and the modern pest management. *Bioscience* 20: 543-552.
- Hodek, I. 1973. *Biology of Coccinellidae*. Dr. W. Junk, The Hague and Academia Press, Czechoslovakia. 260 pp.
- Hodek, I., K. S. Hagen, H. F. van Emden. 1972. Methods for studying effectiveness of natural enemies. In: *Aphid Technology* (H. F. van Emden, ed.), Academic Press, Ltd., London. pp. 147-188.
- Hollingsworth, R. G., B. E. Tabashnik, D. E. Ullman, M. W. Johnson, and R. Messing. 1994. Resistance of *Aphis gossypii* (Homoptera: Aphididae) to insecticides in Hawaii: Spatial patterns and relation to insecticide use. *J. Econ. Entomol.* 87: 293-300.
- Hussey, N. W. 1985. Integrated programmes for specific crops - cucumbers. In: *Biological Pest Control - The Glasshouse Experience* (N. W. Hussey and N. Scopes, eds.). Blandford Press, Dorset, U.K. 175-179.
- Jacobson, R. 1993. Banking on pest predators. *Grower (U.K.)* 11: 19-21.
- Jackson, H. B. and R. D. Eikenbary. 1971. Bionomics of *Aphelinus asychis* (Hymenoptera: Eulophidae) an introduced parasite of the sorghum greenbug. *Ann. Entomol. Soc. Am.* 64: 81-85.
- Jensen, E. 1992. Integrated pest management at the grower level. *Pestic. Sci.* 36: 355-357.
- Kennedy, J. S., M. F. Day, and V. F. Eastop. 1962. *A Conspectus of Aphids as Vectors of Plant Viruses*. Commonwealth Agricultural Bureaux, London. 114 pp.
- Khalil, S. K., J. Bartos, and Z. Landa. 1985. Effectiveness of *Verticillium lecanii* to reduce populations of aphids under glasshouse and field conditions. *Agri. Ecosystems Environ.* 12: 151-156.

Kitajima, E. W. 1976. Isometric, viruslike particles in the green peach aphid, *Myzus persicae*. *J. Invertebr. Pathol.* 28: 1-10.

Kitajima, E. W., C. L. Costa, C. M. Sá. 1978. Baculovirus-like particles in two aphid species. *J. Invertebr. Pathol.* 31: 123-125.

Kring, J. B. 1959. The life cycle of the melon aphid, *Aphis gossypii* Glover, an example of facultative migration. *Ann. Entomol. Soc. Am.* 52: 284-286.

Kring, T. J., F. E. Gilstrap, and G. J. Michels, Jr. 1985. Role of indigenous coccinellids in regulating greenbugs (Homoptera: Aphididae) on Texas grain sorghum. *J. Econ. Entomol.* 78: 269-273.

Latgé, J. P. and B. Papierok. 1988. Aphid pathogens. In: *World Crop Pests - Aphids: Their Biology, Natural Enemies and Control* (A.K. Minks and P. Harrewijn, eds.). Elsevier, The Netherlands. pp. 323-335.

Li, Zhao-Hua, F. Lammes, J. C. van Lenteren, P. W. T. Huisman, A. van Vianen, and O. M. B. dePonti. 1987. The parasite-host relationship between *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera, Aleyrodidae). XXV. Influence of leaf structure on the searching activity of *Encarsia formosa*. *J. Appl. Ent.* 104: 297-304.

Lipa, J. J. 1985. History of biological control in protected culture-eastern Europe. In: *Biological Pest Control - The Glasshouse Experience* (N. W. Hussey and N. Scopes, eds.). Blandford Press, Dorset, U.K. pp. 23-29.

Mackauer, M. 1968. Insect parasites of the green peach aphid, *Myzus persicae* Sulz., and their control potential. *Entomophaga* 13: 91-106.

Mackauer, M. and F. J. Chow. 1986. Parasites and parasite impact on aphid populations. In: *Plant Virus Epidemics - Monitoring, Modelling and Predicting Outbreaks* (G. D. McLean, R. G. Garrett, and W. G. Ruesink, eds.) Academic Press, New York. pp. 95-118.

Mackauer, M. and M. J. Way. 1976. *Myzus persicae* Sulz., an aphid of world importance. In: *Studies in Biological Control* (V. L. Delucchi, ed.). Cambridge University Press, London. pp. 51-119.

Markkula, M. and K. Tiitanen. 1985. Biology of the midge *Aphidoletes* and its potential for biological control. In: *Biological Pest Control - The Glasshouse Experience* (N. W. Hussey and N. Scopes, eds.). Blandford Press, Dorset, U.K. pp. 74-81.

Markkula, M., K. Tiittanen, M. Hämäläinen, and A. Forsberg. 1979. The aphid midge *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae) and its use in biological control of aphids. *Annls. Ent. Fenn.* 45: 89-98.

Martin, H. and C. R. Worthing (eds.). 1977. *Pesticide Manual*. 5th edition. British Crop Protection Council, U.K. 593 pp.

Matthews, R. E. F. 1991. *Plant Virology*. 3rd edition. Academic Press, New York. 835 pp.

McLean, G. D., R. G. Garrett, and W. G. Ruesink (eds.). 1986. *Plant Virus Epidemics - Monitoring, Modelling and Predicting Outbreaks*. Academic Press, Australia. 550 pp.

Meadow, R. H., W. C. Kelly, and A. M. Shelton. 1985. Evaluation of *Aphidoletes aphidimyza* (Dip.: Cecidomyiidae) for control of *Myzus persicae* [Hom.: Aphididae] in greenhouse and field experiments in the United States. *Entomophaga* 30: 385-392.

Metcalf, R. L. 1989. Insect resistance to insecticides. *Pestic. Sci.* 26: 333-358.

Metcalf, R. L. 1980. Changing role of insecticides in crop protection. *Ann. Rev. Entomol.* 25: 219-256.

Miesner, H. 1975. Einfluss unter schiedlicher Beuteverteilung auf den Sucherfolg von *Aphidoletes aphidimyza* (Rond.) (Diptera: Cecidomyiidae). Diss. Univ. Göttingen. 81 pp.

Milner, R. J. and G. G. Lutton. 1986. Dependence of *Verticillium lecanii* (Fungi: Hyphomycetes) on high humidities for infection and sporulation using *Myzus persicae* (Homoptera: Aphididae) as host. *Environ. Entomol.* 15: 380-382.

Minks, A. K. and P. Harrewin (eds.). 1988. *World Crop Pests - Aphids: Their Biology, Natural Enemies, and Control*. Volume 2A. Elsevier, Amsterdam.

- Moericke, V. 1963. Über 'Virusartige Körper' in Organen von *Myzus persicae* (Sulz.). Z. PflKrankh. PflPath. PflSchutz 70: 464-470.
- Moran, N. A. 1992. The evolution of aphid life cycles. Ann. Rev. Entomol. 37: 321-348.
- Needham, P. H. and R. M. Sawicki. 1971. Diagnosis of resistance to organophosphorous insecticides in *Myzus persicae* (Sulz.). Nature 230: 125-126.
- Niemczyk, E. and A. F. G. Dixon (eds.). 1988. *Ecology and Effectiveness of Aphidophaga*. SPB Academic Publishing, The Hague, The Netherlands. 341 pp.
- O'Brien, P. J., Y. A. Abdel-Aal, J. A. Ottea, and J. B. Graves. 1992. Relationship of insecticide resistance to carboxylesterases in *Aphis gossypii* (Homoptera: Aphididae) from mid-south cotton. J. Econ. Entomol. 85: 651-657.
- Parrish, W. B. and J. D. Briggs. 1966. Morphological identification of virus-like particles in the corn leaf aphid, *Rhopalosiphum maidis* (Fitch.). J. Invertebr. Pathol. 18: 122-123.
- Peters, D. 1965. The purification of virus-like particles from the aphid *Myzus persicae*. Virology 26: 159-161.
- Pickett, J. A., L. J. Wadhams, and C. M. Woodcock. 1992. The chemical ecology of aphids. Ann. Rev. Entomol. 37: 67-90.
- Pirone, T. P. and K. F. Harris. 1977. Nonpersistent transmission of plant viruses by aphids. Ann. Rev. Phytopathol. 15: 55-73.
- Plumb, R. T. and J. M. Thresh (eds.). 1983. *Plant Virus Epidemiology-The Spread and Control of Insect-Borne Viruses*. Blackwell Scientific Publications, London. 377 pp.
- Portree, J. (ed.). 1993. *Greenhouse Vegetable Production Guide for Commercial Growers*. Province of British Columbia, Ministry of Agriculture, Fisheries, and Food. Victoria, British Columbia. 86 pp.
- Pree, D. J., D. E. Archibald, and R. K. Morrison. 1989. Resistance to insecticides in the common green lacewing *Chrysoperla carnea*

- (Neuroptera: Chrysopidae) in southern Ontario. *J. Econ. Entomol.* 82: 29-34.
- Price, P. W., C. E. Bouton, P. Gross, B. A. McPheron, J. N. Thompson, A. E. Weis. 1980. Interactions between insect herbivores and natural enemies. *Ann. Rev. Ecol. Syst.* 11: 41-65.
- Quaglia, F., E. Rossi, R. Petacchi, and C. E. Taylor. 1993. Observations on an infestation by green peach aphids (Homoptera: Aphididae) on greenhouse tomatoes in Italy. *J. Econ. Entomol.* 86: 1019-1025.
- Ramakers, P. M. J. 1982. Proc. Symp. Integrated Crop Protection, CEC, Valence, France. pp. 265-70.
- Ramakers, P. M. J. 1992. Proc. Int. Symp. 'Biological Control and Integrated Crop Protection: Towards Environmentally Safer Agriculture', Veldhoven, The Netherlands, 8-13 September 1992.
- Rice, A. D., R. W. Gibson, and M. F. Stribley. 1983. Effects of deltamethrin on walking, flight and potato virus transmission by pyrethroid-resistant *Myzus persicae*. *Ann. Appl. Biol.* 102: 229-236.
- Riechert, S. E. and L. Bishop. 1990. Prey control by an assemblage of generalist predators: Spiders in garden test systems. *Ecology* 71: 1441-1450.
- Rochow, W. F. 1972. The role of mixed infections in the transmission of plant viruses by aphids. *Ann. Rev. Phytopathol.* 10: 101-124.
- Roush, R. T. and J. A. McKenzie. 1987. Ecological genetics of insecticide and acaricide resistance. *Ann. Rev. Entomol.* 32: 361-380.
- Roush, R. T. and B. E. Tabashnik (eds.). 1990. *Pesticide Resistance in Arthropods*. Chapman and Hall, London. 303 pp.
- Rybicki, E. P. 1984. *Investigations of Viruses Affecting South African Small Grains*. Ph.D. thesis, University of Cape Town.
- Rybicki, E. P. and M. B. von Wechmar. 1982. Characterization of an aphid-transmitted virus disease of small grains: Isolation and partial characterization of three viruses. *Phytopathol. Z.* 103: 306-322.
- Samson, R. A., H. C. Evans, and J. P. Latgé. 1988. *Atlas of Entomopathogenic Fungi*. Springer, New York. 187 pp.

Samson, R. A., E. H. S. Hoekstra, C. A. N. Oorschot. 1980. *Introduction to Food-borne Fungi*. Centraal Bureau voor Schimmelcultures, Baarn, The Netherlands.

Samson, R. A. and M. L. Rombach, 1985. Biology of the fungi *Verticillium* and *Aschersonia*. In: *Biological Pest Control - The Glasshouse Experience* (N. W. Hussey and N. Scopes, eds.). Blandford Press, Dorset, U.K. pp. 34-42.

Sawicki, R. M. and A. D. Rice. 1978. Response of susceptible and resistant peach-potato aphids *Myzus persicae* (Sulz.) to insecticides in leaf dip bioassay. *Pestic. Sci.* 9: 513-516.

Schlinger, E. I. and M. J. P. Mackauer. 1963. Identity, distribution, and hosts of *Aphidius matricariae* Haliday, an important parasite of the green peach aphid, *Myzus persicae* (Hymenoptera: Aphidiidae-Homoptera: Aphidoidea). *Ann. Entomol. Soc. Am.* 56: 648-653.

Schneider, F. 1969. Bionomics and physiology of aphidophagous Syrphidae. *Ann. Rev. Entomol.* 14: 103-24.

Scopes, N. E. A. 1969. The potential of *Chrysopa carnea* as a biological control agent of *Myzus persicae* on glasshouse chrysanthemum. *Ann. Appl. Biol.* 64: 433-439.

Scott, S. M. and C. A. Barlow. 1986. Effect of prey availability on foraging and production efficiencies of larval *Metasyrphus corollae* [Dipt.: Syrphidae]. *Entomophaga* 31: 243-250.

Seaman, D. and R. P. Warrington. 1972. Slow release pirimicarb formulations: Measurements of release rate under field conditions. *Pestic. Sci.* 3: 799-804.

Sell, P. 1976. Monogenie bei *Aphidoletes aphidimyza* (Rond.) (Diptera: Cecidomyiidae). *Z. Angew. Ent.* 82: 58-61.

Silver, A. R. J. 1984. The biochemical nature of pirimicarb resistance in two glasshouse strains of *Aphis gossypii* (Glover). Ph.D. thesis, University of Reading, U.K.

- Sun, Y.-Q., G.-L. Feng, J.-G. Yuan, P. Zhu, and K.-Y. Gong. 1987. Biochemical resistance of cotton aphids to organophosphorous insecticides. *Acta Entomologica Sinica* 30: 13-20.
- Sundby, R. A. 1966. A comparative study of the efficiency of three predatory insects - *Coccinella septempunctata* L., (Coleoptera, Coccinellidae), *Chrysopa carnea* St. (Neuroptera, Chrysopidae) and *Syrphus ribesii* L. (Diptera: Syrphidae) - at two different temperatures. *Entomophaga* 2: 395-404.
- Suzuki, K., H. Hama, and Y. Konno. 1993. Carboxylesterase of the cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), responsible for fenitrothion resistance as a sequestering protein. *Appl. Entomol. Zool.* 28: 439-450.
- Swenson, K. G. 1968. Role of aphids in the ecology of plant viruses. *Ann. Rev. Phytopathol.* 6: 351-374.
- Takada, H. and Y. Murakami. 1988. Esterase variation and insecticide resistance in Japanese *Aphis gossypii*. *Entomol. Exp. Appl.* 48: 37-41.
- Tanada, Y. and H. K. Kaya. 1993. *Insect pathology*. Academic Press, New York. 666 pp.
- Tauber, M. J., C. A. Tauber, and S. Gardescu. 1993. Prolonged storage of *Chrysoperla carnea* (Neuroptera: Chrysopidae). *Environ. Entomol.* 22: 843-848.
- Tisdale, C. A. 1990. In: *Critical Issues in Biological Control* (M. Mackauer, L. E. Ehler, and J. Roland, eds.). Intercept, Andover, Hants, U.K. pp. 301-316.
- Tulisalo, U. 1984. Biological control in the greenhouse. In: *Biology of Chrysopidae* (M. Canard, Y. Séméria, and T. R. New, eds.), Dr. W. Junk, The Hague, The Netherlands. pp. 228-233.
- Uygun, N. 1971. Der Einfluss der Nahrungsmenge auf Fruchtbarkeit und Lebensdauer von *Aphidoletes aphidimyza* (Rondani 1847) (Diptera: Itonididae). *Z. Angew. Ent.* 69: 234-258.
- van den Bosch, R., E. I. Schlinger, E. J. Dietrick, J. C. Hall, and B. Puttler. 1964. Studies on succession, distribution, and phenology of imported

- parasites of *Therioaphis trifolii* (Monell) in southern California. Ecology 45: 602-621.
- van Emden, H. F., V. F. Eastop, R. D. Hughes, M. J. Way. 1969. The ecology of *Myzus persicae*. Ann. Rev. Entomol. 14: 197-270.
- van Lenteren, J. C. 1990. Proc. Int. Symp. on Biological Control Implementation, McAllen, Texas, 4-6 April 1989. NAPPO Bulletin 6: 50-70.
- van Lenteren, J. C. 1992. Biological control in protected crops: Where do we go? Pestic. Sci. 36: 321-327.
- van Lenteren, J. C. and J. Woets. 1988. Biological and integrated pest control in greenhouses. Ann. Rev. Entomol. 33: 239-269.
- van Schelt, J., J. B. Douma, and W. J. Ravensberg. 1990. Recent developments in the control of aphids in sweet peppers and cucumbers. SROP/WPRS Bulletin XIII/5: 190-193.
- van Steekelenburg, N. A. M. 1992. Novel approaches to integrated pest and disease control in glasshouse vegetables in The Netherlands. Pestic. Sci. 36: 359-362.
- van Steenis, M. J. 1992. Biological control of the cotton aphid, *Aphis gossypii* Glover (Hom., Aphididae): Pre-introduction evaluation of natural enemies. J. Appl. Entomol. 114: 362-380.
- van Steenis, M. J. 1993a. Introduction frequency is not everything. Groenten & Fruit 3: 14-15 (original in Dutch).
- van Steenis, M. J. 1993b. Suitability of *Aphis gossypii* Glov., *Macrosiphum euphorbiae* (Thom.) and *Myzus persicae* Sulz. (Hom.: Aphididae) as host for several aphid parasitoid species (Hym.: Braconidae). SROP/WPRS Bulletin XVI/2: 157-160.
- Vinson, S. B. 1976. Host selection by insect parasitoids. Ann. Rev. Entomol. 21: 109-133.
- Volk, S. 1964. Untersuchungen zur Eiablage von *Syrphus corollae* Fahr. (Diptera: Syrphidae). Z. Angew. Entomol. 54: 365-386.

- von Wechmar, M. B., J. M. Laubscher, and M. A. Jaffer. 1991. Association of aphid lethal paralysis virus with Entomophthorales species parasitizing cereal aphids. Abstract no. 156 in Program and Abstracts of XXIV Annual Meeting of the Society for Invertebrate Pathology, Northern Arizona University, 4-9 August 1991, Flagstaff, Arizona.
- Wardlow, L. R. 1992. Proc. Int. Symp. 'Biological Control and Integrated Crop protection: Towards Environmentally Safer Agriculture', Veldhoven, The Netherlands, 8-13 September 1992.
- Wardlow, L. R. and T. M. O'Neill. 1992. Management strategies for controlling pests and diseases in glasshouse crops. *Pestic. Sci.* 36: 341-347.
- Ware, G. W. 1991. *Fundamentals of Pesticides*. 3rd edition. Thomson Publications. Fresno, California. 307 pp.
- Williamson, C., E. P. Rybicki, G. G. F. Kasdorf, and M. B. von Wechmar. 1988. Characterization of a new picorna-like virus isolated from aphids. *J. Gen. Virol.* 69: 787-795.
- Williamson, C., M. B. von Wechmar, and E. P. Rybicki. 1989. Further characterization of *Rhopalosiphum padi* virus of aphids and comparison of isolates from South Africa and Illinois. *J. Invertebr. Pathol.* 54: 85-96.
- Woets, J. 1985. Integrated programmes for specific crops - tomatoes. In: *Biological Pest Control - The Glasshouse Experience* (N. W. Hussey and N. scopes, eds.). Blandford Press, Dorset, U.K. pp166-174.
- Wyatt, I. J. 1985. Insecticide resistance in aphids on chrysanthemums. *Proceedings of the 3rd British Insecticide and Fungicide Conference*. pp. 52-55.
- Wyatt, I. J. and S. J. Brown. 1977. The influence of light intensity, daylength, and temperature on increase rates of four glasshouse aphids. *J. Appl. Ecol.* 14: 391-399.