Evaluation and application of parasitoids for biological control of *Aphis gossypii* in glasshouse cucumber crops

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Proefschrift

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Stellingen

1 Met de huidige door de producenten van natuurlijke vijanden voorgeschreven preventieve sluipwespintroducties kan de snelle remming van de bladluispopulatiegroei, die noodzakelijk is voor een goede biologische bestrijding, niet met zekerheid bereikt worden.
Dit proefschrift

2 De stelling van Minkenberg (1990) dat populatiegroeisnelheden van sluipwespen gebruikt kunnen worden als selectiecriterium, moet met de nodige argwaan tegemoet getreden worden.
Dit proefschrift
MINKENBERG, O.P.J.M. (1990). On seasonal inoculative control. Thesis Department of Entomology, Agricultural University Wageningen.

3 In het gebruikswaardeonderzoek van nieuwe komkommerrassen zou ook de mate van resistentie tegen katoenluis een duidelijke plaats moeten krijgen.

4 De sluipwespdichtheid op een bepaalde plaats wordt niet alleen bepaald door het op afstand lokaliseren van bladluiskolonies, ook de snelheid waarmee de sluipwespen een bladluiskolonie van een bepaalde grootte verlaten is van groot belang.
Dit proefschrift
SHEEHAN, W. en SHELTON, A.M. (1989). Parasitoid response to concentration of herbivore food plants: finding and leaving plants. Ecology ***70: 993-998.***

5 Het gezegde: "wie het kleine niet eert is het grote niet weerd" is bij *Aphidius colemani* totaal onbekend.
Dit proefschrift

6 Ten opzichte van de huidige introductiemethodes, geeft het introduceren van sluipwespen door middel van open kweken in de kas een duidelijke verbetering van de biologische bladluisbestrijding.
Dit proefschrift
Bennison, J.A. (1992). Biological control of aphids on cucumbers: use of open rearing systems or "banker plants" to aid establishment of Aphidius matricariae *and* Aphidoletes aphidimyza. Mededelingen van de Faculteit Landbouwwetenschappen Universiteit Gent ***57/2b: 457-466.***

7 Het gebruik van gemiddelde temperaturen bij klimaatmodellen geeft een foutieve voorspelling van de invloed van klimaatveranderingen op ecosysteemniveau.
SCHERM H. en VAN BRUGGEN, A.H.C. (1994). Global warming and nonlinear growth: how important are changes in average temperature? Phytophatology ***84: 1380-1384.***

8 Alleen leugenaars, gekken en oplichters kunnen aardbevingen voorspellen.
Carl Richter

9 Met het oog op de overbevolking en woningnood zou de kinderbijslag omgezet moeten worden in een kindertoeslag.

10 Milieuconferenties zouden alleen georganiseerd mogen worden als de te verwachten baten (in de vorm van harde afspraken) opwegen tegen de door de deelnemers veroorzaakte milieuvervuiling.

11 De duidelijke dosis-respons curves die bij onderzoek naar giftige stoffen gevonden worden, zijn een sterk argument tegen de grondbeginselen van de klassieke homeopathie.

12 E-mail beperkt de volledigheid en betrouwbaarheid van toekomstige biografieën.

13 Er is niets zo onzeker als het gemiddelde.

Stellingen behorend bij het proefschrift:

Evaluation and application of parasitoids for biological control of *Aphis gossypii* in glasshouse cucumber crops

Wageningen, 13 september 1995 Machiel van Steenis

CONTENTS

VOORWOORD

En dan zit het er bijna op. Alles tig keer doorgelezen en steeds maar weer foutjes vinden. Wat nog rest is het schrijven van een voorwoord, misschien wel het lastigste stukje van het hele proefschrift. De lijst met mensen die ik wilde bedanken bleef maar groeien en zelfs nu ben ik er niet zeker van dat ik niemand overgeslagen heb.
In 1990 ben ik begonnen met het onderzoek naar biologische bestrijding van katoenluis in komkommer. Het grootste deel van het werk is uitgevoerd op het Proefstation voor Tuinbouw onder Glas te Naaldwijk, hoewel ik officieel in dienst was bij de vakgroep Entomologie van de Landbouwuniversiteit. In de loop van de jaren is me duidelijk geworden dat bladluizen een heel aparte plaats innemen binnen de plagen die in kassen voorkomen. Door de grote voorplantingscapaciteit hoef je bij wijze van spreken maar even met je ogen te knipperen en het gewas staat op instorten. Deze explosieve groei maakt het voor een onderzoeker alleen maar interessanter en ik heb dan ook met veel plezier mijn steentje bijgedragen aan de biologische bladluisbestrijding.
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Hoewel komkommers vanzelf groeien als ze maar water krijgen, is het onderhouden van het gewas een kunst op zich. Jan van Loenen heeft tijdens de kasproeven gezorgd voor het snoeien en oogsten van de komkommers.
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Machiel van Steenis Naaldwijk, juli 1995

SAMENVATTING

Introductie
Bladluizen vormen een belangrijke plaag in de Nederlandse groenteteelt onder glas. Al bij lage dichtheden kan economische schade ontstaan door vervuiling van vruchten en bladmisvormingen. In paprikateelten wordt de perzikluis (*Myzus persicae* Sulzer (Homoptera: Aphididae)) al geruime tijd met succes bestreden door het inzetten van sluipwespen (*Aphidius matricariae* Haliday (Hymenoptera: Braconidae)) en galmuggen (*Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae)). Bij een zeer snelle ontwikkeling van de bladluispopulatie kan de groei plaatselijk onderdrukt worden door toepassing van het selectieve bladluismiddel pirimicarb. De biologische bestrijding van andere plagen (zoals trips en witte vlieg) wordt door dit middel niet in gevaar gebracht. Biologische bestrijding van katoenluis (*Aphis gossypii* Glover (Homoptera: Aphididae)) met bovengenoemde natuurlijke vijanden, bleek echter niet goed te werken. Bovendien is katoenluis resistent tegen pirimicarb zodat alleen breedwerkende insekticiden ingezet kunnen worden. Dit bemoeilijkt het gebruik van biologische bestrijding tegen andere plagen. Het is daarom noodzakelijk om ook voor katoenluis een goede biologische bestrijdingsmethode te hebben.
De eerste stap van dit project bestond uit een literatuuronderzoek naar de biologie van *A. gossypii* en zijn natuurlijke vijanden (hoofdstuk 1). Het bleek dat de biologie van katoenluis slechts in een klein aantal gevallen in detail bestudeerd was. De eerste proeven richtten zich dan ook op een gedetailleerde beschrijving van de biologie van katoenluis op komkommer.
Het resterende onderzoek kan in twee delen gesplitst worden. Als eerste moet een aantal natuurlijke vijanden getoetst worden op hun geschiktheid voor biologische bestrijding van katoenluis in kassen. Bladluizen hebben een groot aantal natuurlijke vijanden, zowel zeer specifieke als generalistische soorten. Er kunnen drie groepen onderscheiden worden: pathogenen (vnl. insekteparasitaire schimmels), predatoren (zoals lieveheersbeestjes, gaasvliegen en zweefvliegen) en sluipwespen. Op basis van een aantal criteria bleek uit het literatuuronderzoek dat sluipwespen de beste kansen op succesvolle bestrijding van katoenluis bieden.
Pathogenen hebben hoge luchtvochtigheden nodig om te kunnen kiemen en nieuwe sporen te vormen. In kassen is een hoge luchtvochtigheid moeilijk lange tijd te handhaven en werkt bovendien het ontstaan van schimmelziektes in de hand.
Bij de predatoren zijn het meestal de larven die de meeste bladluizen eten. Predatoren hebben lagere populatiegroeisnelheden dan sluipwespen en zullen daarom niet zo snel op een toename van het aantal bladluizen kunnen reageren. Bovendien moeten de larven van predatoren tijdens hun ontwikkeling veel bladluizen eten, wat problemen zou kunnen geven op momenten dat er weinig bladluizen zijn. Ten slotte is het kweken van predatoren moeilijk en duur (met uitzondering van de galmug *A. aphidimyza*).
Er zijn twee families waarin bladluissluipwespen voorkomen: de Aphelinidae en de Braconidae (onderfamilie Aphidiinae). Deze sluipwespen leggen een ei in de bladluis. De larve van de sluipwesp eet de bladluis van binnenuit op, verpopt zich en kruipt als volwassen sluipwesp weer uit de bladluis. De ontwikkeling van ei tot volwassen sluipwesp duurt kort waardoor een sluipwesppopulatie snel in aantal kan toenemen. Op grond van deze hoge vermenigvuldigingscapaciteit en de relatief eenvoudige massaproduktie concentreert het onderzoek zich op het gebruik van sluipwespen voor de biologische bestrijding van katoenluis.

Wanneer bekend is welke natuurlijke vijand gebruikt gaat worden, moet ten tweede een efficiënte introductiemethode worden ontwikkeld. In kassen zijn vaak grote fluctuaties van het aantal bladluizen zichtbaar. Een eis die aan de natuurlijke vijanden gesteld wordt, is dat ze goed kunnen zoeken. Daarbij blijven er bij succesvolle bestrijding slecht weinig bladluizen in het gewas over. Omdat de sluipwesplarven zich alleen in bladluizen kunnen ontwikkelen betekent dit dat na verloop van tijd ook het aantal natuurlijke vijanden afneemt. Wanneer op dit moment bladluizen van buiten de kas naar binnen komen, zullen er niet voldoende natuurlijke vijanden zijn om de groei van de bladluispopulatie meteen af te remmen. Een meer betrouwbare situatie kan worden gecreëerd door gedurende het hele seizoen regelmatig een groot aantal natuurlijke vijanden in de kas los te laten. Dit zou echter veel geld kosten. Een oplossing zou het inzetten van planten met bladluizen die geen schade aan het gewas toebrengen, kunnen zijn. De natuurlijke vijanden kunnen zich dan op deze bladluizen in stand houden, ook als er vrijwel geen katoenluis in de kas aanwezig is. Dit resulteert in een constante aanwezigheid van een groot aantal natuurlijke vijanden.
In het nu volgende deel wordt eerst de biologie van katoenluis beschreven, waarna de twee deelvragen ((a) wat is de beste parasiet en (b) wat is de beste introductiemethode) aan bod zullen komen.

Biologie van Aphis gossypii
In hoofdstuk 2 wordt de invloed van temperatuur (20 tot 30 °C), komkommerras en parasitering op de biologie van katoenluis beschreven. Door een korte ontwikkeling van de onvolwassen stadia en een hoge dagelijkse reproduktie bij 25 °C, is de maximale groeisnelheid van een katoenluispopulatie het grootst bij deze temperatuur. De gegevens die in het laboratorium gevonden zijn, komen goed overeen met de biologie van katoenluis in een kas.
De ontwikkelingsduur verschilt op verschillende komkommerrassen. Het gebruik van partieel resistente rassen zou de biologische bestrijding van katoenluis eenvoudiger maken.
Bladluizen die door de sluipwesp *Aphidius colemani* Viereck (Hymenoptera: Braconidae) geparasiteerd zijn, produceren alleen jongen wanneer de parasitering in het vierde nymfstadium of in volwassen bladluizen plaats vindt. Deze bladluizen produceren nog een aantal dagen na de parasitering jongen. Door de korte ontwikkelingsduur van de jongen is de bijdrage van geparasiteerde bladluizen aan volgende bladluisgeneraties nog steeds zeer groot.

Evaluatie van sluipwespen
Van een aantal sluipwespen is de geschiktheid voor biologische bestrijding van katoenluis bekeken (hoofdstuk 3). Bij de sluipwespen van de onderfamilie Aphidiinae (Braconidae) gaf een laboratorium experiment een goede indicatie van het succes van de sluipwespen in de kas. Van de vier sluipwespsoorten die bekeken zijn, is *A. colemani* de beste biologische bestrijder. Deze soort vindt meer bladluiskolonies in kassen en heeft in bladluiskolonies een hoger parasiteringspercentage dan *A. matricariae* Haliday, *Ephedrus cerasicola* Starý en *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae).
Het vergelijken van *A. colemani* met de sluipwesp *Aphelinus varipes* Förster is niet mogelijk in het laboratorium door de grote verschillen in de voortplantingsstrategie. *Aphidius* sluipwespen kunnen dagelijks veel bladluizen parasiteren gedurende een eilegperiode van enkele dagen. *Aphelinus* sluipwespen parasiteren dagelijks wat minder bladluizen omdat er continu eirijping plaats vindt. De eilegperiode is voor deze soorten echter wel een stuk langer. Bovendien doden

Aphelinus soorten nog een aantal bladluizen per dag om zich mee te voeden. Er is daarom voor gekozen om meteen op kleine schaal kasproeven te doen. Het gecombineerde effect van *A. varipes* and *A. colemani* resulteert in een betere bestrijding dan wanneer alleen *A. colemani* wordt gebruikt. Door de langere levensduur overleeft *A. varipes* periodes met lage bladluisdichtheid beter dan *A. colemani*.

Biologie van sluipwespen
In hoofdstuk 4 is van een aantal sluipwespsoorten de biologie nader onderzocht. Zowel *A. colemani* als *L. testaceipes* parasiteren dagelijks veel bladluizen en hebben een korte ontwikkelingsduur van ei tot volwassen sluipwesp. De maximale populatiegroeisnelheden zijn iets lager dan die van *A. gossypii*. De levensduur van de sluipwespen is slechts enkele dagen. Dit kan problemen geven wanneer sluipwespen preventief (voordat er bladluizen aanwezig zijn) ingezet worden, omdat het aantal sluipwespen na een introductie snel af zal nemen. De levensduur van *A. varipes* is aanzienlijk langer dan die van *A. colemani*. Deze soort zal dan ook beter in staat zijn om een periode van lage bladluisdichtheid te overleven. De dagelijkse reproduktie van *A. varipes* is lager dan die van *A. colemani*. De ontwikkeling van ei tot volwassen sluipwesp van *A. varipes* is, bij temperaturen hoger dan 25 °C, gelijk aan die van *A. colemani*. Bij lagere temperaturen is de ontwikkeling van *A. colemani* duidelijk sneller.

Zoekgedrag van Aphidius colemani
Een beter begrip van het zoekgedrag van *A. colemani* kan meer inzicht geven in de processen die leiden tot succesvolle bestrijding van *A. gossypii* en duidelijk maken welke manier van introduceren de beste resultaten zal geven. Een aantal aspecten van het zoekgedrag van *A. colemani* wordt beschreven in hoofdstuk 5.
Na een klein aantal parasiteringen verandert het gedrag van de volwassen sluipwespen. De activiteit wordt groter en een groter percentage van de sluipwespen bezoekt planten. De sluipwespen kunnen de aanwezigheid van bladluizen op een blad van een afstand waarnemen. Voor de verandering van het zoekgedrag maakt het niet uit of de sluipwespen eerst katoenluis of de graanluis *Rhopalosiphum padi* Linnaeus (Homoptera: Aphididae) geparasiteerd hebben.
De functionele respons (de reactie van individuele sluipwespen op het aantal aanwezige bladluizen) van *A. colemani* is sigmoïde. Tot een dichtheid van tien bladluizen per bladponsje nemen de parasiteringspercentages met toenemende katoenluisdichtheid toe. Bij hogere bladluisdichtheden nemen de parasiteringspercentages weer af. Wanneer een sluipwesp een bezoek brengt aan een blad waar de sluipwesp al eerder is geweest, is de duur van het bezoek duidelijk korter dan de duur van het eerste bezoek. Er zijn geen aanwijzingen gevonden dat de sluipwesp bezochte bladeren of bladluiskolonies markeert, dus is ontmoeting met geparasiteerde gastheren waarschijnlijk de oorzaak van het kortere bladbezoek.
Het zoekgedrag van *A. colemani* is ook onderzocht op intacte komkommerbladeren. Op bladeren met een hoge gastheerdichtheid (100 bladluizen) is de kans op weggaan van de sluipwespen kleiner dan op bladeren met minder dan 100 gastheren (0, 1 of 10). Opvallend is dat het voor de kans op weggaan (en dus de opgeeftijden) niet uitmaakt of er 0, 1 of 10 bladluizen op het blad zitten.
Het afwijzen van bladluizen (wat vaak gebeurt bij geparasiteerde bladluizen) en de aanwezigheid van een andere bladluiskolonie (vlakbij de kolonie waar de sluipwesp aan het zoeken) is, hebben geen invloed op de kans op weggaan. De invloed van het aantal ontmoette gastheren tijdens

een bladbezoek hangt af van het aantal aanwezige katoenluizen. Bij een dichtheid van minder dan tien bladluizen is de kans op weggaan na 30 ontmoetingen veel groter dan daarvoor. Bij een dichtheid van 100 bladluizen neemt de kans op weggaan pas toe na 100 ontmoetingen. Herhaalde bezoeken aan een bladluiskolonie met tien ongeparasiteerde gastheren resulteren in een toename van de kans op weggaan na ongeveer tien bladbezoeken. De resultaten duiden erop dat de sluipwespen waarschijnlijk een 'aangeboren' verwachting hebben van de ruimtelijke verdeling van bladluizen en ze hun tijd voornamelijk doorbrengen bij kolonies met veel bladluizen.

Toepassing van Aphidius colemani
In hoofdstuk 6 worden verschillende methodes om *A. colemani* in kassen te introduceren met elkaar vergeleken. Bij herhaalde loslatingen van volwassen sluipwespen hangt het slagen van de biologische bestrijding af van het moment en de grootte van de introducties. De natuurlijke vijanden moeten snel na het in de kas komen van katoenluis in grote aantallen aanwezig zijn. Bij introductie van een te klein aantal natuurlijke vijanden wordt een deel van de bladluiskolonies niet meteen gevonden. Hierdoor kan de katoenluispopulatie nog doorgroeien en wordt pas een goede bestrijding verkregen als de eerste nakomelingen van de uitgezette sluipwespen uitkomen. In de zomer is biologische bestrijding moeilijker te realiseren door de grotere snelheid waarmee een katoenluispopulatie bij hogere temperaturen groeit.
Met introductie van sluipwespen door een open kweek met graan en graanluis (*R. padi*) in de kas, wordt meteen een hoog parasiteringspercentage van katoenluiskolonies verkregen. De bestrijding van katoenluis verloopt met deze methode dan ook beter dan met regelmatige introducties van volwassen sluipwespen. Aan het eind van het seizoen kunnen problemen met hyperparasieten ontstaan. Hyperparasieten parasiteren door *A. colemani* geparasiteerde bladluizen en kunnen zich dus ook uitstekend in stand houden op de open kweken. Door het grote aantal hyperparasieten neemt het aantal *A. colemani* af, wat weer wordt gevolgd door een toename van het aantal katoenluis. Hyperparasieten zijn voornamelijk laat in het seizoen een probleem, op het moment dat hyperparasieten in te grote aantallen voorkomen zou kunnen worden overgeschakeld op een predator, zoals *A. aphidimyza*.
Naast katoenluis komt een aantal andere bladluissoorten regelmatig in kassen voor. De belangrijkste soorten zijn de aardappeltopluis, *Macrosiphum euphorbiae* Thomas (Homoptera: Aphididae) en de groene perzikluis *M. persicae*. Voor de sluipwespsoorten die al eerder zijn genoemd (*A. colemani, A. matricariae, E. cerasicola* en *L. testaceipes*) is gekeken of deze bladluissoorten ook goede gastheren zijn. Geen van de sluipwespsoorten parasiteert de aardappeltopluis met succes. Verder is *A. colemani* de enige soort die zowel katoenluis als perzikluis zeer goed parasiteert en is dus het meest geschikt is voor bestrijding van zowel katoenluis als groene perzikluis.

Het gebruik van verschillende criteria voor evaluatie van natuurlijke vijanden wordt bediscussieerd in de algemene discussie (hoofdstuk 7). Het gebruik van biologische parameters als ontwikkelingsduur en reproduktie is niet betrouwbaar gebleken. Deze gegevens waren voor *A. colemani* en *L. testaceipes* vrijwel gelijk, terwijl in de kas zeer grote verschillen in effectiviteit te zien waren. Er wordt ook duidelijk gemaakt dat het vergelijken van sluipwespen met een duidelijk verschillende biologie in het laboratorium moeilijk is omdat het belang van individuele criteria moeilijk is in te schatten. Bovendien is het belang van individuele criteria afhankelijk van het systeem dat bestudeerd wordt en het soort biologische bestrijding dat het uiteindelijke doel

is. Bij bestrijding van bladluizen in kassen is het erg belangrijk dat de bladluispopulatie op een laag niveau blijft. Een efficiënt zoekgedrag (het snel lokaliseren van bladluiskolonies) is onder deze omstandigheden een zeer belangrijk kenmerk van een succesvolle natuurlijke vijand. Bladluiskolonies moeten snel gevonden worden om te voorkomen dat ze te groot worden. Omdat sluipwespen in staat zijn om de bladluispopulatie tot zeer lage niveaus terug te brengen (waardoor na verloop van tijd ook slechts een klein aantal sluipwespen aanwezig zal zijn) is het systeem erg gevoelig voor binnenkomende katoenluizen. De enige manier om goede bestrijding te krijgen is door er voor te zorgen dat er altijd een voldoende hoeveelheid sluipwespen aanwezig is. Wanneer dit lukt kan door het inzetten van *A. colemani* een goede katoenluisbestrijding verkregen worden.

SUMMARY

Introduction

Aphids are an important problem in glasshouse vegetables. Already at low aphid densities fruits can get contaminated with honeydew, which decreases the economical value of the fruits. When aphids feed on the growing tips of the plants, the new shoots can get heavily distorted and plant growth is reduced. At the time this project was started integrated aphid control in cucumber and sweet pepper crops consisted of introduction of the parasitoid *Aphidius matricariae* Haliday (Hymenoptera: Braconidae) and the predatory gall midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae). Integrated control of *Myzus persicae* Sulzer (Homoptera: Aphididae) in sweet pepper was effective, but *A. gossypii* was little affected by the introduced parasitoids. Additional control with the selective aphicide pirimicarb was also not possible since cotton aphid has developed resistance against this chemical. Aphid control with non-selective insecticides inhibits the use of biological control of other pests (like thrips and whitefly) in the glasshouse, which is applied on a large scale in the Netherlands. To be able to keep using biological control of other pests it is, therefore, necessary to develop an effective biological control programme for cotton aphid as well. In Chapter 1 the biology of cotton aphid and its most important natural enemies is described. This literature review showed that detailed data on the biology of *A. gossypii* were scarce. Therefore, the first experiments consisted of detailed research on the biology of cotton aphid.

Research to develop biological control of *A. gossypii* can be divided into two main lines. First of all a selection of (a) potential candidate(s) for the control of *A. gossypii* has to be made. Many natural enemies of aphids are known, ranging from monophagous to polyphagous species. The natural enemies can be divided into three groups: pathogens (mainly parasitic fungi), predators (like ladybeetles, lacewings and hoverflies) and parasitoids. Based on several criteria, a literature survey indicated that parasitoids seemed most promising.

Insect pathogens need very high humidities for successful germination and sporulation. These humidities are difficult to maintain in glasshouses for sufficiently long periods and can cause plant diseases.

Predators have lower population growth rates than parasitoids and will, therefore, not be able to react to increasing aphid densities as quickly as parasitoids. Additionally, predator larvae need many aphids for successful development which might give problems during periods of low aphid density. Finally, predators are more expensive to culture (with the exception of *A. aphidimyza*), because of the cannibalistic habits of the larvae. Parasitoid populations can multiply rapidly because of a short development time, and parasitoids need only one aphid for successful development. Based on the high reproductive capacity and the possibility of rearing parasitoids in large quantities, parasitoids seem to be the most promising group of aphid natural enemies.

Secondly, an efficient method has to be developed for the introduction of natural enemies in a glasshouse. In glasshouses the interaction between aphids and natural enemies is wave-like. The natural enemies are efficient searchers and are able to destroy the aphid population almost completely. When few aphids are present, most of the natural enemies will die and the aphid population can grow again once few aphids have entered the glasshouse from outside. A more stable situation can be created by introducing many parasitoids very frequently, but this would be very expensive. A second solution is the creation of a refuge for the parasitoids in the form of banker plants with aphids, which are harmless to the crop. On these refuges the parasitoids

can multiply independently of the presence of aphids in the crop. As a consequence a continuous presence of a large number of natural enemies is ensured during the entire cropping period.

In the next section the life history of *A. gossypii* will be described. Thereafter the two lines of research ((a) what is the best parasitoid and (b) what is the best introduction method) will be dealt with.

Life history of Aphis gossypii

In Chapter 2 the influence of temperature, host plant cultivar and parasitism on the life history data of the cotton aphid are described. The potential population growth of a cotton aphid population is highest at 25 °C, because of a shorter development time and a higher daily reproduction at this temperature. There is a good agreement between life history data in the laboratory and in glasshouses. The development times on two cucumber cultivars differs markedly. Partial host plant resistance can be a useful tool for improving biological control of cotton aphid.

Aphids, successfully parasitized by *Aphidius colemani* Viereck (Hymenoptera: Braconidae) only reproduce when they are parasitized in the fourth instar or as adult. These aphids produce nymphs for several days but, because of the short development time of the nymphs, they still have a large contribution to the growth of the aphid population.

Evaluation of parasitoids

The evaluation of several parasitoids is described in Chapter 3. For aphidiine parasitoids a small laboratory experiment gives a good indication on the usefulness of the parasitoids in glasshouses. Out of four parasitoid species *A. colemani* is the most promising control agent. This species finds more aphid colonies in glasshouses and higher parasitization rates are obtained than for *A. matricariae*, *Ephedrus cerasicola* Starý and *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae).

Because of the different reproduction strategies, comparison of *Aphelinus varipes* Förster (Hymenoptera: Aphelinidae) with aphidiine parasitoids is not possible in the laboratory. Aphidiine parasitoids have a higher daily reproduction but a shorter reproduction period compared to aphelinids. Therefore, *A. varipes* was compared with *A. colemani* in small glasshouses. The combined effect of *A. varipes* and *A. colemani* results in better and more stable control than when *A. colemani* is introduced alone.

Life history of parasitoids

For several parasitoids life history data were collected in more detail (Chapter 4). Both *A. colemani* and *L. testaceipes* have a very high daily reproduction and a short development period. The population growth rates are slightly lower than for *A. gossypii*. The life span of the parasitoids is only a few days. This might create problems when these parasitoids are used for preventive introductions in glasshouses, because the introduced parasitoids will be present for a short period only. *Aphidius*-species can parasitize many aphids during a reproduction period of a few days, whereas *Aphelinus*-parasitoids parasitize less aphids daily over a longer reproduction period. Development of *A. varipes* takes longer than the development of the aphidiine parasitoids at 20 °C, but at temperatures above 25 °C the development times and population growth rates are equal. The life span of *A. varipes* is considerably longer than for *A. colemani*.

Aphelinus varipes parasitoids will survive periods of low aphid density for a longer period.

Searching behaviour of Aphidius colemani

The searching behaviour of *A. colemani* is described in Chapter 5. Few oviposition experiences increases the responsiveness of females to host plants. The parasitoids are able to detect the presence of aphids on a leaf from a short distance even if no directed air current is present. When the parasitoids can choose between a clean and an aphid infested leaf, most of the parasitoids fly to the aphid infested leaf. Oviposition experiences on the grain aphid *Rhopalosiphum padi* Linnaeus (Homoptera: Aphididae) do not change the in-flight host location by *A. colemani*. Therefore, the use of banker plants with *R. padi* will probably not influence the searching behaviour of *A. colemani*.

Once in an aphid colony the functional response (the reaction of individual parasitoids to the number of aphids present) of *A. colemani* is sigmoid. The increase of the parasitization rates is clearest at densities of up to ten aphids per leaf disk. At higher aphid densities the parasitization rate decreases gradually. After re-entering a recently visited leaf disk the parasitoid stays for a much shorter time than the first visit. No evidence of patch marking is found, so the reduction of visiting times is probably caused by encounters with parasitized hosts.

Also the time allocation of individual *A. colemani* female parasitoids foraging for *A. gossypii* nymphs on cucumber leaves has been investigated. The leaving tendency only decreases on leaves with a high host density (100 aphids), thus increasing the giving up time since the latest encounter. Rejection of aphids and the nearby presence of another aphid colony has no influence on the leaving tendency. The effect of the number of hosts encountered differs among aphid densities. When less than ten aphids are present the leaving tendency is much larger after 30 encounters than beforehand. At a density of 100 aphids the leaving tendency is lower than at the other aphid densities and increases only after 100 encounters. Repeated visits to leaves with ten unparasitized aphids results in an increase in the leaving tendency after approximately ten visits. These results can be explained by assuming that the parasitoids have some innate expectancy of the spatial distribution of hosts (which is likely to be clustered) and concentrate their searching time on high density patches.

Application of Aphidius colemani

In Chapter 6 application of *A. colemani* is studied. The effect of repeated introductions of parasitoids depends highly on the timing and size of the introductions. Natural enemies have to be present in large numbers to obtain sufficient and immediate control. With lower introduction rates not all aphids will be parasitized. As a consequence the aphid population keeps on growing. Sufficient control is only obtained when the parasitoid population has built up sufficiently, which might be too late to prevent damage to the crop. Especially in summer successful control will be difficult to obtain because at the higher temperatures the colonies which are not found by the parasitoids will grow much faster.

An open rearing with wheat plants and grain aphids (*R. padi*) can be used to maintain a parasitoid population, independent of the occurrence of cotton aphid in the glasshouse. Compared to weekly introductions the open rearing method gives initially a much better aphid control, mainly because of the high number of parasitoids than can be reared on the open rearings. At the end of the cucumber cropping hyperparasitoids can occur on the open rearing of the parasitoids. At this point the number of parasitoids will decrease, followed by an increase

in aphid numbers. If hyperparasitoids start to increase, other natural enemies (like the gall midge, *A. aphidimyza*) can also be introduced with the open rearing method. In glasshouses with repeated introductions the influence of hyperparasitoids is much less, even though they do also occur in these glasshouses.

Apart from *A. gossypii* several other aphid species frequently are a pest in glasshouses. The most important species are the tomato aphid, *Macrosiphum euphorbiae* Thomas (Homoptera: Aphididae) and the peach aphid *M. persicae*. A short test, as done for evaluation of parasitoids in Chapter 4 is used to test whether *A. colemani*, *A. matricariae*, *E. cerasicola* and *L. testaceipes* can be useful for control of these aphids too. None of the parasitoids produces mummies on *M. euphorbiae*. Only *A. colemani* parasitizes *A. gossypii* and *M. persicae* successfully and it is concluded that *A. colemani* seems to be the most suitable species for control of both cotton and green peach aphid.

In the general discussion (Chapter 7) it is concluded that evaluation of parasitoids based on several individual criteria can give erroneous results. Life history data of *A. colemani* and *L. testaceipes* are not very different, whereas there is a large difference in the effectivity in glasshouses. Also it is made clear that evaluation of different types of parasitoids is difficult in the laboratory. Additionally, the importance of individual evaluation criteria will depend on the system that is studied and the type of control that has to be obtained. For aphid control in glasshouses it is important that a rather constant low aphid level is maintained. A good searching capacity (finding aphid colonies quickly) is a very important characteristic of a successful natural enemy. Aphid colonies have to be found quickly to prevent the colonies from becoming too large. Because aphid parasitoids are able to reduce the aphid population to very low levels (where also only a small amount of parasitoids will be present) the system is very sensitive to incoming aphids. The only way to obtain sufficient control is by ensuring a continuous presence of a sufficient amount of parasitoids. If this succeeds successful control of *A. gossypii* can be obtained by using the parasitoid *A. colemani*.

Chapter 1

Introduction

1 Introduction

Integrated pest management in glasshouses

In the Netherlands integrated pest management is applied on a large area of glasshouses with vegetables (van Schelt, 1993). Since the late 1960s the two-spotted spider mite *Tetranychus urticae* Koch (Acari: Tetranychidae) was the first pest to be controlled on a large scale with the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae) (Ravensberg *et al*, 1983; van Lenteren & Woets, 1988). Since 1971 whitefly (*Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae)) could be controlled in tomato with the parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) (Koppert, 1978). At present biological control is used on a large area of glasshouse-grown cucumber, sweet pepper and tomato crops (van Schelt, 1993). For example, in 1993 integrated pest management was used on 899 out of 920 ha glasshouse cucumber crops (Ramakers & Rabasse, 1995). The use in smaller crops like eggplant and melon is increasing. Only 6.5% of the glasshouse vegetable growers did not use any biological control method in 1993 (Extension Service Information Bulletin 1994). The amount of glasshouse vegetables under biological control is given in Table 1.

In contrast to the beginning of biological control, when only one or two pests could be controlled with one natural enemy each, many natural enemies are available now to growers. For each pest one to six natural enemies can be used (examples in Table 1), although several of these species are used on a small scale only.

Several factors have contributed to the spread of biological control in glasshouses. First, once the first pests were controlled biologically, the use of pesticides against other pests became limited because application disrupted biological control. In the beginning of the eighties,

Table 1
Natural enemies used in Dutch vegetable cultures and glasshouse vegetable area under biological control.

pest	frequently used natural enemies	incidentally used natural enemies	glasshouse vegetables under biological control (ha (%))
whitefly	*Encarsia formosa*	*Macrolophus carnosum* *Verticillium lecanii* *Delphastus pusillus*	3715 (78.6)
leafminers	*Dacnusa sibirica* *Diglyphus isaea*		2141 (45.3)
aphids	*Aphelinus abdominalis* *Aphidius colemani* *Aphidius matricariae* *Aphidoletes aphidimyza* *Hippodamia convergens*	*Chrysoperla carnea* *Verticillium lecanii*	2543 (53.8)
spider mite	*Phytoseiulus persimilis*		2751 (58.2)
thrips	*Orius laevigatus* *Amblyseius cucumeris* *Amblyseius degenerans*	*Amblyseius spp.* *Orius spp.* *Verticillium lecanii*	2444 (51.7)
caterpillars	*Bacillus thuringiensis*	*Trichogramma evanescens*	2482 (52.5)

for example, the chemical control of leafminers and thrips interrupted the biological control of whitefly (van Lenteren *et al*, 1979; Ravensberg *et al*, 1983). Therefore, alternative methods had to be used for these secondary pests as well (van Lenteren *et al*, 1979; van Lenteren & Woets, 1988; van Schelt, 1993). Second, the occurrence of strains or species of pest insects, which are resistant to commonly used insecticides, has encouraged integrated pest management (IPM) to a large extent (Ramakers, 1989). Third, the application of bumble bees for pollination in tomato, sweet pepper and eggplant crops limits the use of a broad range of chemicals (Ramakers, 1989). Finally, IPM programmes are stimulated by governmental policies to reduce the use of chemicals and by increasing concern over residues remaining on the fruits after a pesticide application (Ramakers, 1989).

At the end of the 1980s, aphids were one of the factors hampering the implementation of IPM. The occurrence of aphids in glasshouses (especially *A. gossypii* in cucumber crops) restricted the use of IPM because biological control was difficult to achieve and chemical control of *A. gossypii* could not be integrated in IPM programmes (Ramakers, 1989).

Pest status of the cotton aphid, Aphis gossypii

The cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), is an important pest on different kinds of crops throughout the world. Its first record as a pest was in cotton in 1854 in South Carolina, U.S.A. (Paddock, 1919). Since then it has spread over the U.S.A. and has caused much damage to cotton, cucumber, melon and orange crops (Paddock, 1919). In 1919

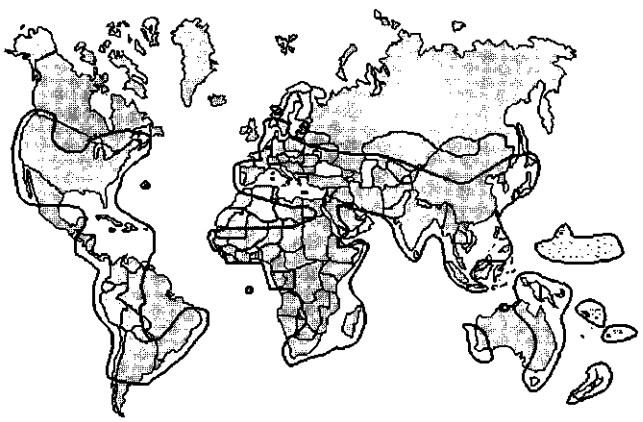

Figure 1
Distribution of the cotton aphid, *Aphis gossypii* Glover (Commonwealth Institute of Entomology, Distribution Maps of Pests, Series A, Map No. 18, 1968). Outside this area (e.g., in Canada, Finland and the United Kingdom) *Aphis gossypii* can occur in glasshouses but no establishment of the aphid has been shown.

A. gossypii also occurred in Africa, South America, Indonesia and the Mediterranean area (Paddock, 1919).

Since the end of the 1980s *A. gossypii* is an important aphid pest on cucumber in the Netherlands (van Schelt *et al*, 1990). Its occurrence in other glasshouse crops, like sweet pepper, is increasing. Scopes & Biggerstaff (1976) demonstrated the serious nature of this pest. Only 35 days after the introduction of two aphids on each cucumber plant (bearing 11 leaves) a total collapse of the crop followed.

Through a combination of biological and chemical control the growers try to keep the aphid population density as low as possible, but even at low aphid densities damage can occur. Most damage is caused by contamination of the fruits with honeydew, which decreases the economic value of the fruits. When aphids feed on the growing tips of the plants the new shoots can get heavily distorted and plant growth is reduced. Also, the cotton aphid is a vector of about 50 plant viruses (Blackman & Eastop, 1984). In cucumber the cucumber mosaic virus is the most important virus. De Brouwer & van Dorst (1975) showed that occurrence of this virus is strongly correlated with the occurrence of *A. gossypii*. At higher aphid densities fungi will grow on honeydew contaminated leaves, decreasing the photosynthetic capacity and yield of the crop (Cichocka *et al*, 1992).

Aphid control

At the time this project was started integrated aphid control in cucumber and sweet pepper crops consisted of introduction of the parasitoid *Aphidius matricariae* Haliday (Hymenoptera: Braconidae) and the predatory gall midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) (van Schelt *et al*, 1990). On a small scale Common green lacewings (*Chrysoperla carnea* Stephens (Neuroptera: Chrysopidae)) and Convergent lady bird beetles (*Hippodamia convergens* Guérin (Coleoptera: Coccinellidae)) were introduced against aphids. Additional control was obtained by using pirimicarb, a selective aphicide.

Integrated control of *Myzus persicae* Sulzer (Homoptera: Aphididae) in sweet pepper was effective (van Schelt *et al*, 1990), but *A. gossypii* was little affected by the introduced parasitoids (Ramakers, 1989). Furthermore, corrective applications of the selective aphicide pirimicarb had no effect on *A. gossypii*, since *A. gossypii* had developed resistance against this chemical (Hardee *et al*, 1990; Grafton-Cardwell, 1991; Grafton-Cardwell *et al*, 1992; Kerns & Gaylor, 1992; Gubran *et al*, 1993; Silver *et al*, 1995). Using less selective pesticides for aphid control results in increasing problems with spider mites (*T. urticae*), whitefly (*T. vaporariorum* and *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae)) and thrips (*Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae)), because their natural enemies are very sensitive to many pesticides. To be able to use biological control of other pests it is therefore necessary to develop an effective biological control programme for aphids as well.

The aim of this project is to evaluate natural enemies that can be used in IPM programmes in cucumber and to develop and implement an efficient method for biological control of aphids. In this first chapter a review of literature data regarding the biology of cotton aphid and its natural enemies will be given. Based on these data a first evaluation of natural enemies can be made and it will be made clear where significant data, which are necessary for a thorough evaluation of natural enemies of aphids, are lacking. With this information a research strategy will be designed for the evaluation of natural enemies and the implementation of biological control with the natural enemies selected.

1.1 *Aphis gossypii* Glover

Introduction

Aphis gossypii is distributed world-wide (Figure 1) and is particularly abundant in the tropics. In temperate regions the species is probably confined to glasshouses (Blackman & Eastop, 1984). North of the 50th parallel the aphid is not found anymore (Starý, 1967). *Aphis gossypii* is closely related to European *Aphis spp.* of the *Aphis frangulae* Kaltenbach-group, which indicates a palaearctic origin (Blackman & Eastop, 1984).

The taxonomic status of *A. gossypii* is still unclear. For this reason some authors prefer to speak of an *A. frangulae-gossypii*-group (e.g., de Brouwer & van Dorst, 1975). Because of the difficulties with the taxonomic status 41 synonyms have been used (Paddock, 1919; Patch, 1925; Börner, 1952; Böhm, 1966; Ilharto & van Harten, 1987). In this thesis the taxonomy according to Blackman & Eastop (1984) will be used:

Order:	Hemiptera
Suborder:	Homoptera
Superfamily:	Aphidoidea
Family:	Aphididae
Subfamily:	Aphidinae
Genus:	*Aphis*
Species:	*Aphis gossypii* Glover 1854

Host range

Aphis gossypii is extremely polyphagous and has been recorded on more than 50 families of host plants (see the Appendix). On a world-wide basis *A. gossypii* comprises an indefinite number of anholocyclic lines, some of which may have particular host plant associations (Blackman & Eastop, 1984). Each line can have distinct and different host plant preferences (Table 2).

Morphology

The apterae are very variable, both in size and in colour. In general their size is between 0.9 and 1.8 mm (Blackman & Eastop, 1984). Under favourable conditions the aphids are large and have a dark green, almost black colour and six segmented antennae (Blackman & Eastop, 1984). Dark siphunculi are present in all morphs (Blackman & Eastop, 1984). Adults produced in crowded colonies or at high temperatures may have a size of less than one mm and are very pale to almost white (Blackman & Eastop, 1984). The temperature has a marked influence on the colour and the size of the aphids. The higher the temperature, the paler (Inaizumi, 1980) and smaller the aphids will

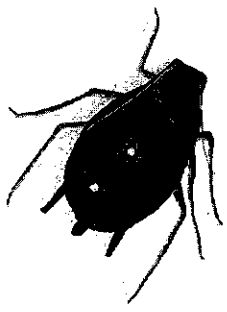

Figure 2
An apterous adult of the cotton aphid, *Aphis gossypii* Glover.

be (Scopes & Biggerstaff, 1977; Aldyhim & Khalil, 1993). A small and yellow aestivating morph with five segmented antennae and short siphunculi can occur in summer (Kring, 1959). The colour and morphology of the aphids are also influenced by the host plant on which the aphids feed (Batchelder, 1927; Inaizumi, 1981; Ekukole, 1990). Body size and length of appendages are directly correlated with colour, the darker morphs being larger (Wall, 1933).

The alatae have shiny bodies with a less variable green to brown colour (Patch, 1925) and a size of 1.1 to 1.8 mm (Blackman & Eastop, 1984). They are produced in crowded colonies and under suboptimal conditions (Reinhard, 1927).

The apterous oviparae and the winged males are dark green (Patch, 1925).

Table 2
Suitability of different host plants for several lines of *Aphis gossypii*.

CRUZ & BERNARDO (1971)

clone	chrysanthemum	citrus	cotton	cucumber	eggplant	hibiscus	melon	potato	strawberry
		– –				+ +	– –		

FURK & HINES (1993)

clone	chrysanthemum	citrus	cotton	cucumber	eggplant	hibiscus	melon	potato	strawberry
80-005	+ +		+ –	– –					
81-171	– –		+ +	+ +					
85-015	+ +		+ +	– –					
87-043	– –		+ +	+ +					

SAITO (1991)

clone	chrysanthemum	citrus	cotton	cucumber	eggplant	hibiscus	melon	potato	strawberry
M-1				+ +	– –		+ +	+ –	+ +
C-1				+ +	– –		+ +	– –	+ +
E-1				+ –	+ +		– –	+ +	+ +
E-10				+ +	+ +		– –	+ +	+ +
P-1				+ –	+ +		+ –	+ +	+ +
VM-6				+ +	– –		+ +	– –	+ –
VM-8				+ +	– –		+ +	– –	+ +
VE-5				+ –	+ +		– –	+ –	+ –
HE-2				+ –	+ +		– –	+ +	+ –
S-4				– –	+ –		– –	+ –	+ –

+ + suitable
+ – reasonably suitable
– – not suitable

Table 3
Life history data of *Aphis gossypii*.

(a) Influence of different constant temperatures on the life history data of *Aphis gossypii* feeding on cucumber (*Cucumis sativus* cv. 'Sandra')

temperature (°C)	devel. time (days)	imm. mort. (%)	pre-repr. period (days)	repr. period (days)	life-time fecundity (nymphs/♀)	reference
10.0	75.9		18.5	35.5	35.7	Kocourek *et al* (1994)
17.0	10.7		1.7	37.0	61.3	Kocourek *et al* (1994)
20.0	7.9		1.0	21.1	55.7	Kocourek *et al* (1994)
25.0	6.0		1.0	22.0	53.6	Kocourek *et al* (1994)
30.0	5.1		0.9	22.0	76.1	Kocourek *et al* (1994)

(b) Influence of host plant species on the life history data of *Aphis gossypii* at a constant temperature of 20 °C

host plant	devel. time (days)	imm. mort. (%)	pre-repr. period (days)	repr. period (days)	life-time fecundity (nymphs/♀)	reference
Citrus unshiu[a]	7.6[b]	8.7		25.7[c]	63.6	Komazaki (1982)
Cucumis melo					80.4	Narai & Murai (1991)
Cucumis sativus	7.9		1.0	21.1	55.7	Kocourek *et al* (1994)
Cucurbita pepo	8.7	0.0	1.9	20.5	44.4	Aldyhim & Khalil (1993)
Gossypium hirsutum	7.9			50.0[b,c]	71.3	Barkay (unpublished)[d]
Guava	8.0			26.2	34.0	Liu & Hwang (1991)
Veronica persica	5.1	0.0			61.6	Nozato (1987)[d]

a at 19.8 °C; b including pre-reproductive period; c including post-reproductive period; d partly extracted from graphs

(c) Influence of melon cultivar (*Cucumis melo*) on the life history data of *Aphis gossypii* on melon at a temperature fluctuating between 15 and 25 °C

cultivar	devel. time (days)[a]	imm. mort. (%)	pre-repr. period (days)	repr. period (days)	life-time fecundity (nymphs/♀)	reference
'Akikei No. 1'	6.0			17.2	81.1	Shinoda & Tanaka (1987)
'Charentais T'	6.0			14.7	75.2	Shinoda & Tanaka (1987)
'Honeydew'	6.1			14.3	71.5	Shinoda & Tanaka (1987)
'PMAR No. 5'	6.7			14.1	46.0	Shinoda & Tanaka (1987)

a including pre-reproductive period

Biology

Relatively few publications with detailed information have appeared on the biology of *A. gossypii* and for the target crop in the Netherlands, cucumber, only data from two publications are available (Wyatt & Brown, 1977; Kocourek *et al*, 1994). On cucumber the life span of the adults varies from about five weeks at 10 to 17 °C to about three weeks at 20 to 30 °C (Table 3). The life-time fecundity is little influenced by temperatures of up to 30 °C, only at very low temperatures the life-time fecundity is lower (Table 3). At temperatures from 17 to 30 °C the pre-reproductive period is one to two days, below this temperature the pre-reproductive period can be several days (Table 3). The post-reproductive period is much longer and takes two to eight days at 20 to 25 °C (Kennedy & Kishaba, 1976; Aldyhim & Khalil, 1993). Alatae live shorter and produce less offspring than apterae (Khalifa & Sharaf El-Din, 1964; Nozato, 1987).

The development time, life-time fecundity and life span differs among host plant species (Table 3). Also among cultivars of one host plant species differences in suitability for cotton aphid can occur (Table 3). The effects of temperature, host plant species and host plant cultivar on the population growth rate of *A. gossypii* are given in Figure 3.

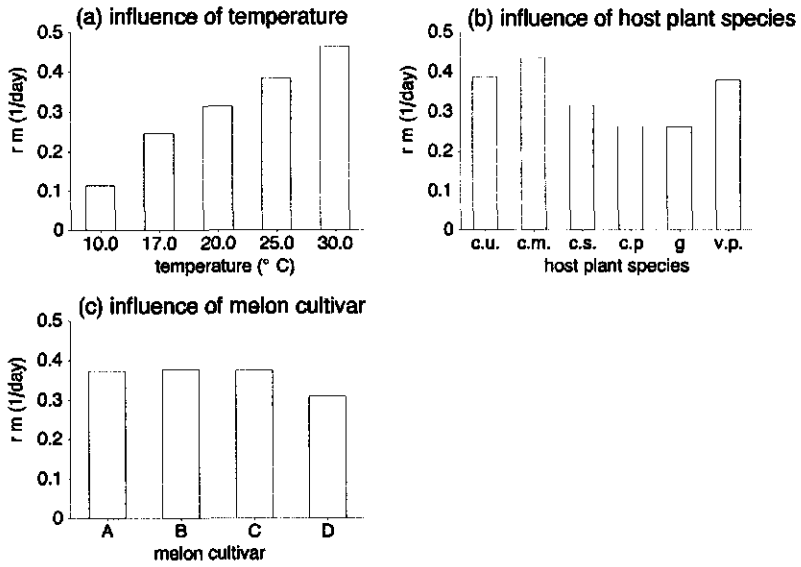

Figure 3
Influence of (a) temperature, (b) host plant species at 21 °C (c.u. = *Citrus unshiu*, c.m. = *Cucumis melo*, c.s. = *Cucumis sativus*, c.p. = *Cucurbita pepo*, g = Guava and v.p. = *Veronica persicae*) and (c) melon cultivar at 15 to 25 °C (A = 'Akikei No. 1', B = 'Charentais T', C = 'Honeydew' and D = 'PMAR No. 5') on the population growth rates of *Aphis gossypii* (a constant reproduction and an immature mortality of 10% was assumed).

On suitable host plants like cucumber or eggplant the development time is five to nine days at average glasshouse temperatures of 20 to 25 °C (Table 3). On suitable host plants the immature mortality is low. Only below 10 °C and above 30 °C a considerable mortality occurs during the immature stages (Aldyhim & Khalil, 1993).

Life cycle

The way of overwintering in areas where the aphid only seems to occur in glasshouses is still unknown. Outside glasshouses *A. gossypii* might overwinter in a holocyclic or in an anholocyclic way and with (heteroecious) or without (monoecious) a change of host plant (Figure 4).

If the aphid population overwinters in a heteroecious holocyclic way the fall eggs are laid by oviparous (egg-laying) and sexually reproducing females on the primary host plants (Patch, 1925; Kring, 1959; Komazaki *et al*, 1979; Blackman & Eastop, 1984) (Figure 4). The primary host plants can include *Catalpa bignonioides* (Bignoniaceae) (Kring, 1959), *Celastrus orbiculatus* (Celastraceae) (Inaizumi, 1981), *Citrus* trees (Rutaceae) (Komazaki *et al*, 1979), *Hibiscus syriacus* (Malvaceae) (Inaizumi & Takahashi, 1988), *Rhamnus nipponica* (Rhamnaceae) (Inaizumi, 1981), *Rubia cordifolia* (Rubiaceae) (Inaizumi, 1981) and *Sedum purpureum* (Crassulaceae) (Patch, 1925). The overwintered eggs hatch next spring. The hatched fundatrices are virginoparous (asexually reproducing) and viviparous. The fundatrices produce the second generation at the primary host plants until, at high aphid densities, many alatae are formed which move to the secondary host plants (Komazaki *et al*, 1979). More than 50 families

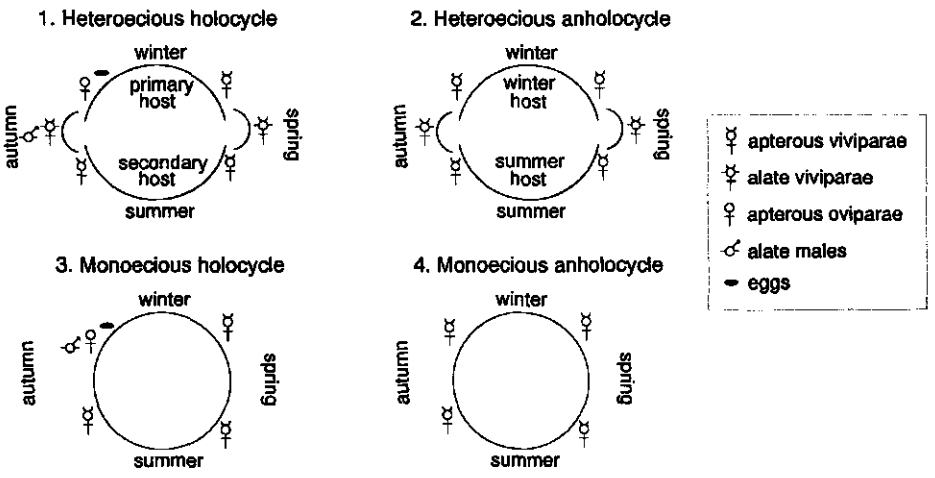

Figure 4
Various annual life cycles as found for *Aphis gossypii* (after Kring (1959) and Inaizumi (1981)).

of plants can serve as secondary host plants for cotton aphid, the Malvaceae and Cucurbitaceae being the most important families (see the Appendix). In autumn winged males and winged viviparous autumn migrants (gynoparae) are produced on the secondary host plants. After migration to the primary host the oviparous offspring of the gynoparae mate with the males and eggs are produced (Kring, 1959; Inaizumi, 1981; Blackman & Eastop, 1984). O'Brien *et al* (1990) found males and oviparae on cotton in Mississippi.

A holocyclic overwintering without a switch of host plants (monoecious) is also possible. In this case the aphids go through the same cycle as described above but stay on the primary host plant throughout the year (Inaizumi, 1981) (Figure 4).

If overwintering is monoecious and anholocyclic, the cotton aphid populations consist of virginoparous females throughout the year and no winter eggs are produced (Figure 4). Anholocyclic overwintering can include a switch from a summer to a winter host (heteroecious) (Figure 4). Kring (1959) demonstrated overwintering as adult in Connecticut, U.S.A., with *C. bignonioides* and *H. syriacus* utilized as winter host. Also in Texas and Florida the normal form of reproduction is asexual throughout the year (Paddock, 1919; Goff & Tissot, 1932). Gillette (1908) could not discover males, oviparous females or eggs in outdoor populations, even when in December temperature was below zero for several nights. The overwintering adults are covered with white wax and are smaller (Inaizumi, 1986).

For glasshouse populations the situation can be more complex. Börner (1952) reports that *A. gossypii* from cucumber nurseries was found to be anholocyclic. However, in his studies of the *A. frangulae-gossypii* problem, Böhm (1966) comes to the conclusion that part of the population on crops in the cucumber family is holocyclic (overwintering on Rhamnaceae), a smaller part is anholocyclic (overwintering in glasshouses) and a considerable part is killed by frost together with the host plant.

1.2 Natural enemies

In the field, aphid numbers increase only with a fraction of their potential rates of increase (Frazer, 1988b). Without natural enemies, aphid populations soon reach very high numbers (Way & Banks, 1968; Tamaki & Weeks, 1972; Maelzer, 1977). Also simulation models showed that natural enemies can have a large impact on the growth of aphid populations (Frazer *et al*, 1981; Raworth, 1984; Gutierrez *et al*, 1990). Many natural enemies of aphids are known, ranging from monophagous to polyphagous species. It is, of course, not possible to thoroughly evaluate all these species for their use in glasshouse biological control programmes in a reasonable amount of time. The most important groups of natural enemies which are more or less specific for aphids and seem to have the best prospects, will be discussed here.

One of the main problems is that only for a few natural enemies biological data with *A. gossypii* as host are available. *Aphis gossypii* is a relatively new glasshouse pest (van Schelt *et al*, 1990) and until recently most research has concentrated on natural enemies of the green peach aphid (*M. persicae*), bean aphids and cereal aphids. For oligophagous natural enemies (like most of the parasitoid species) the biology with these aphids as host is likely to differ from the biology on *A. gossypii* (Starý, 1988a; Starý, 1988b). Even from polyphagous predators, that might also attack insect groups other than aphids, it is known that some aphid species are more suitable as food than others (Scopes, 1969; Gurney & Hussey, 1970; Chambers, 1988).

Three main groups of natural enemies can be distinguished:

1. fungi:
   - Entomophthorales (Zygomycetes)
   - *Verticillium lecanii* (Deuteromycetes)
2. predators:
   - Cecidomyiidae (Diptera)
   - Chrysopidae (Neuroptera)
   - Coccinellidae (Coleoptera)
   - Hemerobiidae (Neuroptera)
   - Syrphidae (Diptera)
3. parasitoids:
   - Aphelinidae (Hymenoptera)
   - Aphidiinae (Hymenoptera: Braconidae)

These groups will be discussed more thoroughly in the next chapter. Apart from the groups listed, several other predators do consume aphids occasionally. Among these are (1) bugs (Hemiptera: Anthocoridae, Miridae, Nabidae) (Goodarzy & Davis, 1958; Way & Banks, 1968; Tamaki & Weeks, 1972; Bouchard *et al*, 1988; Hodgson & Aveling, 1988; Snodgrass, 1991; Bush *et al*, 1993), (2) beetles (Coleoptera: Staphilinidae) (Holmes, 1984), (3) phytoseiid mites (Hoda *et al*, 1986; Golovach, 1989), (4) tetranychid mites (Zhang *et al*, 1993) and (5) lycosid, micryphantid and liniphiid spiders (Mansour & Heimbach, 1993). They do, however, not consume large quantities and will probably not contribute to the regulation of aphid populations (Tamaki & Weeks, 1972).

1.2.1 Pathogens

Fungi are considered to be the principal aphid attacking group of pathogens. Viruses, protozoa, bacteria and nematodes also infest aphids, but no epizootics caused by bacteria, viruses, protozoa or nematodes have been reported from aphids (Hagen & van den Bosch, 1968; Latgé & Papierok, 1988). Laubscher & von Wechmar (1992) found that Aphid lethal paralysis virus reduced the fecundity of *R. padi*.

Several abiotic factors govern the presence and development of fungal pathogens in aphid populations. Relative humidity is the most critical environmental factor (Latgé & Papierok, 1988). Moisture and temperature requirements differ from one fungal species to another, but in general the relative humidity has to be high (90%) for a certain period to enable successful germination (Wilding, 1969; van der Geest *et al*, 1980; Latgé & Papierok, 1988). It is possible to select strains with variable effectiveness towards an aphid clone (Latgé & Papierok, 1988).

Entomophthorales (Zygomycetes) and the Deuteromycete *Verticillium lecanii* (Zimmermann) Viégas are the most important and virulent species under field and glasshouse conditions (Latgé & Papierok, 1988; Hayden *et al*, 1992).

Zygomycetes

Introduction

The most important fungi from the Zygomycetes belong to five genera of the order Entomophthorales: *Conidiobolus*, *Entomophthora*, *Erynia*, *Neozygites* and *Zoophtera* (Latgé & Papierok, 1988). Under suitable environmental conditions entomophthoraceous fungi can cause

a high mortality in aphid populations (Gustafsson, 1971). Entomophthorales are identified by the shape and size of the different spore types (Latgé & Papierok, 1988).

Host range

The host range of a fungus is species dependent (Latgé & Papierok, 1988). Some species attack a wide range of insect orders while others are more or less specific for aphids or even only a few aphid species (Latgé & Papierok, 1988). Different strains of a fungus species can show a difference in aggressiveness towards aphids (Latgé & Papierok, 1988). Most of the aphid-attacking species are rather selective (Zimmermann, 1983). Also clones of the same aphid species can have a different susceptibility to a fungus (Briese, 1986; Latgé & Papierok, 1988). Entomophthorales are not obligate parasites since most of these fungi can be cultured on artificial substrates (Hagen & van den Bosch, 1968; Latgé & Papierok, 1988).

Biology

A high relative humidity (90% or more) is a prerequisite for sporulation and germination of resting spores (Hagen & van den Bosch, 1968; Wilding, 1969). The most favourable temperature, humidity and nutrient conditions vary among strains and species (Latgé & Papierok, 1988). Fungal disease outbreaks are associated with high aphid densities (Hagen & van den Bosch, 1968). Yearly outbreaks of Entomophthorales in populations of cereal aphids were observed by Feng *et al* (1992).

Infection results from contact with spores which are air-dispersed or by contact with fungus-bearing material (Latgé & Papierok, 1988). Two to four days after infection the aphids die (Wilding, 1969).

Life cycle

The infection starts with the germination of a spore on the integument of a host (Zimmermann, 1978). The resulting germ tube penetrates the aphid cuticle, after which the fungus develops in the haemocoel and subsequently invades the other tissues (Latgé & Papierok, 1988). After the host died, the hyphae penetrate the integument again and start producing new spores (Zimmermann, 1978). Under unfavourable conditions resting spores are produced through asexual or sexual reproduction inside the host (Zimmermann, 1978).

Aphid control

Successful introductions of Entomophthorales are rare (Zimmermann, 1983). This could be contributed to the fact that epizootics occur only when aphid density is high (Latgé & Papierok, 1988) and because of the high humidity that is necessary for germination of spores (Hagen & van den Bosch, 1968; Wilding, 1969). Dedrijver (1979) had reasonable results when *Entomophthora fresii* was used against *Aphis fabae* on broad beans. Sprinkling during the night raised the humidity and improved control (Dedrijver, 1979).

Entomophthorales can be useful in biological control of aphids because the spores are discharged actively and in some species are disseminated by air (Zimmermann, 1983). The resting spores, which are more stable, can be used for storage (Zimmermann, 1983). Parasitoid larvae are also killed when the aphid is infected by *Entomophthora*-fungi. *Entomophthora*-species can survive several months at low humidity inside the mummified aphids (Wilding, 1973).

Entomophthora and *Neozygites*-species are difficult to culture on artificial media and are therefore difficult to rear in large quantities (Latgé & Papierok, 1988). *Conidiobolus*, *Erynia* and *Zoophtera* species can be cultivated in specific artificial media more easily (Latgé & Papierok, 1988).

Deuteromycetes

Introduction

One species of the Deuteromycetes frequently infects aphids: *Verticillium lecanii* (Zimmermann) Viégas. Synonyms of *V. lecanii* are given by Schuler *et al* (1991). *Verticillium lecanii* occurs mainly in tropical and subtropical regions, especially on aphids and scale insects (Zimmermann, 1983).

Host range

The most frequently recorded hosts are scale insects and aphids, but also other insect orders (like Coleoptera and Diptera) are reported as hosts (Hall, 1981b). Not only does *V. lecanii* infest many different kinds of insects (Zimmermann, 1983), also fungi, nematodes, spiders (Aranaea) and mites (Acari) can serve as hosts (Schuler *et al*, 1991). Furthermore the fungus can live saprophagously (Schuler *et al*, 1991). Not all aphid species are equally susceptible to the fungus (Hall & Burges, 1979) and virulence differs among strains (Hall, 1982).

Biology

After application the spores start to germinate under favourable conditions. Spores are not readily released into the air, hence spread of the fungus occurs only if a healthy aphid comes into contact with a diseased one or its footsteps (Burges & Hall, 1976).

Milner & Lutton (1986) showed that maximum infection by the pathogen occurs when the relative humidity is 100% and free water is present. Lower humidities inhibit infection and sporulation, with almost no transmission or sporulation at a relative humidity below 93% (Milner & Lutton, 1986).

Temperature is also important for the development of the fungus. The temperature range in which *V. lecanii* is able to grow depends on the origin of the strain (Schuler *et al*, 1991). The lower range differs from 1 to 5 °C, while the upper temperature range differs from 30 to 37 °C (Schuler *et al*, 1991). The fungus is able to withstand temperatures beyond this range for a short period (Schuler *et al*, 1991). The optimum temperature for spore germination and colony growth is 20 to 25 °C (Hall, 1981b).

Life cycle

Reproduction of *V. lecanii* is asexual (Schuler *et al*, 1991). The germinated spores infect the aphid by hyphal penetration through the cuticle. Dead aphids covered by the fungus can be observed one to two weeks later (Helyer & Wardlow, 1987). The spores are divided into blastospores and conidiospores. Blastospores are bigger than conidiospores (Hall, 1979).

Aphid control

A natural infestation in glasshouses occurs only at high aphid densities (Burges & Hall, 1976). The fungus is sprayed as a spore preparation (Helyer & Wardlow, 1987). *Verticillium lecanii* has given good control of aphids in some cases (Helyer & Wardlow, 1987), but is not always effective because of the difficulty of maintaining the humidity essential for germination and sporulation (Milner & Lutton, 1986). Ekbom (1981) showed that a daily humid period of 16 hours was necessary for mycelial growth and whitefly death. But even with misting control is not always sufficient (Gardner *et al*, 1984). Nor is *V. lecanii* as effective against *A. gossypii* as it is against *M. persicae* (Hall, 1985; Helyer & Wardlow, 1987). This may be due to the sedentary nature of *A. gossypii* which inhibits the spread of an infection (Hall, 1981b; Hall, 1982; Milner & Lutton, 1986; Helyer & Wardlow, 1987). Aphid mortality rises with increasing spore density but in glasshouses this effect is quickly masked by the spread of the fungus (Hall, 1980). In commercial formulations a growth substrate is added to the spores. In this way limited saprophytic fungal growth and sporulation on the leaf surface is possible (Hall, 1982).

Fungicides can reduce the effectiveness of *V. lecanii* application (Gardner *et al*, 1984), but if a careful selection of pesticides and fungicides is made *V. lecanii* can be incorporated in IPM programmes (Hall, 1981a).

The fungus can easily be reared on artificial media (Schuler *et al*, 1991). Conidiospores can be stored and remain viable up to six months at 2 to 10 °C and three months at 20 to 25 °C (Khalil *et al*, 1990).

1.2.2 Predators

Cecidomyiidae (Diptera)

Introduction

This family of the order Diptera consists of 4000 mainly phytophagous species. Some species are saprophagous, zoophagous or endoparasitic. *Endaphis* Kieffer and *Pseudendaphis* Barnes species are internal parasites of aphids, but seem to be more rare than the predacious species (Harris, 1973). A gall midge feeding on aphids was observed first in 1847 by Rondani (Harris, 1982). In the following decennia many more species and genera were described based on the false assumption that gall midges feeding on different aphid species had to be different species (Harris, 1982). Barnes (1929) described 37 specific and 10 generic names divided over 12 genera. At this moment five aphidophagous species are recognized: *Aphidoletes abietis* (Kieffer), *A. aphidimyza* Rondani, *A. urticariae* (Kieffer), *A. thompsoni* (Möhn) and *Monobremia subterranea* (Kieffer) (Harris, 1982). Of these species *A. aphidimyza* is the most widespread and common (Harris, 1982) and will be dealt with here in more detail. Harris (1973) lists 33 synonyms of *A. aphidimyza*.

Host range

Only the larvae are predatory, the adults feed on honeydew (Kuo-Sell, 1987). *Aphidoletes aphidimyza* is polyphagous on Aphidoidea (62 species listed), including *M. persicae* and *A. gossypii* (Harris, 1973).

Morphology

The adults are red-brown midges of about 2.5 mm long (Nijveldt, 1988). The size of the adults depends on the aphid species preyed upon (Kuo-Sell, 1989a, 1989b). Eggs are oval, about 0.3*0.1 mm and orange-red in colour (Nijveldt, 1988). Newly hatched larvae are transparent orange. Depending on the body content of the prey the colour of the larvae can change into yellow, orange, red, brown and even greyish (Nijveldt, 1988). It is assumed that there are three larval instars. The full-grown larvae are about 2.5*0.7 mm and have thirteen body segments (Nijveldt, 1988). They usually descend to the soil to pupate in the upper layer in an oval, brown silk cocoon with a length of about 2 mm (Nijveldt, 1988). Sometimes cocoons can be found on the plant (Nijveldt, 1988).

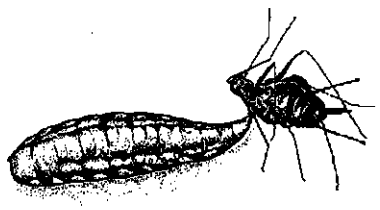

Figure 5
A larva of *Aphidoletes aphidimyza* feeding on an aphid (from Nijveldt (1988)).

Table 4
Life history data of *Aphidoletes aphidimyza*.

(a) Influence of different constant temperatures on the life history of *Aphidoletes aphidimyza* females feeding on *Acyrthosiphon pisum*

temperature (°C)	devel. time (days)	imm. mort. (%)	repr. per. (days)	life-time fecundity (eggs/♀)	reference
17	34.4	35.7			Havelka & Zemek (1988)
20	19.5	19.5			Havelka & Zemek (1988)
25	14	41.7	9.9	139.4	Havelka & Zemek (1988)

(b) Influence of prey aphid species on the life history of *Aphidoletes aphidimyza* at a constant temperature of 20 °C

aphid species	devel. time (days)	imm. mort (%)	repr. per. (days)	life-time fecundity (eggs/♀)	reference
Acyrthosiphon pisum	19.5	19.5			Havelka & Zemek (1988)
Metopolophium dirhodum	17.9[a]	10.0	13.2[b]	224	Kuo-Sell (1987)
Myzus persicae	18.1[a]	13.0	9.8	100	Kuo-Sell (1987)
Rhopalosiphum padi	16.8[c]	9.0			Kuo-Sell (1989b)
Sitobion avenae	16.4[c]	12.0			Kuo-Sell (1989b)

a without egg-stage; b lifespan; c pupal period only

Biology

Aphidoletes aphidimyza adults are nocturnal (Uygun, 1971; Mansour, 1976). Females live 10-15 days at 21 °C (Table 4), males live several days shorter (Uygun, 1971; Sell, 1984; Kuo-Sell, 1987). Without any food females live at average three days (Uygun, 1971). The presence of aphids and/or honeydew lengthens the longevity of females and supports the maturing of eggs (Uygun, 1971).

A female deposits her eggs only close to or in dense colonies of *A. gossypii* (Scopes, 1981). Eggs are deposited on the lower leaf surface (El Titi, 1973; Mansour, 1975) and are laid singly or in clusters among the aphids (Nijveldt, 1988). Honeydew and the presence of dead aphids stimulate egg laying but in the presence of living aphids most eggs are deposited (El Titi, 1974b). One female deposits 100 to 250 eggs during her life (Table 4). Most of the eggs are deposited during the first eight days of the oviposition period (Havelka & Růžička, 1984). The total number of eggs produced by a female midge depends on larval feeding and on honeydew intake by the adult (Kuo-Sell, 1987). The number of eggs deposited by a female can depend on the aphid species (Havelka & Růžička, 1984; Kuo-Sell, 1989a). Preference for oviposition on a certain host plant species is present and can be changed in several generations towards the species the gallmidges are cultured on (Mansour, 1975).

The progeny of individual females is unisexual (monogenic), apparently the males have no influence on the sex of their progeny (Sell, 1976). Nevertheless, mating is necessary for production of fertile eggs (Sell, 1976). Overall the sex ratio is 50 to 70% females (Uygun, 1971; Havelka & Zemek, 1988).

The egg stage lasts three to four days (Wilbert, 1973). Immediately after hatching the larvae start searching for aphids (Wilbert, 1973). Once they find an aphid they paralyse and hold it when extracting body fluids (Wilbert, 1973). The larvae are able to recognize aphids from a short distance by olfaction, maybe visual cues also play a role (Wilbert, 1974). The young larva has a very limited searching area, therefore it is very important that eggs are deposited close to

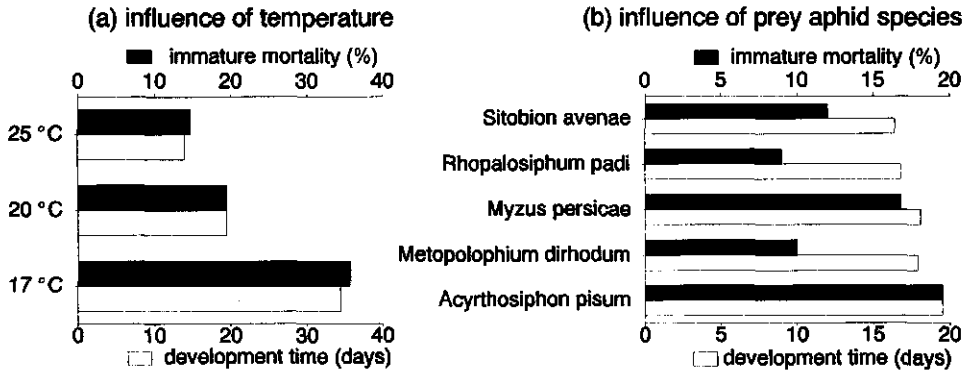

Figure 6
Influence of (a) temperature and (b) prey aphid species at 20 °C on the development time and immature mortality of *Aphidoletes aphidimyza* (data from Havelka & Zemek (1988) and Kuo-Sell (1989b)).

or in aphid colonies (Wilbert, 1973). The development from egg to adult takes about 17 days at 21 °C (Table 4). With rising temperatures the development time shortens (Figure 6) (Table 4) and the development time and immature mortality can change when different aphid species are offered as host (Figure 6). The development time and the optimal temperature for development differs among populations (Havelka & Zemek, 1988).

The number of aphids killed during the larval stages is rather variable and depends on the size of the aphids (Nijveldt, 1988; Uygun, 1971), aphid species (Kuo-Sell, 1987; Nijveldt, 1988; Table 4) and temperature (Uygun, 1971). Larval voracity ranges from 30 to 130 aphids in different studies (Table 4). If there is an abundant supply of aphids the midge larvae can kill and feed on more aphids than they need for their development (Uygun, 1971). Through the aphid and its honeydew the host plant can influence larval weight, adult longevity and egg production (Kuo, 1977; Havelka & Růžička, 1984).

Life cycle

In spring adult midges emerge from the diapausing pupae in the soil (Harris, 1973). Larvae can be found from the end of May (Harris, 1973). The midge enters diapause in the beginning of September. Diapause is induced in the last instar, one day before the cocoon is built and in the cocoon (Forsberg, 1980). Among populations, differences in daylength needed for diapause induction exist (Havelka & Zemek, 1988).

Aphid control

Aphidoletes aphidimyza is used for biological control of *A. gossypii* and *M. persicae*, often in combination with the parasitic wasps *A. colemani* and *A. matricariae* (Markkula *et al*, 1979b; van Schelt *et al*, 1990; van Schelt, 1993). Efficient mass rearing methods have been developed (Rimpiläinen, 1980; van Lieburg & Ramakers, 1984). Cocoons readily withstand transport and distribution (Markkula & Tiitanen, 1985). Markkula & Tiitanen (1980) compared several predators and came to the conclusion that only *A. aphidimyza* was able to develop a continuous population for the whole growing season in the glasshouse. Even with successful control a complete destruction of the aphid population is not achieved and continuous introductions of gall midges will have to be made (El Titi, 1974a). In the case of control of *A. gossypii* in cucumber problems can rise due to the enormous reproductive capacity of this aphid. Only regular releases (once a week) at high predator-prey ratio (8-10 cocoons/m²) can prevent the increase of *A. gossypii* on chrysanthemums (Scopes, 1981; Chambers, 1990). The midges can also be introduced through an open rearing unit with cereal aphids (Kuo-Sell, 1989b).

In practice, results are not always satisfactory, partly because the midge enters diapause in the beginning of September, resulting in a rapid increase of the aphid density (Hofsvang & Hågvar, 1982). Additional light (with low intensity) in the glasshouse can prevent diapause (Gilkeson & Hill, 1986a; Gilkeson, 1990). The problem of diapausing midges might also be solved by selecting for non-diapausing populations. Havelka & Zemek (1988) showed differences in the photophase necessary for the onset of diapause among different populations. Indeed, Gilkeson & Hill (1986b) were able to select a non-diapausing population without any change in morphology, sex ratio or fecundity. The effect of relaxing pressure was a gradual increase in diapause incidence, until after eight generations the former diapause incidence was present again (Gilkeson & Hill, 1986b). Induced diapause can be used for long-term storage of pupae (Forsberg, 1980; Tiitanen, 1988).

Another problem occurring in glasshouses is the absence of suitable pupation substrates in glasshouses where plants are grown on rockwool and the floor is covered with plastic (Buxton *et al*, 1990; Gilkeson, 1990; van Schelt *et al*, 1990). Some kind of protection for the pupae like sawdust or peat could be advantageous (Markkula *et al*, 1979a; Gilkeson, 1990).

Finally pirimicarb treatments can cause problems because pirimicarb treated plants are repellent to gall midge females for at least three weeks (Gilkeson, 1990).

Chrysopidae (Neuroptera)

Introduction

The Chrysopidae are a family belonging to the order Neuroptera. Although green lacewings are polyphagous they are frequently found in association with aphids (New, 1988). Green lacewings are distributed throughout the world and have occasionally been found to be important aphid predators, especially in temperate regions (New, 1988).

Host range

Chrysopids are polyphagous predators and accept aphids as part of a broad spectrum of mainly soft-bodied and slow-moving prey (New, 1988). Adults feed on honeydew and pollen (e.g., *Chrysoperla carnea* Stephens) (New, 1988) or on aphids and other prey (e.g., *Chrysopa oculata* Say) (Burke & Martin, 1956). The larvae are always predaceous. Not all aphid species are equally suitable as prey (Canard, 1970). In absence of prey cannibalism occurs (Canard & Duelli, 1984) and newly hatched larvae may suck out other eggs (Bänsch, 1964).

Morphology

The wings of the adults are usually large and broadly oval, with a rich and regular venation (Barnard, 1984). Eggs are placed on a stalk (the pedicel) to prevent predation and cannibalism (Duelli, 1984b). There are three larval stages followed by a prepupa and a pupa (Canard & Principi, 1984). In many chrysopids the larvae cover themselves with debris as protection against predators (Canard & Principi, 1984). Others (like *C. carnea*) have naked larvae, which are active hunters, characterized by swift movements, aggressive behaviour and fast growth (Canard & Duelli, 1984). The third instar spins a cocoon in which the pupation occurs (Canard & Principi, 1984). The site selected for cocoon spinning differs among species and can be attached to leaves or twigs, in trunks or in the soil (Canard & Principi, 1984). Before moulting into adult the pupa emerges from the cocoon in search for a good moulting site (Canard & Principi, 1984).

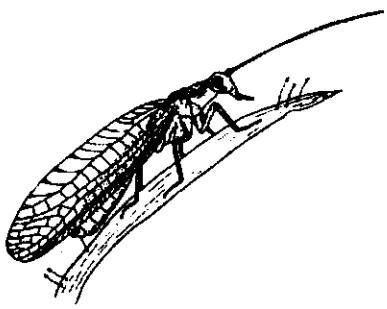

Figure 7
An adult *Chrysopa sp.* (from New (1988)).

Biology

In general the longevity of adults is several months (Table 5), but can be up to seven months for diapausing adults (Canard & Principi, 1984). There are no differences in lifespan between males and females (Samson & Blood, 1979). The pre-oviposition period in non-diapausing adults

Table 5
Life history data of Chrysopidae.

(a) Life history data of several Chrysopidae species feeding on aphids at a constant temperature of 20 to 22 °C

species	development time (days)			imm. mort (%)	life-time fec. (eggs/♀)	sex ratio (%♀)	larval voracity (aphids)	reference
	egg	larva	pupa					
Chrysoperla carnea		14.0	16.9	27.0		46.0		Obrycki *et al* (1989)
Chrysopa oculata		12.5	11.8	18.8		44.0		Obrycki *et al* (1989)
Chrysopa perla	4.2	12.9		4.0	350	50.0		Canard (1970)

(b) Influence of different constant temperatures on the life history data of *Chrysoperla carnea* feeding on aphids

temperature (°C)	development time (days)			imm. mort (%)	life-time fec. (eggs/♀)	sex ratio (%♀)	larval voracity (aphids)	reference
	egg	larva	pupa					
15.5		29.5					371	Scopes (1969)
16.0	<<	69.0	>>				298	Sundby (1966)
20.0		13.6					233	Zaki (1987)
21.0	5.6	14.6	14.9	18.2	477		393	Sundby (1966)
22.0		14.0	16.9	27.0		46.0		Obrycki *et al.* (1989)
25.0	<<	25.0	>>	35.5	772.3	61.5		Grafton-Cardwell & Hoy (1986)
30.0		8.4					273	Zaki (1987)

a lifespan

(c) Influence of prey aphid species on the life history data of *Chrysopa perla* at a constant temperature of 20 °C

prey aphid species	development time (days)			imm. mort (%)	life-time fec. (eggs/♀)	sex ratio (%♀)	larval voracity (aphids)	reference
	egg	larva	pupa					
Aphis sambuci	6.0	14.0		31.0	141	34.8		Canard (1970)
Brevicoryne brassicae	10.3	19.2		53.0	45	22.2		Canard (1970)
Macrosiphum rosae	5.4	13.4		10.0	191	45.0		Canard (1970)
Megoura viciae	8.0	15.0		27.0	4	35.0		Canard (1970)
Myzus persicae	4.2	12.9		4.0	350	50.0		Canard (1970)

in general takes four to ten days (Duelli, 1984b), but also a pre-oviposition period of 39 days has been recorded (Burke & Martin, 1956). Most species lay their eggs singly, but also groups or clusters with the stalks more or less joined can be found in some species (Gepp, 1984). Egg deposition occurs in the evening and at night (Duelli, 1984b). Twenty to forty eggs are deposited per night (Duelli, 1984b). One female can produce several hundreds of eggs (Table 5). In general the sex ratio is approximately 50% (Table 5). The female of *C. carnea* deposits her eggs in the vicinity of aphids (Sundby, 1966). Females of *C. carnea* are attracted by the scent of honeydew of a number of homopteran insects (Duelli, 1984a; Hagen *et al*, 1976) and possibly by some habitat kairomones (Duelli, 1984a).

Unmated females deposit only a few infertile eggs per night (Duelli, 1984b). Unfertilized eggs are sterile (Canard & Principi, 1984). Under normal conditions the mortality of *C. carnea* eggs is 10 to 15% (Sundby, 1966; Grafton-Cardwell & Hoy, 1986).

The larval mortality of *C. carnea* is seven percent (Grafton-Cardwell & Hoy, 1986). When only water is available larvae live 3.8 days, when both water and honey is available the duration of the larval stage is 24.3 days (Sundby, 1966).

The larva of *C. carnea* consumes 200 to 400 aphids during development (Table 5), of which more than 80 percent is consumed during the third instar (Scopes, 1969). Rates of predation of *C. carnea* larvae increase when prey kairomones are present (Lewis *et al*, 1977), but prey location itself is at random (Canard & Duelli, 1984). The aphid species or honeydew eaten influences the development and reproduction (Canard, 1970; Principi & Canard, 1984; Şengonca *et al*, 1987; Kaya & Oncuer, 1988) (Figure 8). Unsuitable prey may lead to a high larval and pupal mortality or to male sterility (Principi & Canard, 1984). The pupal mortality is 21.5% at 25 °C (Grafton-Cardwell & Hoy, 1986).

Many predators and insect parasitoids attack the various stages of chrysopids (Alrouechdi *et*

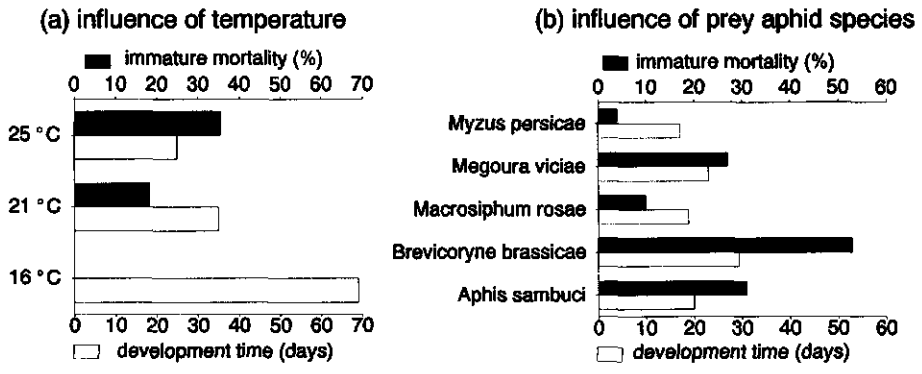

Figure 8
Influence of (a) temperature on the development and reproduction of *Chrysoperla carnea* (see Table 5) and (b) prey aphid species (at a constant temperature of 20 °C) on the egg and larval development time, voracity and reproduction of *Chrysopa perla* (data from Canard (1970)).

al, 1984). Predators play a minor role, but larval and pupal parasitoids can be a significant mortality factor, with parasitization rates of 10 to 80% in field populations (Alrouechdi *et al*, 1984; Gerling & Bar, 1985). Also egg parasitoids can be found (Gerling & Bar, 1985).

Life cycle

Overwintering in temperature regions can occur (i) as adults (*Chrysoperla* type), (ii) as free-living larvae (*Anisochrysa* type) or (iii) as prepupae (*Chrysopa* type) or pupae (*Hypochrysodes* type) inside the cocoon (Canard & Principi, 1984). When the chrysopids overwinter as adults or larvae some food is needed during diapause (Canard & Principi, 1984). Diapause is induced by a short photoperiod, the larva always is the most sensitive stage (Canard & Principi, 1984).

Aphid control

For biological control of aphids most attention has been paid to the common green lacewing *C. carnea*. *Chrysoperla carnea* is a cosmopolitan species (Séméria, 1984). In greenhouses, larvae of *C. carnea* have been successfully used to control *M. persicae* in chrysanthemums and sweet pepper (Scopes, 1969; Hassan, 1977). In chrysanthemums best control was obtained when the chrysopid larvae were introduced close to dense aphid colonies, at low aphid densities the searching capacity of the larvae is insufficient and aphid control fails (Scopes, 1969). On cucumber predation is ineffective because locomotion of the larvae is inhibited by the hairiness of the leaf (Scopes, 1969). The larvae are unable to adhere to the leaf surface by the adhesive anal secretion commonly used in locomotion and anchorage (Spiegler, 1962).

The lacewing population does not renew itself spontaneously and introductions have to be repeated every three to four weeks (Tulisalo & Tuovinen, 1975). With introduction of eggs high egg/aphid ratios are necessary to compensate for mortality and cannibalism (Tulisalo & Tuovinen, 1975). Even with regular releases of eggs, chemical control cannot be avoided (Tulisalo & Tuovinen, 1975).

An advantage of using *C. carnea* in a biological control programme is the resistance of the eggs to many insecticides (Bartlett, 1964; Bigler, 1984). The larvae are apparently not killed by systemic insecticides that are injurious to other predators (Bigler, 1984). Also chrysopids are relatively resistant to many non-systemic insecticides (Bigler, 1984). Furthermore, resistance in *C. carnea* can be induced through selection (Grafton-Cardwell & Hoy, 1986).

Chrysoperla carnea larvae feed also on parasitized aphids, thus reducing the efficiency of parasites (Akinlosotu, 1978; New, 1988), but mummified aphids are not attacked (Akinlosotu, 1978).

Rearing methods (including mass-rearing) of *C. carnea* are described by Tulisalo (1978, 1980), Tulisalo & Korpela (1973), Hassan (1975) and Morrison *et al* (1975). Eggs can be kept at 8-10 °C for several weeks, while recently spun non-diapausing cocoons of *C. perla* can be kept at 6 °C for more than six months, without a reduction in emergence rates (Canard & Principi, 1984). A rearing method for *Chrysopa californica* was described by Finney (1948). Nevertheless, it is difficult to maintain a mass rearing with good quality for longer periods (Tulisalo, 1984). Fecundity, longevity, feeding capacity and searching ability can decrease during mass rearing (Tulisalo, 1984).

Coccinellidae (Coleoptera)

Introduction

Aphidophagous coccinellids are found throughout the world in association with aphids. More than 5000 species of Coccinellidae have been described (Frazer, 1988a). Aphidophagous coccinellids are primarily found in the subfamily Coccinellinae (Frazer, 1988a). Coccinellids have been studied intensively but their role in aphid population dynamics so far remains obscure (Frazer, 1988a). Already in 1908 coccinellids (*Hippodamia convergens* Guérin) were released in North America to control *A. gossypii* on cantaloupes (Hagen, 1962). The adults disappeared within three days and control failed (Hagen, 1962).

Host range

Most species are predators of various Homoptera but they will accept a wide range of food (Frazer, 1988a). Hagen (1962) lists 60 species of aphidophagous Coccinellidae for which the biology has been more or less investigated. Feeding habits vary from monophagy in some coccinellids to polyphagy in most coccinellids (Hagen, 1962). Pollen, fungi and nectar frequently make up part of their diet, although it is not complete enough for egg-production (Hagen, 1962). Different aphid species have different suitabilities, resulting in differences in development time, immature mortality and adult weight (Blackman, 1965; Olszak, 1988). Even aphid species which are toxic to some coccinellids (e.g., *Megoura viciae* Buckton to *Adalia bipunctata* (Linnaeus)) can be a suitable prey for other coccinellids (e.g., *Coccinella septempunctata* Linnaeus) (Blackman, 1965, 1967b). The coccinellids do not avoid feeding on toxic aphids (Blackman, 1967a).

Morphology

Eggs are laid in batches and are mostly attached to leaves with aphids (Blackman, 1967a). The larvae are black with orange dots on the dorsal side. The size and placement of the dots differ among species. In general four larval instars are present (Hagen, 1962; Frazer, 1988a). Adults are easily recognized, because of their brightly coloured and spotted elytra.

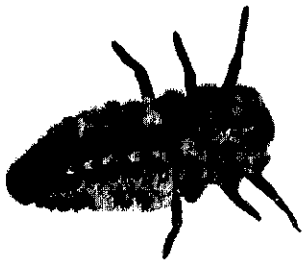

Figure 9
A coccinellid larva.

Biology

Aphids are necessary for the production of eggs (Sundby, 1968). If no aphids are available the adults can survive on a diet of sugar and water (Gurney & Hussey, 1970; Hemptinne & Desprets, 1986), although oviposition is severely reduced on such a diet (Dixon, 1959). Oviposition is resumed within one week after feeding on aphids (Sundby, 1968; Gurney & Hussey, 1970; Hemptinne & Desprets, 1986). The pre-oviposition period is one to two weeks at 20 °C and three weeks at 15 °C (El Hariri, 1966). During the reproductive period of several months hundreds of eggs are produced (Table 6). Daily egg production ranges from 4 to 28

Table 6
Life history data of Coccinellidae.

(a) Life history data of Coccinellidae feeding on *Myzus persicae* at a constant temperature of 20 or 21 °C

species	development time (days)			imm. mort. (%)	repr. per. (days)	life-time fec. (eggs/♀)	references
	egg	larva	pupa[a]				
Adalia bipunctata		10.4		17.8[b]	76.2[c]	676.2	Blackman (1965, 1967b)
Coccinella septempunctata	5	15	8.5	62.0	65	814	Sundby (1966)
Coleomegilla maculata	5.1	17.0	5.1	33.3[d]	73.8[c]	162.6	Wright & Laing (1978)
Cycloneda sanguinea	3.0	16.0	6.0				Gurney & Hussey (1970)

a including the pre-pupa; b larval mortality; c longevity; d without mortality of eggs

(b) Influence of different constant temperatures on the life history data of *Coleomegilla maculata* feeding on *Myzus persicae*

temperature (°C)	development time (days)			imm. mort. (%)	repr. period (days)	life-time fecundity (eggs/♀)	references
	egg	larva	pupa[a]				
16.0	3.0	40.0	5.0				Gurney & Hussey (1970)
19.0	6.9	28.4	7.7	72.6[b]	73.3[c]	74.7	Wright & Laing (1978)
21.0	5.1	17.0	5.1	33.3[b]	73.8[c]	162.6	Wright & Laing (1978)
23.0	3.8	13.7	4.3	32.8[b]	77.2[c]	93.7	Wright & Laing (1978)
25.0	3.0	11.4	3.4	12.9[b]	44.8[c]	85.3	Wright & Laing (1978)
27.3	2.5	9.6	2.9	11.6[b]	79.7[c]	349.5	Wright & Laing (1978)

a including the pre-pupa; b without mortality of eggs; c longevity

(c) Influence of prey aphid species on the life history data of *Coccinella septempunctata* at a constant temperature of 20 °C

prey species	development time (days)			imm. mort. (%)	repr. period (days)	life-time fecundity (eggs/♀)	references
	egg	larva	pupa[a]				
Acyrthosiphon pisum	«	26.7[b]	»	20.0[b]			Olszak (1988)
Aphis fabae		13.6		9.1[c]			Blackman (1965)
Aphis pomi				100.0[b]			Olszak (1988)
Brevicoryne brassicae		16.1		26.1[c]			Blackman (1965)
Dysaphis plantaginae	«	25.0[b]	»	0.0[b]			Olszak (1988)
Megoura viciae		14.8		13.4[c]			Blackman (1965)
Myzus persicae		13.0		12.5[c]			Blackman (1965)

a including the pre-pupa; b without development and mortality of eggs; c larval mortality

eggs (Sundby, 1966; Gurney & Hussey, 1970). The fecundity of the adults depends on the aphid species fed upon (El Hariri, 1966; Blackman, 1967b). The post-oviposition period is short (El Hariri, 1966). Mating is not necessary for egg production but unfertilized eggs are sterile (El Hariri, 1966). The adults often prefer oviposition in colonies of a certain aphid species (Gurney & Hussey, 1970). Males live as long as females (El Hariri, 1966).

About 50% of the eggs of *C. septempunctata* hatch at 21 °C (Sundby, 1966, 1968). The duration of the immature stages depends on temperature, coccinellid and aphid species (Blackman, 1965; Olszak, 1988) (Figure 10) (Table 6). If the number of aphids available is low, development of the larvae takes longer and mortality is higher than in the presence of an abundant amount of aphids (Dixon, 1959). Under favourable conditions and a temperature of 20 to 25 °C development from egg to adult takes 15 to 30 days (Table 6). The immature mortality is very variable and depends on experimental conditions and prey species (Figure 10 and Table 6).

The young coccinellid larvae usually pierce and suck the contents from their prey, often accompanied by periodic regurtation into the prey's body (Hagen, 1962). The number of aphids killed depends on the size and species of aphid and on the stage of the coccinellid (Olszak, 1988). Several hundreds of aphids can be consumed during the larval stages (Table 6). About 80% of the total food eaten is consumed by the fourth instar (Blackman, 1967b). The adult also consumes a considerable amount of aphids (Olszak, 1988).

Coccinellids seem to be able to detect their prey from a short distance (about 1 cm) (Stubbs, 1980; Nakamuta, 1983; Nakamuta, 1984; Frazer, 1988a). After finding a prey the search path of the larvae and adults changes from one of rapid and random movement to one of more extensive search as reflected by more frequent turns (Hagen, 1962; Marks, 1977; Carter & Dixon, 1982; Nakamuta, 1982). The duration of area-restricted searching behaviour following

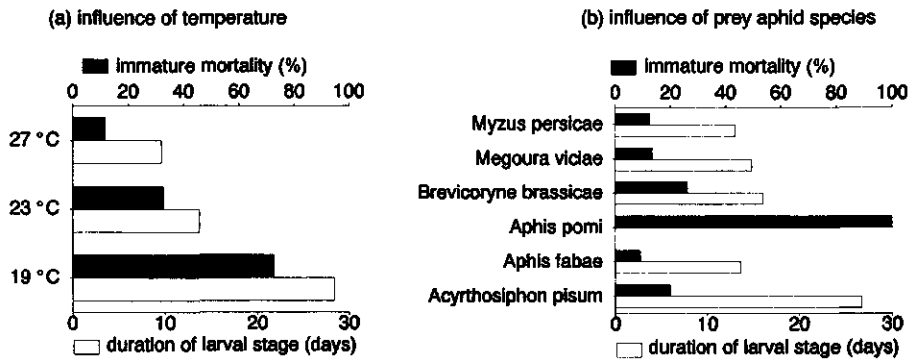

Figure 10
Influence of (a) temperature on the development time and immature mortality of *Coleomegilla maculata* (Wright and Laing, 1978) and (b) prey aphid species on the development time and immature mortality of *Coccinella septempunctata* at 20 °C (Blackman, 1965; Olszak, 1988).

prey encounter increases with increasing hunger (Carter & Dixon, 1982). Plants previously searched unsuccessfully are recognized by detection of a chemical marker, probably secreted via the anal disk during searching (Marks, 1977).

In the presence of prey cannibalism occurs on a small scale (Şengonca & Frings, 1985). Eggs are eaten by all stages, this partly explains the high mortality of the eggs (Şengonca & Frings, 1985). When prey is absent, egg and larval cannibalism increases (Şengonca & Frings, 1985; Takahashi, 1987).

The effect of natural enemies (both predators and parasitoids) on the population dynamics of the lady beetles and aphids is unknown (Frazer, 1988a). Many larval, pupal and adult parasitoids are present (Iperti, 1966), but only from the parasitoid *Perilitus coccinellae* (Schrank) it is known that it can be a significant mortality factor (Frazer, 1988a). Parasitization rates in outdoor populations of *C. septempunctata* can be very high in some years (Semyanov, 1986). The adults can also be attacked by nematodes and fungi (Iperti, 1966).

Life cycle

Many species in the temperate zone hibernate. The intensity of their dormancy varies, even though most species do not oviposit or feed during the winter (Hagen, 1962).

Coccinella septempunctata hibernates in the adult stage and moves from the hibernating quarters in April or early May (Sundby, 1966). The hibernating adults of *C. septempunctata* start feeding as soon as aphids are available in spring. The females produce their progeny during the summer and die (Sundby, 1968). Photoperiod has the most important influence on diapause (Hodek, 1986). Temperature, food availability and population density modify the photoperiodic response (Hodek, 1986). The daylength necessary for diapause induction differs among species and populations of the same species (Hodek, 1986).

Depending on its origin *C. septempunctata* has one to several generations a year (Hagen, 1962). Several species are known to have successive generations without diapause (Hagen, 1962).

In Japan *C. septempunctata bruckii* has a photoperiodically regulated aestivation diapause to survive the dry summer period (Hodek, 1986).

Aphid control

Biological control of aphids in glasshouses with coccinellids gave varying results (Gurney & Hussey, 1970; Hämäläinen, 1977). Introduction of larvae gives better control of aphids than introduction of adults (Hämäläinen, 1977). Especially when aphid densities are low the adults do not stay on the plants but tend to leave the glasshouse (Hämäläinen, 1977). Coccinellidae are not able to form a self-perpetuating population in a glasshouse (Hämäläinen, 1977) and repeated introductions have to be made. High temperatures in glasshouses may cause problems since eggs of *A. bipunctata* do not hatch at temperatures above 35 °C (Hämäläinen, 1980).

A simulation model of the population dynamics of pea aphids and coccinellids showed that the coccinellids can be an important aphid mortality factor (Frazer *et al*, 1981). However, field data suggest that without augmentation of coccinellids, their population development lags behind the development of the aphid population and that the subsequent reduction of aphids is too late to get control without considerable damage to the plants (Atwal & Sethi, 1963).

Some coccinellid species can be reared successfully on an artificial diet made from honeybee larvae and pupae (Niijima *et al*, 1986). On an artificial diet mortality is higher, development

takes longer and less eggs are produced (Kariluoto, 1980). Cold storage of adults and larvae of *A. bipunctata* for some weeks is possible (Hämäläinen, 1980). Cold storage of *C. septempunctata* adults causes high mortality, it is however possible to store eggs for one week at 10 °C without a marked decrease in hatchability (Hämäläinen, 1980).

Coccinellids do not discriminate between parasitized and unparasitized aphids, even a small fraction of the mummified aphids will be attacked (Akinlosotu, 1978).

Hemerobiidae (Neuroptera)

Introduction

Most Hemerobiidae or brown lacewings feed on aphids as adults and larvae and are therefore closely associated with aphid populations (Hagen & van den Bosch, 1968; Maelzer, 1977; Samson & Blood, 1979). The genera *Micromus* Rambur and *Hemerobius* Linnaeus are the most widely distributed (New, 1988). Development threshold temperatures are very low and as a consequence hemerobiids can be found throughout the year (New, 1988).

Host range

Apart from aphids also other soft bodied insects, like small caterpillars (Neuenschwander & Hagen, 1980) and eggs of coccinellids, butterflies and their own species (Cutright, 1923) are preyed upon.

Morphology

The eggs are elliptical in shape and, in contrast with chrysopid eggs, not placed on stalks (Smith, 1923). The eggs are laid horizontally (Moznette, 1915), on the underside of the leaves and in irregular groups of 1 to 13 eggs (Cutright, 1923). Their colour is light yellow to greyish (Smith, 1923).

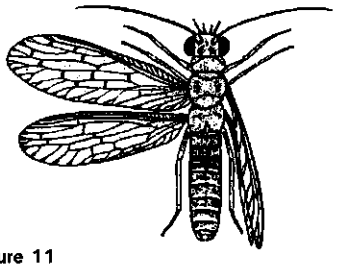

Figure 11
An adult *Micromus sp.* (from New (1988)).

The newly hatched larva is white and 2 mm in length (Moznette, 1915). Three larval stages are recognized, part of the third stage is spent as a pre-pupa inside the cocoon (Moznette, 1915). Full grown larvae are 4 to 7 mm in size and have a greyish colour, sometimes with some reddish spots (Smith, 1923). In a protected place the cocoon is spun, in which the larva pupates (Smith, 1923; Miller & Cave, 1987). The cocoon is 5 mm and light brown (Moznette, 1915). The adults are light brown with hyaline wings with brown spots (Moznette, 1915).

Biology

Mating does not occur before five to six days after emergence (Miermont & Canard, 1975). Without mating only few infertile eggs are produced (Miermont & Canard, 1975). One female produces several hundred to more than 1000 eggs (Table 7). The longevity of the adults is

several weeks (Table 7) and does not differ between males and females (Laffranque & Canard, 1975; Miller & Cave, 1987; Stelzl & Hassan, 1992).

During one day 15 to 25 eggs can be deposited (Stelzl & Hassan, 1992). Depending on environmental conditions the pre-oviposition period is from several days to two weeks (Cutright, 1923; Neuenschwander, 1976; Stelzl & Hassan, 1992). The sex ratio is 50% (Samson & Blood, 1979). Larvae are very active searchers, which can readily disperse (New, 1988). The larvae search for prey by shifting the head jerkily from side to side (Cutright, 1923). The larval voracity is between 40 and 200 aphids (Moznette, 1915; Cutright, 1923; Samson & Blood, 1979). At 20 °C the development from egg to adult takes three to five weeks (Table 7). The development thresholds and development times can differ among species (Samson & Blood, 1979) (Table 7). There are no differences in the development times between males and females (Samson & Blood, 1979).

Larvae can be parasitized by ichneumonid and figitid parasitoids, but in cotton fields parasitization rates were low (Miller & Cave, 1987).

Life cycle

Many Hemerobiidae undergo a winter diapause, sometimes as adult (New, 1988). Adult diapause is induced by short daylength and is expressed by extension of the maturation period, which is in nature followed by thermal quiescence (Miermont & Canard, 1975). At low

Table 7
Life history data of Hemerobiidae.

(a) Life history data of Hemerobiidae feeding on aphids at a constant temperature of 18 to 20 °C

species	temp. (°C)	development time (days)			imm. mort (%)	repr. period (days)	life-time fecundity (eggs/♀)	reference
		egg	larva	pupa				
Boriomyia subnebulosae	20	7	10	16.5[a]	4	53[b]	1045	Laffranque & Canard (1975)
Eumocromus angulatus	20	7.5	8.2	5.1[a]		20	±2000	Miermont & Canard (1975)
Hemerobius pacificus	18.3					71.8[b]	714.8	Neuenschwander (1976)
Micromus tasmaniae	18	5.6	7.1	13.3				Samson & Blood (1979)

a including pre-pupa; b oviposition period

(b) Influence of temperature on the life history data of *Micromus tasmaniae* feeding on *Aphis gossypii*

temperature (°C)	development time (days)			imm. mort (%)	repr. period (days)	life-time fecundity (eggs/♀)	reference
	egg	larva	pupa				
5		49.4	64.7				Samson & Blood (1979)
18	5.6	7.1	13.3				Samson & Blood (1979)
23	4	5.8	10.6				Samson & Blood (1979)
28	4.8	5.8	9.1		27	613	Samson & Blood (1979)

temperatures a short day length lengthens the pre-oviposition period, at higher temperatures no influence of daylength is observed (Neuenschwander, 1976).

Aphid control

Although recognized as aphid predators the use of Hemerobiidae in biological control programmes is very limited. Neuenschwander & Hagen (1980) released eggs of *Hemerobius pacificus* Banks to control *M. persicae* in artichoke fields with good results. During the winter this hemerobiid was the only common active predators (Neuenschwander & Hagen, 1980). A method for mass rearing *M. angulatus* was described by Stelzl & Hassan (1992).

Syrphidae

Introduction

More than 4700 syrphid species have been described world-wide (Chambers, 1988). Most aphidophagous species are found in two tribes of the subfamily Syrphinae: the Syrphini and the Melanostomi, both of world-wide distribution (Chambers, 1988). Syrphids can make up a large part of the aphid predator population in the field (Mahmoud *et al*, 1981; Lazzari, 1985).

The most intensively studied syrphid is *Metasyrphus corollae* (Fabricius). Four other species which may be of economic importance because of their habit of ovipositing at low aphid densities are *Platycheirus peltatus* (Meigen), *P. manicatus* (Meigen), *Melanostoma mellinum* (L.) and *M. scalare* (Fabricius) (Chandler, 1968a, 1968b, 1968c; Chambers, 1988).

Host range

Syrphid species can be carnivorous, phytophagous or scavengers (Schneider, 1969). The larvae of aphidophagous species feed on aphids while the adults feed on pollen and nectar (Schneider, 1969). Uptake of nectar, honeydew and pollen is necessary for ovarial maturation (Schneider, 1969) and as a consequence syrphids are commonly observed feeding on flowers (Chandler, 1968a). A great variety of aphid species is accepted, but a certain preference is also present (Yakhontov, 1966; Schneider, 1969). Some aphid species are unsuitable as food (Chambers, 1988). In the absence of prey cannibalism occurs (Schneider, 1969).

Morphology

The eggs are white and about 1 mm long (Chambers, 1988). The eggs of *M. corollae* are attached to the leaf horizontally (Tawfik *et al*, 1974). The larvae feed on aphids and pass three instars. Full grown they are grey, yellow, green or brown coloured and have a size of 1 to 2 cm (Scott, 1939; Chambers, 1988). The pupae have a length of 5 to 8 mm and are brown to almost black (Scott, 1939). Pupae can

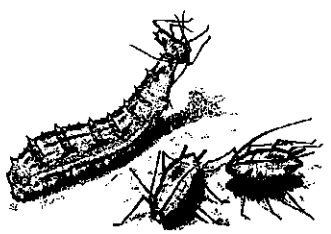

Figure 12
A larva of *Metasyrphus corollae* feeding on aphids (from Chambers (1988)).

be found in the soil surface for some species and attached to the plant for others (Chambers, 1988). The abdomen of the adults is frequently brightly coloured (Chambers, 1988).

Biology

At 20 to 25 °C females live one to three weeks (Sundby, 1966) (Table 8). The longevity of males is slightly shorter (Lal & Lal Gupta, 1953; Lal & Haque, 1955; Tawfik *et al*, 1974). The pre-oviposition period is about one week (Sundby, 1966; Tawfik *et al*, 1974). One female produces 30 to 50 eggs (Table 8), on some occasions several hundreds of eggs were produced (Barlow, 1961; Sundby, 1966). Most of the oviposition occurs during daytime (Bombosch, 1962b; Peschken, 1964). Eggs are laid singly or in groups (Scott, 1939; Chandler, 1968c). Oviposition is elicited by olfactory stimuli originating from exuviae, aphid honeydew or from the cornicles (Volk, 1964; Chambers, 1988). The effect of the presence of aphids as an oviposition eliciting cue differs among the species. Oviposition by *Syrphus spp.* is closely related to the presence of aphids ('aphidozetic'), whilst *M. scalare*, *M. mellinum* and *P. peltatus* lay their eggs mostly on uninfested plants ('phytozetic') (Chandler, 1968a, 1968b, 1968c). The higher the honeydew concentration or the more aphids are present the more eggs are deposited (Chandler, 1968b; Budenberg & Powell, 1992), but the number of eggs per aphid decreases with increasing aphid density (Itô & Iwao, 1977).

Of the eggs of *Syrphus ribesii* L. 67.2% hatches (Sundby, 1966). Syrphid larvae search by "casting": the hind part of the body grips the substrate while the anterior end is extended forward and laterally in search of prey (Chambers, 1988). The larvae puncture the body-wall of

Table 8
Life history of Syrphidae.

(a) Life history data of Syrphidae females feeding on aphids at a constant temperature of 25 to 26 °C

species	temp. (°C)	development time (days)	life span (days)	life-time fecundity (eggs/♀)	larval voracity (aphids)	reference
Allograpta oblique	25	17.9				Simpson & Burkhardt (1960)
Metasyrphus corollae	26.2	16.4	12.4			Tawfik *et al* (1974)
Sphaerophoria scutellaris	25.0		12.3	27.8		Lal & Haque (1955)

(b) Influence of different constant temperatures on the life history data of *Sphaerophoria scutellaris* females feeding on aphids

temperature (°C)	development time (days)	life span (days)	life-time fecundity (eggs/♀)	larval voracity (aphids)	reference
16.2	21.8	13.3	29.0		Lal & Lal Gupta (1953)
19.8		18.1	40.8	416.9	Lal & Haque (1955)
22.2				321.8	Lal & Haque (1955)
25.0		12.3	27.8		Lal & Haque (1955)
30.0		9.5			Lal & Haque (1955)

the aphid and extract the fluid contents (Chambers, 1988). The larvae do not perceive their prey at a distance, aphids are located by direct contact. Under normal conditions the larval mortality is about 10% (Sundby, 1966).

Eighty to ninety percent of the total aphid consumption is done by the 3rd instar (Chambers, 1988). At lower humidity the number of aphids consumed is higher than at higher humidity (Bombosch, 1962a, 1963). If aphids are abundant more aphids are killed, but larger aphid carcasses are left (Scott & Barlow, 1986). One larva can eat several hundreds of aphids during its development (Bombosch, 1962a; Sundby, 1966; Agarwala & Saha, 1986; Kotwal *et al*, 1989) (Table 8).

Nine families of hymenopterous parasitoids attack the larvae (Scott, 1939; Schneider, 1969; Chambers, 1988). Most parasitoids are monophagous, a few are oligophagous (Rotheray, 1984). It is not known whether the voracity of the larvae is affected if they are parasitized (Chambers, 1988).

Life cycle

The occurrence of diapause and the number of generations a year depend upon the species (Chambers, 1988). Most syrphid species overwinter as diapausing larvae (Hagen & van den Bosch, 1968; Dušek & Láska, 1986). The larvae drop to the ground together with the leaves, after which the larvae pupate early in May (Sundby, 1966). Also overwintering in the pupal stage (Scott, 1939) or as adult (Schneider, 1969) occurs.

In some syrphid species there may be up to five or six generations a year, depending on the temperature (Hagen & van den Bosch, 1968), but one or two generations occur as well (Dušek & Láska, 1986).

Aphid control

Control of *A. gossypii* on isolated cucumber plants was successful after females of *M. corollae* were allowed to oviposit on the plants for 24 hours, providing less than nine aphids were present per egg (Chambers, 1986). *Metasyrphus corollae* larvae of one, two and three days old prevented aphid increase unless there were more than 15, 26 or 41 aphids per larva, respectively, at the time of introduction (Chambers, 1986). When aphid density declined after a few days, the larvae of *M. corollae* tended to move away, after which the aphid density increased again (Chambers, 1986). Continuous control of *A. gossypii* on single caged cucumber plants was possible, providing that the presence of one gravid female of *M. corollae* was maintained (Chambers, 1986). However, complete eradication of aphids occurred very rarely (Chambers, 1986). Chambers (1986) suggests that *M. corollae* could be used for a quick reduction of aphid numbers after which other natural enemies can be used to keep the aphid density low.

At present there is no insecticide which is sufficiently effective on the basis of contact toxicity to kill aphids, but preserve syrphids. Syrphids are susceptible to a wide range of chemicals (Horn & Wadleigh, 1988). Even the commonly used aphicide pirimicarb is harmful to hoverflies (Proctor & Baranyovitz, 1969; Láska, 1973), although the puparia are better able to survive contact with a range of pesticides than the larvae (Láska, 1973).

With the exception of *M. corollae* syrphids are difficult to rear in large quantities (Hodek & Honěk, 1988).

Aphids containing eggs or larvae of parasitoids are also preyed upon (Akinlosotu, 1978).

1.2.3 Parasitoids

Aphelinidae (Hymenoptera)

Introduction

Of the aphelinids, only part has become associated with aphids as primary or secondary hosts (Viggiani, 1984). The most common aphid attacking genera are *Aphelinus* Dalman and *Mesidia* Förster of the subfamily Aphelininae (Mackauer, 1972). The taxonomy of the Aphelinidae is still unclear. Many species have a similar morphology but their clearly different host ranges might indicate the existence of true species (Mackauer, 1968b). For some aphelinid species morphological characteristics are very variable and depend on the host aphid species (Hennesey, 1981). On the other hand two strains of *Aphelinus varipes* Förster, which were separated by mating incompatibilities, could not be distinguished through electrophoresis (Strong, 1993). Also reproductive barriers between different lines of the same species can be present (Haardt & Höller, 1992).

Few aphelinids are known to parasitize *A. gossypii* successfully. Only *Aphelinus asychis* Walker (= *A. flavipes* (Förster) = *A. semiflavus* Howard) has been used for biological control of *A. gossypii* (Wyatt, 1969; Lyon, 1976).

Host range

All hosts of the aphidophagous Aphelinidae belong to the Aphidoidea and the majority of the host aphid species belong to the Aphididae (Starý, 1988a). Adults feed on the body fluids of aphids (Starý, 1988a). Aphelinids also accept honeydew as food (Starý, 1988a). Most of the time aphelinids have a distinct host preference (Kuo-Sell & Kreisfeld, 1987; Starý, 1988a). The suitability of and preference for certain host species can change dramatically within a few generations in association with host availability (Michel, 1971). Some aphid species are accepted as host but no larva develops because the egg is encapsulated (Carver & Woolcock, 1985). In other aphid species the larva does develop but most of the time dies within the dead or dying, non-mummified host before the mummy stage (Carver & Woolcock, 1985).

Morphology

All aphidophagous Aphelinidae are solitary endoparasitoids, usually less than 1 mm in size (Starý, 1988a). The size of the adult depends on the aphid species used as host (Lajeunesse & Johnson, 1992). The egg is oval with a length of 0.2 mm (Lundie, 1924). At first the larva is long and narrow, but before mummification the larva fills the entire aphid body (Lundie, 1924). Before mummification the parasitoid larva attaches the mummy to the leaf through the ventral side of the mummy (Hamilton, 1973). Aphelinid mummies are black and not swollen. The adults emerge through a circular hole in the dorsum of the aphid mummy (Hagen & van den Bosch, 1968).

Biology

At the moment the parasitoid emerges from the mummy only 6 to 14 eggs are present in the ovaries, after some time 10 to 24 eggs are available (Michel, 1973). Oogenesis is a continuous process (Schlinger & Hall, 1959). After an encounter the aphid is tapped with the antennae. If the host is suitable the female quickly turns 180 degrees and inserts the ovipositor in the aphid

(Starý, 1988a). The aphid is not paralysed during oviposition (Boyle & Barrows, 1978). All instars are accepted as host but first and second instar nymphs are preferred (Schlinger & Hall, 1959; Hamilton, 1973; Cate *et al*, 1977; Starý, 1988a). For successful oviposition the ovipositor has to be inserted for at least one minute (Wilbert, 1964; Hamilton, 1973; Michel, 1973; Boyle & Barrows, 1978). Aphelinids in general seem to avoid multi- and superparasitism (Mackauer, 1982; Starý, 1988a). They also recognize aphids parasitized by braconid parasitoids (Bai & Mackauer, 1991). Only at high parasitoid-aphid ratios superparasitism occurs more often (Bai & Mackauer, 1990a).

Table 9
Life history parameters of Aphelinidae known to parasitize *Aphis gossypii* successfully.

(a) Life history data of Aphelinidae parasitizing suitable hosts at a constant temperature of 20 to 21 °C

species	devel. time (days)	imm. mort. (%)	repr. per. (days)	life-time fec. (eggs/♀)	sex ratio (% ♀)	r_m	reference
Aphelinus abdominalis	23.5[a]				66.2		Haardt & Höller (1992)
Aphelinus asychis	20.8	12.4	55.2[b]	411.4	67.5		Kuo (1986)
Aphelinus mali	23.0						Bonnemaison (1965)
Aphelinus semiflavus	18.3[a]	0.0	46.0[b]	879.2	51.0	0.24	Force & Messenger (1964a, 1964b)

a mummy mortality; b longevity of females; c mummies per female

(b) Influence of different constant temperatures on the life history data of *Aphelinus semiflavus* parasitizing *Therioaphis maculata*

temperature (°C)	devel. time (days)	imm. mort. (%)	repr. per. (days)	life-time fec. (eggs/♀)	sex ratio (% ♀)	r_m	reference
10.0	> 60.0[a]						Force & Messenger (1964a, 1964b)
15.6	38.4[a]	21.8	70.4[b]	429.4	16.0	0.09	Force & Messenger (1964a, 1964b)
21.1	18.3[a]	0.0	46.0[b]	879.2	51.0	0.24	Force & Messenger (1964a, 1964b)
22.3	12.6	22.7					Manglitz & Schalk (1970)
26.7	11.3[a]	20.0	19.9[b]	385.2	84.0	0.34	Force & Messenger (1964a, 1964b)
29.4	10.4[a]	7.7	16.0[b]	274.9	20.0	0.30	Force & Messenger (1964a, 1964b)
32.2	10.0	94.1	4.9	4.8	0	<0	Force & Messenger (1964a, 1964b)

a mummy mortality; b mummies per female

(c) Influence of host aphid species on the life history data of *Aphelinus asychis* at an average constant temperature of 23.9 °C

host aphid species	devel. time (days)	imm. mort. (%)	repr. per. (days)	life-time fec. (eggs/♀)	sex ratio (% ♀)	r_m	reference
Rhopalosiphum maidis	16.6	24.0[a]	13.5[b]	52.0[c]	64.0		Raney *et al* (1971)
Schizaphis graminum	15.8	21.0[a]	17.8[b]	82.0[c]	63.0		Raney *et al* (1971)
Sipha flava	17.1	28.0[a]	16.8[b]	10.0[c]	57.0		Raney *et al* (1971)

a mummy mortality; b longevity of females; c mummies/female

The fecundity is species dependent. Under suitable conditions one female can produce almost 1000 eggs (Table 9). The sex ratio is usually biased towards females (Table 9). Males are haploid, being derived from unfertilized eggs (Flanders, 1953). However, in some *A. semiflavus* and *A. abdominalis* strains thelytokous-parthenogenetic reproduction seems to occur, with males being produced only in exceptional cases (Schlinger & Hall, 1959; Force & Messenger, 1964b; Mackauer, 1968; Haardt & Höller, 1992).

The initial phase of host feeding resembles oviposition. However, insertion of and stabbing with the ovipositor takes much longer (6 to 10 minutes) and the aphid is paralysed (Michel, 1973). No eggs are deposited before host feeding (Wilbert, 1964; Esmaili & Wilde, 1972). Usually one or two aphids per day are killed for host feeding (Hamilton, 1973; Kuo, 1986; Kuo-Sell & Kreisfeld, 1987; Bai & Mackauer, 1990b). There is a positive correlation between the number of aphids fed upon and the number of eggs laid, indicating that host feeding is necessary to produce eggs (Hamilton, 1973). Adult longevity depends on available food and temperature (Viggiani, 1984). Females live considerably longer than males (Kuo, 1986).

The development time from egg to adult is influenced by host aphid species and inversely related to temperature (Table 9). Below 20 °C several weeks are necessary to complete development but above 25 °C the development time is only 10 to 11 days (Table 9).

Through the aphids the suitability of the host plant can influence the development, reproduction, life span, sex ratio and size of the aphelinids (Kuo, 1986; Haardt & Höller, 1992). Several Pteromalidae, Charipidae, Cynipidae and Encyrtidae are hyperparasitic upon *Aphelinus spp.* (Schlinger & Hall, 1959; Carver, 1992).

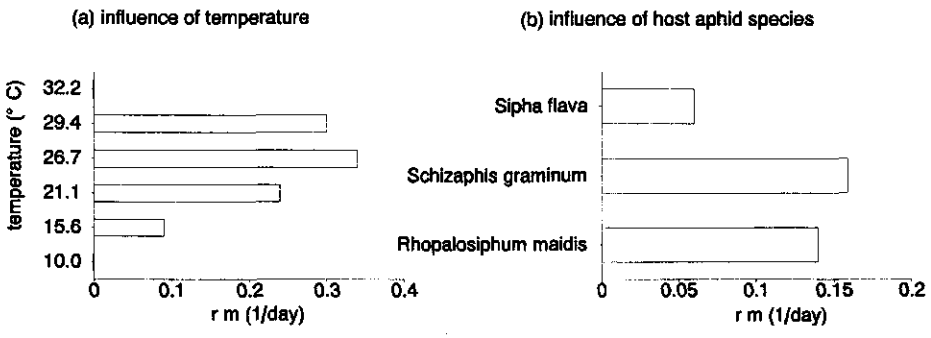

Figure 13
Influence of (a) temperature on the population growth rate of *Aphelinus semiflavus* (Force & Messenger, 1964a, 1964b) and (b) host aphid species on the population growth rates of *Aphelinus asychis* at 23.9 °C (Raney *et al*, 1971). In figure b it is assumed that reproduction is constant during the life span of the parasitoids and that all parasitoids die at average age.

Life cycle

As long as aphids are present a continuous host-parasitoid interaction during the season is possible (Starý, 1988a). Overwintering occurs in the pupal stage inside the mummy (diapause) or as adult (hibernation) (Spencer, 1926; Bonnemaison, 1965; Hamilton, 1973). Overwintering females do not contain mature eggs, but they do continue their host feeding activities (Hamilton, 1973).

Aphid control

The parasitoid *Aphelinus* sp. aff. *flavipes* which was used in cotton aphid control experiments spreads very slowly (Wyatt, 1970) and only introductions with high parasitoid-host ratio can give reliable control (Wyatt, 1971).

The population growth of *A.* sp. aff. *flavipes* was insufficient to control *A. gossypii* on glasshouse grown cucumber, eggplant or sweet pepper (Wyatt, 1969; Lyon, 1976). In smaller trials, *A. asychis* has successfully been used to control *M. persicae*, *Schizaphis graminum* (Rond.) and *Macrosiphum solanifolii* (Ashmead) (Richardson & Westdal, 1965). At lower temperatures (19 °C) the parasitoids overtook the aphids before the infestation was severe (Wyatt, 1969). Still *A. gossypii* is not as susceptible to attack by *A. asychis* as *M. persicae* (Lyon, 1976). Even though high parasitization rates were obtained in the laboratory, *Aphelinus abdominalis* ((Dalman) did not control wheat aphids in the field (Höller & Haardt, 1993). *Aphelinus abdominalis* is used to control *Macrosiphum euphorbiae* (Thomas) in glasshouses (Höller & Haardt, 1993; van Schelt, 1993).

Aphidiinae (Hymenoptera: Braconidae)

Introduction

The Aphidiinae are a subfamily of the Braconidae. Members of this subfamily are solitary endoparasitoids of aphids (Mackauer, 1968a) and include many important genera for biological control like *Aphidius*, *Ephedrus*, *Lysiphlebus*, *Monoctonus* and *Trioxys*. One of the earliest attempts to use Aphidiinae for control of pest aphids was the use of *Lysiphlebus testaceipes* Cresson against the greenbug, *Schizaphis graminum* (Rondani), in the midwestern United States around 1910 (Kelly, 1917). The Aphidiinae are a relatively uniform group of Hymenoptera, this feature seems to be due to their full adaptation to parasitism on a single group of hosts, the aphids (Starý, 1988b). About 400 species, divided over 60 genera and subgenera, have been described (Starý, 1988b). Aphidiinae occur throughout the world, closely following their aphid hosts (Starý, 1988b). Most of the species occur in the temperate and subtropical zones of the northern hemisphere, relatively few species are endemic to the tropics (Starý, 1988b).

Several species are known to parasitize *A. gossypii*. Most of these belong to the genera *Aphidius*, *Lysiphlebus* and *Trioxys*.

Host range

Most Aphidiinae are oligophagous, only parasitizing a small range of host species (Starý, 1988b). In the host range, preference of certain aphid species may occur (Starý, 1988b). Certain parasitoid strains of one species may prefer a certain group of host aphids within the overall host range of the species (Schlinger & Mackauer, 1963; Pungerl, 1984; Powell &

Wright, 1988; Hågvar & Hofsvang, 1991). Also different lines of the same aphid species may differ in suitability for a parasitoid species (Ankersmit *et al*, 1986).

Starý *et al* (1985) showed that strains that prefer a certain host aphid can be distinguished by electrophoretic analysis, indicating a (partly) genetic difference. Sometimes it is not clear whether these different strains represent different species (Höller, 1991). In some aphid-parasitoid associations the egg or larva of the parasitoid is encapsulated during a cellular immune response (Carver & Sullivan, 1988) or die during the mummy stage (Carver, 1984; Starý, 1989).

Morphology

The adults are small, their size ranging from one to several mm (Spencer, 1926). The size of the adults depends on the size of the host (Hight *et al*, 1972; Starý, 1988b). Prevailing colours are combinations of black, brown, orange and yellow (Spencer, 1926; Starý, 1988b).

In the ovary the size of the egg is 50 by 20 micrometer (Spencer, 1926). Once within the aphid, the egg osmotically absorbs liquid from the aphid and expands to 130 by 60 micrometer (Spencer, 1926). After hatching of the egg four larval instars follow, which can be distinguished by size and by shape (Spencer, 1926; Hofsvang & Hågvar, 1978). O'Donnell (1987) found only three larval instars in *Aphidius colemani* Viereck. By the last instar the aphid has usually become adult and the parasitoid larva has consumed all the internal tissues of the aphid, completely filling its cuticle (Rabasse & Wyatt, 1985). The larva then cuts a hole in the underside of the aphid and attaches the cuticle of the aphid to the leaf by silk (Rabasse & Wyatt, 1985). Then the larva forms a cocoon and pupates. At this stage the parasitized aphid can be recognized because it looks like a swollen papery aphid: the mummy (Rabasse & Wyatt, 1985). Some parasitoid species can be recognized through the form and colour of the mummy and the shape of the emergence hole (Rabasse & Wyatt, 1985; Mackauer & Kambhampati, 1988).

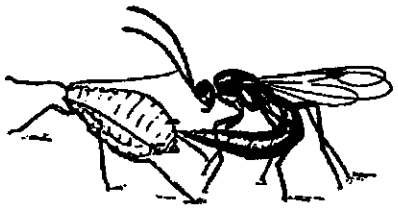

Figure 14
***Lysiphlebus testaceipes* parasitizing an aphid (from Sweetman (1936)).**

Biology

Aphidiinae are solitary endoparasitoids of aphids (Starý, 1988b). The female inserts her ovipositor in the aphid by bending her abdomen between her legs (Rabasse & Wyatt, 1985). Oviposition may occur quite soon after emergence (Starý, 1988b) and takes less than a second in some species ('t Hart *et al*, 1978) and up to 12 seconds in others (Chow & Mackauer, 1986; Hofsvang & Hågvar, 1986).

Females live for one to two weeks at a temperature of 20 °C (Table 10). When only water is offered, the longevity is only a few days (Hofsvang & Hågvar, 1975a). When aphids are

Table 10
Life history data of several aphidiine parasitoids (Hymenoptera: Braconidae).

(a) Life history data of Aphidiinae parasitizing suitable hosts at a constant temperature of 20 to 21 °C

species	devel. time (days)	imm. mort. (%)	repr. per. (days)	life-time fecundity (eggs/♀)	sex ratio (% ♀)	r_m	reference
Aphidius colemani	15.6	25.0[a]	5.6[b]	46[c]	52.0		Hofsvang & Hågvar (1975a, 1975b)
A. ervi	19.9	50.0[a]	10.6[b]				Hofsvang & Hågvar (1975a)
A. gifuensis			14.9	531.5			Fukui & Takada (1988)
A. matricariae	13.4		10.8	309.0[c]	57.3	0.29	Shalaby & Rabasse (1979b)
A. nigripes		7.6[a]	19.8[b]	338.2[c]	35.0		Cloutier *et al* (1981)
A. smithi	12.5	15.0[a]	7.2[b]				Wiąckowski (1962)
A. sonchi	12.4	2.8[a]					Liu Shu-Sheng & Hughes (1984)
A. urticae	16.0						Dransfield (1979)
A. uzbekistanicus	13.9						Dransfield (1979)
Diaeretiella rapae	14.1	12.0[a]					Bernal & González (1993)
Ephedrus californicus	16.1	4.6[a]					Cohen & Mackauer (1987)
E. cerasicola	21.6	12.5	16.9[b]	961.0	50.0	0.29	Hofsvang (1985); Hågvar & Hofsvang (1986, 1990)
E. plagiator	17.6	5[a]		183.0[c]	30.0		Rogers *et al* (1972)
Lysiphlebus delhiensis			8.8[b]	270.8[c]	59.0	0.31	Mishra & Singh (1991)
L. mirzai		14.7[a]	6.4	169.2[c]	64.0	0.24	Tripathi & Singh (1990)
L. testaceipes	13.2	5.0			62.0		Hight *et al* (1972)
Praon palitans	17.2[d]	45.5[d]	18.2	578.5	44.4	0.24	Force & Messenger (1964a, 1964b)
Trioxys communis	16						Shi Da-San (1984)
T. utilis	14.4[d]	12.0[d]	14.3	493.3	52.8	0.48	Force & Messenger (1964a, 1964b)

a mummy mortality; b life span; c number of mummies; d of females

(b) Influence of different constant temperatures on the life history data of *Trioxys utilis* parasitizing *Therioaphis maculata*

temperature (°C)	devel. time (days)	imm. mort. (%)	repr. per. (days)	life-time fecundity (eggs/♀)	sex ratio (% ♀)	r_m	reference
10.0	> 62.0[a]						Force & Messenger (1964a, 1964b)
15.6	26.9[a]	16.3[b]	14.1	457.7	57.9	0.18	Force & Messenger (1964a, 1964b)
18.3		1.1[b]		844.7	58.9	0.38	Force & Messenger (1964a, 1964b)
21.1	14.4[a]	12.0[b]	14.3	493.3	52.8	0.48	Force & Messenger (1964a, 1964b)
23.9		31.6[b]		335.9	50.8	0.43	Force & Messenger (1964a, 1964b)
26.7	9.7[a]		7.9	62.9	0	<0	Force & Messenger (1964a, 1964b)
29.4	9.3[a]		6.5				Force & Messenger (1964a, 1964b)
32.2	10.5[a]		2.6				Force & Messenger (1964a, 1964b)

a of females; b mummy mortality

(c) Influence of host aphid species on the life history data of *Ephedrus plagiator* at a constant temperature of 21.0 °C

host aphid species	devel. time (days)	imm. mort. (%)	repr. per. (days)	life-time fecundity (eggs/♀)	sex ratio (% ♀)	r_m	reference
Macrosiphum avenae	17.2	5.0[a]		60.0[b]	22.0		Rogers *et al* (1972)
Rhopalosiphum maidis	17.6	5.0[a]		183.0[b]	30.0		Rogers *et al* (1972)
Rhopalosiphum padi	16.7	7.0[a]		162.0[b]	13.0		Rogers *et al* (1972)
Schizaphis graminum	17.2	6.0[a]		255.0[b]	24.0		Rogers *et al* (1972)

a mummy mortality; b number of mummies

offered, the longevity is shorter than when honey and water is offered as food (Wiąckowski, 1962; Hofsvang & Hågvar, 1975a). Longevity can be influenced by the host plant species the aphids feed on (Hofsvang & Hågvar, 1975a; Bhatt & Singh, 1989). The pre- and post-oviposition periods are very short (Shirota *et al*, 1983; Hågvar & Hofsvang, 1991).

Some aphid parasitoid species are attracted to host plants, irrespective of the presence of aphids (Read *et al*, 1970; Starý, 1970; Singh & Sinha, 1982a; Goff & Nault, 1984). Others respond to odours from aphids (Pandey *et al*, 1984; Bouchard & Cloutier, 1985; Hardie *et al*, 1991) or to both odour sources (Powell and Zhang Zhi-Li, 1983; Guerriri *et al*, 1993). The exact searching strategy might be related to the degree of specificity of the parasitoid and the host aphid (Powell & Wright, 1992). The searching behaviour on the leaf is random. From a short distance vision, tactile responses and aphid movement may play a role in locating the host (Starý, 1970; Singh & Sinha, 1982a). The presence of aphids or aphid related products stimulate searching on a leaf (Bouchard & Cloutier, 1984; Gardner & Dixon, 1985; Ayal, 1987; Decker, 1988; Budenberg, 1990; Cloutier & Bauduin, 1990; Budenberg *et al*, 1992; Battaglia *et al*, 1993). As a consequence the wasps accumulate on honeydew-contaminated plants (Hågvar & Hofsvang, 1987).

Certain instars are preferred for oviposition although any instar is usually acceptable (Rabasse & Wyatt, 1985). In general young aphids are preferred over adults (Mackauer, 1973; Shirota *et al*, 1983; Liu Shu-Sheng *et al*, 1984), because adult aphids are more easily disturbed and show a more vigorous defence behaviour (Fox *et al*, 1967).

Aphidiinae are able to distinguish between parasitized and unparasitized hosts ('t Hart *et al*, 1978; Singh & Sinha, 1982b; Shirota *et al*, 1983, Mackauer, 1983; Chow & Mackauer, 1984;

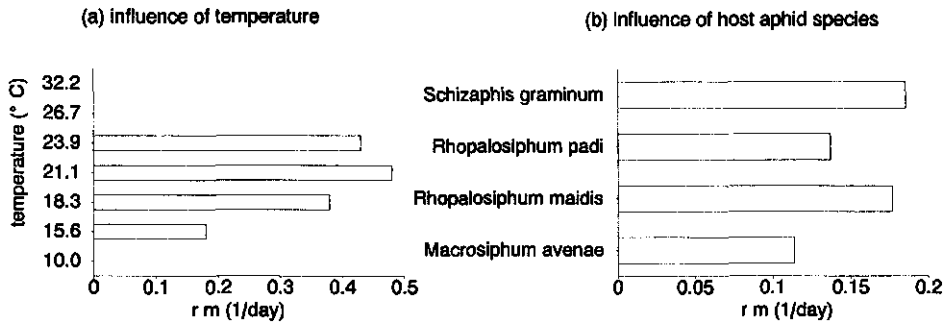

Figure 15
Influence of (a) temperature on the population growth rate of *Trioxys utilis* (Force & Messenger, 1964a, 1964b) and (b) host aphid species on the population growth rates of *Ephedrus plagiator* at 21 °C (Rogers *et al*, 1972). In figure b it is assumed that daily reproduction is constant during the oviposition period and that all parasitoids die at average age.

Chow & Mackauer, 1986; Hofsvang & Hågvar, 1986; Hofsvang, 1988; Völkl & Mackauer, 1990; Bai & Mackauer, 1991; McBrien & Mackauer, 1991; Mishra & Singh, 1993). This does not imply that superparasitization does not occur. Especially at low aphid densities wasps tend to superparasitize (Hofsvang & Hågvar, 1983; Cloutier, 1984; Liu Shu-Sheng & Morton, 1986; Völkl & Mackauer, 1990; Mackauer *et al*, 1992; Mishra & Singh, 1993). In aphids superparasitized by two aphidiine species, the older larva usually eliminates a younger competitor (Chow & Mackauer, 1984, 1986).

The fecundity ranges between several hundred to more than 1000 eggs per female (Hågvar & Hofsvang, 1991) (Table 10). The number of eggs in the ovaries at emergence is lower than the realized fecundity, indicating maturation of eggs during life (synovigenic) (Starý, 1962; Shirota *et al*, 1983). A significant positive correlation is present between parasitoid size and mature egg load after emergence (Collins & Dixon, 1986). The number of eggs deposited can be influenced by the host plant species the aphids are bred upon (Bhatt & Singh, 1989). At night and also during dark days the wasps are inactive (Spencer, 1926).

The sex ratio tends to be female biased at 60 to 70% females (Table 10), but may depend on environmental conditions, population density and host size (Cloutier *et al*, 1981; Wellings *et al*, 1986; Starý, 1988b; Bhatt & Singh, 1989; Shukla &Tripathi, 1993). Fertilized eggs develop into females and unfertilized eggs develop into males. Females mate only once but a mated female produces mainly males at the end of her life due to exhaustion of the sperm supply (Starý, 1962; Cloutier *et al*, 1981; Shirota *et al*, 1983; Starý, 1988b; Tripathi & Singh, 1990). In some species or populations of one species, however, males do not occur at all (Rosen, 1967; Starý, 1970; Carver, 1984).

The first three larval stages feed on the hosts haemolymph while the fourth instar feeds actively destroying the remaining tissue (Starý, 1988b; Hågvar & Hofsvang, 1991). Development from egg to adult takes about two weeks at 20 °C and shortens with increasing temperatures (Table 10). The development time of the parasitoids can be influenced by the host plant species the aphids feed on (Hofsvang & Hågvar, 1975a) (Table 10). In general males emerge shortly before females (Hofsvang & Hågvar, 1975a).

Dispersal of the parasitoid takes place by the flying adult or within parasitized aphids, especially if they are winged (Vater, 1971; Starý, 1988b). Parasitoid larvae can change the behaviour of the aphids prior to mummification (Brodeur & McNeil, 1989).

Apart from the mortality caused by the parasitization, a parasitoid causes additional mortality among the aphids as an effect of the searching behaviour. After disturbance by a parasitoid, the aphids dislodge themselves from the leaves and fall on the soil (Tamaki *et al*, 1970). If they are not able to find a host plant quickly enough they will die (Hight *et al*, 1972; Ruth *et al*, 1975).

Hyperparasitoids of Aphidiinae are found in the families Charipidae (Carver, 1992), Cynipidae (*Charips* Haliday) (Paetzhold & Vater, 1967; Gutierrez & van den Bosch, 1970; Sullivan, 1986), Encyrtidae (Sullivan, 1986), Eulophidae (Sullivan, 1986), Megaspilidae (Sullivan, 1986) and Pteromalidae (*Pachyneuron* Walker, *Asaphes* Walker) (Paetzhold & Vater, 1967; Sullivan, 1986). There is a large degree of host specificity in several hyperparasitoid species (Sullivan, 1986).

Life cycle

Aphidiinae may survive unfavourable conditions by going into diapause as a larva or pre-pupa inside the aphid (Webster & Phillips, 1912; Singh & Sinha, 1980). The seasonal history of Aphidiinae depends primarily on the aphid host (Starý, 1988b; Polgár *et al*, 1991) and is

therefore not a species attribute but may be limited to local populations (Flint, 1980; Bernal & González, 1993).

Aphid control

A number of Aphidiinae-species have been or are used in biological control of aphids, both in outdoor and in glasshouse cultures (Halfhill & Featherston, 1973; Carver, 1989; Gilkeson, 1990; van Schelt, 1993). On several occasions releases of parasitoids were made to control introduced aphid pests in classical biological control programmes (Starý *et al*, 1985; Costa & Starý, 1988).

In glasshouses biological control of aphids almost always includes releases of the parasitoids *A. colemani* and *A. matricariae* (van Schelt, 1993). Parasitoids are introduced preventively at a rate of 0.1/m^2/week. Once aphids are observed in the glasshouse the release rate is increased to 0.5/m^2/week and gall midges are introduced too (van Schelt, 1993). In glasshouses the parasitoids do not enter diapause (Hofsvang & Hågvar, 1982).

In the mummy the parasitoid larva is protected against some pesticides (Binns, 1968; Lingappa *et al*, 1972; Chao Yen Hsieh & Allen, 1986; Hardee *et al*, 1990; Shean & Cranshaw, 1991).

Storage of mummies at low temperatures is possible for several days without a marked increase in mortality (Archer *et al*, 1973; Hofsvang & Hågvar, 1977; Shalaby & Rabasse, 1979a; Polgár, 1986; Singh & Srivastava, 1988; Jarry & Tremblay, 1989). Also the performance of the adult does not seem to be hampered by a short period of cold storage (Jarry & Tremblay, 1989).

1.3 Pre-introduction selection of (a set of) natural enemy(ies)

The failure of biological control of *A. gossypii* in cucumber crops so far may be attributed to (a combination of) the following factors:

1. The natural enemies that are used do not perform well enough on *A. gossypii*, this in contrast to their performance on for example *M. persicae*.
2. The population growth of *A. gossypii* is faster than that of other aphids.
3. Mechanical and physiological properties of the cucumber host plants influence the natural enemy population in a negative way.
4. The introduction methods used at present do not prevent the initial explosion of the aphid population, so that an effective reduction cannot be obtained in time.

The above problems force the research into two different directions:

1. Try to find a more efficient (set of) natural enemy(s) (factor 1, 2 and 3).
2. Try to find a more efficient introduction method of the natural enemies (factor 4).

Consequences of these directions for the research programme will be discussed below.

Selection of a (set of) natural enemy(s)

The extensive list of natural enemies makes it impossible to evaluate all candidates for their effectiveness in biological control of cotton aphid. Furthermore, it is difficult to select potentially good natural enemies from the literature because data are scarce and often not sufficiently indicative due to the different circumstances at which they were collected. However, it might

be possible to identify promising groups of natural enemies and to identify areas where important data are lacking.

Evaluation and selection of natural enemies can be performed with a holistic or a reductionist approach (Waage & Mills, 1992). A holistic approach focuses on the interactions between the pest and its natural enemy complex (Waage, 1990). The best control is thought to be given by a complex of natural enemies with complementary characteristics (Waage, 1990). Often more than one natural enemy is introduced without a thorough pre-introduction evaluation. In many cases the releases of the natural enemy species resulted in sufficient long-term control (DeBach, 1964).

Although the debate on the usefulness of multiple introductions is ongoing (Waage & Mills, 1992), it can be questioned whether this approach will be applicable to biological control in glasshouses. Apart from the practical problems that arise when a complex of natural enemies has to be released on a regular basis, it is difficult to identify processes that lead to (un)successful control. Because in glasshouses control has to be effective from the start, understanding the way in which biological control acts is very important to identify the most effective release strategy. Further this approach is based on identifying promising agents for classical biological control (Ehler, 1982; González & Gilstrap, 1992). In this case it can be important to find a natural enemy that fits into the natural enemy complex that might already be present (González & Gilstrap, 1992), a concept that does not apply to the short term control that has to be obtained in glasshouse crops.

In the reductionist approach, a thorough pre-introduction selection of natural enemies is made (Waage & Mills, 1992). What started as comparing control agents on individual characteristics, has developed into comparison of control agents through integration of individual attributes (van Lenteren, 1986, 1993). The comparison of natural enemies is based on biologic, ecologic and economic characteristics of the species.

Van Lenteren & Woets (1988) give several criteria for pre-introduction evaluation of natural enemies for biological control in glasshouses: (1) internal synchronization with the host, (2) a good climatic adaptation, (3) no negative effects, (4) a good culture method, (5) a high reproductive potential and kill-rate and (6) a good searching efficiency. The importance of each characteristic will more or less depend on the type of control that has to be achieved. Efficiently searching natural enemies are able to reduce the pest population to low levels but may also be a cause of instability (Murdoch *et al*, 1985). Inefficiently searching natural enemies can keep the pest population stable, but probably on a much higher level. As a consequence there is a trade-off between stability and maintenance of a low pest density (Murdoch *et al*, 1985). In glasshouses the amount of aphids that can be tolerated is low and therefore a good searching capacity and large population growth rate are important characteristics of an efficient natural enemy. The instability that can occur has to be compensated for by introducing the right amount of natural enemies at the right time.

Laboratory measures of effectivity are likely to be different from the real effectivity in a more complex field environment (Kennedy, 1965; Waage & Mills, 1992). It is possible to measure parameters in the field too, but comparisons among species remain difficult because these attributes cannot be compared independently (Waage & Mills, 1992). The combination of all individual characteristics will determine the overall effectivity and trade-offs between characteristics are likely to occur (Waage & Mills, 1992). Nevertheless, the use of pre-introduction evaluations makes it possible to identify the most promising (group of) natural

enemies, or at least can make it clear which (groups of) natural enemies can be disregarded (van Lenteren, 1993). Therefore, the criteria given by van Lenteren & Woets (1988) will be evaluated with respect to an aphid-natural enemy system. The conclusions are summarized in Table 11.

1. Internal synchronization with the host

Internal synchronization is not important in an aphid-natural enemy system because in general all aphid stages are suitable hosts or prey and because in aphid populations all aphid stages are present at the same time. A problem that can occur is diapause induction in autumn. *Aphis gossypii* develops continuously in glasshouses, this means that at the end of the cropping period aphids are still present while natural enemies might go into diapause. This kind of problems were for example observed when the gall midge *A. aphidimyza* was used to control aphids in glasshouses (Hofsvang & Hågvar, 1982; Gilkeson & Hill, 1986a; Gilkeson, 1990). *Aphidoletes aphidimyza* enters diapause in the beginning of September, resulting in a rapid increase of the aphid density (Hofsvang & Hågvar, 1982).

Diapause in parasitoids is induced by hormonal cues of the aphid host (Polgár *et al*, 1991). As long as suitable aphid stages are available in the glasshouses parasitoids will not go into diapause (Hofsvang & Hågvar, 1982; Starý, 1988a).

2. Climatic adaptation

For fungi the glasshouse climate is not very favourable because of the low humidity during most of the day (Wilding, 1969; van der Geest *et al*, 1980; Ekbom, 1981; Milner & Lutton, 1986; Latgé & Papierok, 1988). At relative humidities below 93% spread of and infection by fungi is inhibited strongly (Hagen & van den Bosch, 1968; Wilding, 1969; Milner & Lutton, 1986).

It is not likely that the population development of parasitoids and predators is hampered by the average glasshouse climate, but high temperatures in summer can reduce population growth of the natural enemies. Population growth of parasitoids is reduced above 25 °C through a higher immature mortality, lower reproduction, shorter life-span or changes in the sex ratio (Wiąckowski, 1962; Force & Messenger, 1964a, 1964b; Raney *et al*, 1971; Liu Shu-Sheng & Hughes, 1984; Kring & Kring, 1988; Bernal & González, 1993) whereas *A. gossypii* populations grow fastest at constant temperatures of 30 °C and do not seem to be hampered by high temperatures (Kocourek *et al*, 1994).

Another problem occurring when *A. aphidimyza* is used is the lack of suitable pupation sites in glasshouses where the plants are grown on artificial substrates (Buxton *et al*, 1990; Gilkeson, 1990; van Schelt *et al*, 1990) and the induction of diapause mentioned above.

3. Negative effect

Although fungi do attack a wide range of organisms, strains of a fungus species are often very specific (Hall, 1982; Zimmermann, 1983; Schuler *et al*, 1991). Also predators are specific to aphids, only chrysopid and hemerobiid species do attack other soft bodied insects (New, 1988; Neuenschwander & Hagen, 1980). Aphid parasitoids are specific to aphids (Starý, 1988a; Starý, 1988b) and no other phytophagous insects or beneficial organisms are attacked. Therefore, it is not likely that natural enemies used for aphid control will interfere with the biological control of other pests. However, a combined use of several natural enemy species against aphids can still result in some kind of interference. This does not have to be a problem

as long as the combined effect is as large as or larger than the effect of a single agent. Fungi and predators do not distinguish between healthy and parasitized aphids (Wilding, 1973; Akinlosotu, 1978; New, 1988) and can, therefore, have a negative influence on the parasitoid population. Only after mummification parasitized aphids will not be attacked by predators anymore (Akinlosotu, 1978).

4. Good culture method

In classical biological control programmes the natural enemies are released only a few times. If the releases are successful and good control is obtained releases of natural enemies are not necessary any more. In seasonal inoculative control as applied in glasshouses, natural enemies are introduced throughout the year and large numbers of natural enemies have to be available at any time. Therefore, a good and efficient culture method is very important (van Lenteren & Woets, 1988).

Most fungi are easy to rear since they can be cultured on artificial media (Hagen & van den Bosch, 1968; Schuler *et al*, 1991). Spores of fungi (especially resting spores) can easily be stored for long periods (Zimmermann, 1983; Khalil *et al*, 1990).

With the exception of *A. aphidimyza* (Rimpiläinen, 1980; van Lieburg & Ramakers, 1984), mass production of predators is difficult and expensive (Tulisalo, 1984; Chambers & Helyer, 1988) because of the cannibalistic habits of many predator species (Canard & Duelli, 1984; Şengonca & Frings, 1985; Takahashi, 1987). Chrysopid and coccinellid eggs can be stored for several days at 10 °C without a marked decrease in hatchability (Hämäläinen, 1980; Canard & Principi, 1984). Diapause induction can be used to store chrysopid pupae for several months (Canard & Principi, 1984).

Cultures of aphid parasitoids are easy to maintain and a high production can be obtained in the case of *A. matricariae* which is used for biological control of aphids in glasshouses (van Schelt, 1993). Storage of parasitoid mummies is possible for several days at 6 to 10 °C without extra mortality (Archer *et al*, 1973; Tyler & Jones, 1974; Hofsvang & Hågvar, 1977; Polgár, 1986; Singh & Srivastava, 1988; Jarry & Tremblay, 1989).

5. High reproductive potential and host kill-rate

Life history parameters on immature and mature life stages of insects can be integrated to the intrinsic rate of increase or r_m-value (Birch, 1948). According to Huffaker *et al* (1976) and van Lenteren & Woets (1988) the r_m-value or host kill-rate of the natural enemies should at least equal the population growth rate of *A. gossypii* to be able for the natural enemies to keep up with the growth of the *A. gossypii* population in seasonal inoculative release programmes. Predator larvae consume a large amount of aphids during development, resulting in a large host kill-rate during one generation. However, population growth rates are always lower than the population growth rates of *A. gossypii* (Figure 16) and predators will need a considerable amount of time to build up large populations. In such cases, frequent inundative releases may be needed for sufficient control.

From literature data it is known that the reproductive potential of aphid parasitoids is large, with r_m-values equal to that of aphids (Figure 16), which means that parasitoids will be able to react to increasing aphid populations rapidly. The exact reproductive potential on cotton aphid has however still to be determined. Due to the close relationship between a parasitoid and its host there can be substantial differences between life history parameters on different aphid

species (Starý, 1988a; Hågvar & Hofsvang, 1991).

The host kill-rate of parasitoids is enlarged by the death of aphids which have fallen to the soil as reaction on the searching parasitoid (Tamaki *et al*, 1970; Hight *et al*, 1972; Ruth *et al*, 1975). Additionally, aphelinid parasitoids daily kill several hosts by host feeding (Hamilton, 1973; Kuo, 1986; Kuo-Sell & Kreisfeld, 1987; Bai & Mackauer, 1990b).

6. Good searching efficiency

In the beginning of the cropping period and when aphid control is successful, the amount of aphids present will be relatively low. In these environments the searching capacity, which is realized under circumstances in which the parasitoids will be used, is a very important feature of a successful natural enemy (Huffaker *et al*, 1977) and research on searching capacity should therefore be included in evaluation of natural enemies. Reliable, easy and effective methods to determine this characteristic are however unknown (van Lenteren, 1986) and can differ among different groups of natural enemies.

Because of the close relationship between the natural enemy and the aphids, most parasitoids and predators are efficient searchers. Predators respond to aphid related chemicals

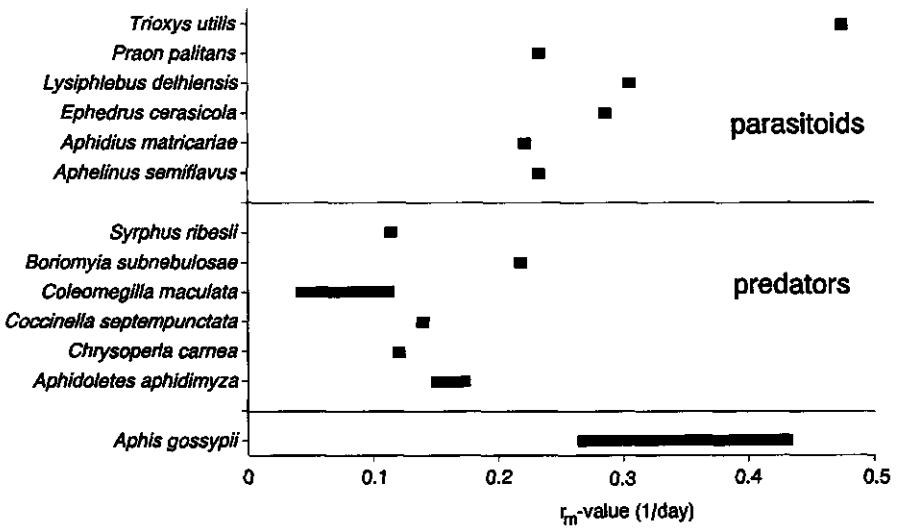

Figure 16
Population growth rates of *A. gossypii* and some of its natural enemies at 20 °C. In some cases its was assumed that there was a constant reproduction during the oviposition period, that all adults died at average life span and that the sex ratio was 50%.

(e.g., Duelli, 1984a; Chambers, 1988; Nijveldt, 1988) and deposit their eggs close to aphid colonies (e.g., Sundby, 1966; Chambers, 1988; Nijveldt, 1988). Also parasitoids use aphid related odours for host location (for a review see Hågvar & Hofsvang (1991)) and aggregate at places with high aphid densities (Hågvar & Hofsvang, 1987).

For several reasons research will concentrate on parasitoids (for a summary see Table 11). Pathogens are not able to develop a large population size in the glasshouse because the spread of the fungi through the glasshouse is insufficient. The sedentary nature of *A. gossypii* prevents spread through the glasshouse (Hall, 1981b; Hall, 1982; Milner & Lutton, 1986; Helyer & Wardlow, 1987). Also the high humidity that is required for germination is often not reached in the glasshouse for sufficiently long periods (Milner & Lutton, 1986). Because pathogens are easy to culture but have a poor capacity for transmission, application of pathogens can be used as a biopesticide when aphid densities are too high (Waage & Mills, 1992). When applied at the right time fungus sprays can cause a considerable immediate mortality (Helyer & Wardlow, 1987).

Also predators do not seem to be very promising for seasonal inoculative releases. First of all the life history parameters suggest that population growth is too low to ensure long lasting control of *A. gossypii* (Figure 16). Compared to aphids, population development is very slow. Secondly, glasshouse experiments showed that very high predator-prey ratios are necessary to control *A. gossypii* successfully (Scopes, 1969; Tulisalo & Tuovinen, 1975). Thirdly, most

Table 11
Evaluation of several groups of natural enemies based on literature data

	synchroni-zation	climatic adaptation	no negative effect	good culture method	high reproductive potential and host kill rate	good searching efficiency
PATHOGENS						
Entomophthora	+ +	− −	+ +	− −	+ −	+ −
Verticillium	+ +	− −	+ +	+ −	+ −	− −
PREDATORS						
Cecidomyiidae	+ +	+ +	+ +	+ +	+ +	+ +
Chrysopidae	+ +	+ +	+ +	− −	+ −	+ +
Coccinellidae	+ +	+ −	+ +	− −	+ −	+ +
Hemerobiidae	+ +	+ +	+ +	− −	+ −	+ +
Syrphidae	+ +	+ +	+ +	− −	+ −	+ +
PARASITOIDS						
Aphelinidae	+ +	+ +	+ +	+ +	+ −	+ +
Aphidiinae	+ +	+ +	+ +	+ +	+ +	+ +

+ + good; + − reasonable; − − bad

predator species do not form continuous populations in glasshouses because predator populations die out at low aphid densities after which an increase of cotton aphid can occur again (Hämäläinen, 1977; Chambers, 1986) and regular releases of many predators are necessary (Tulisalo & Tuovinen, 1975; Hämäläinen, 1977). The latter two points would make biological control with predators very expensive, especially because it is difficult to rear them in large quantities (Tulisalo, 1984; Chambers & Helyer, 1988; Hodek & Honěk, 1988).

Only *A. aphidimyza* is able to develop a continuous population in the glasshouse (Markkula & Tiitanen, 1980). High predator:prey ratios and repeated introductions are necessary (Scopes, 1981; Chambers, 1990), but gall midges can be cultured more easily than other predators. Also in the field aphid predators seem only to follow aphid abundance but arrive too late or leave too early to be effective as regulators of aphid populations (Frazer, 1988b).

Population growth rates of parasitoids are comparable to population growth rates of *A. gossypii* and much larger than for predators (Figure 16), which is mostly due to the shorter development time of parasitoids. Parasitoids are likely to react faster to increased aphid densities and seem therefore better candidates for biological control. Secondly, parasitoids can, even at low aphid densities, form continuous populations in glasshouses because only one aphid is needed for successful development and because they are efficient searchers (for a review see Hågvar & Hofsvang (1991)). Parasitoids are successfully used in many aphid control programmes (Richardson & Westdal, 1965; Carver, 1989; Gilkeson, 1990; van Schelt, 1993).

Based on (scarce) literature data and experiences by other researchers several hymenopterous parasitoids have been selected as possible candidates for biological control of *A. gossypii*: *Aphelinus varipes* (Förster) (Aphelinidae), *Aphidius colemani* Viereck (Braconidae), *A. matricariae* Haliday (Braconidae), *Ephedrus cerasicola* Starý (Braconidae) and *Lysiphlebus testaceipes* Cresson (Braconidae).

Before these natural enemies can be evaluated more detailed information on the pest organism is required. Chapter 2 of this thesis will describe the life history parameters of *A. gossypii* on cucumber which were collected during this project, both in the laboratory and under glasshouse conditions. Evaluation and selection of parasitoids will be described in Chapter 3. Both laboratory and glasshouse experiments were used for evaluation. For the most promising parasitoids the life history parameters were estimated in more detail (Chapter 4). Chapter 5 is concerned with the searching behaviour of the most promising parasitoid.

Development of an efficient method of introduction of natural enemies

An aphid-natural enemy system differs considerably from other pest-natural enemy systems that occur in glasshouses. Pests like leafminers, whitefly and thrips show initially a discrete population growth in which the stages suitable for predation and parasitization are present at certain intervals. Furthermore, the natural enemies used against these pests often attack only a few stages of the pest (Ramakers & Rabasse, 1995). As a consequence total eradication of the pest population (and thus of the natural enemy population) will not easily occur and the pest and its natural enemies will be present continuously.

Aphid-natural enemy complexes are less stable. The natural enemies are efficient searchers and attack all aphid stages. In field populations, at first the aphids increase in numbers very fast. After the natural enemy populations have built up, a population crash follows often caused by deterioration of the host plants (Way & Banks, 1968; van Emden *et al*, 1969). After

destruction the large natural enemy population prevents the aphid population from increasing again (Way & Banks, 1968). However, the crop damage that precedes the crash of the aphid population is often intolerable to growers (van Emden *et al*, 1969).

Because of the fast population growth of aphids, the first aphid entering a glasshouse causes an indiscrete, almost exponential population growth. For effective control the natural enemies have to be present very soon after aphids enter the glasshouse, otherwise the aphid population will grow to such a size that effective control cannot be achieved anymore. After successful suppression of the pest, aphid levels are very low and not many parasitoids and predators will survive, giving a chance to new aphids entering the glasshouse (Ramakers & Rabasse, 1995). During the absence of the natural enemies the aphids are able to multiply to such levels that the next generation of natural enemies is too late to establish efficient control. This delay in the reaction of the parasitoid population to the number of hosts available, causes oscillations (Krebs, 1972; Varley *et al*, 1973). The size of the oscillations increases with increasing growth rates of the host and parasitoid population (Nicholson, 1933). A wave-like population development of the aphids and their natural enemies can often be seen in glasshouses (Ramakers & Rabasse, 1995).

To ensure a continuous presence of natural enemies in time and space, natural enemies should be introduced with very short time intervals and in sufficiently high numbers before a large aphid population is present. Depending on the size of introductions needed, this could be rather expensive and costs may prevent such an introduction system to be implemented. A possible solution to this problem is to create a more or less stable natural enemy population before the aphids enter the glasshouse (van Emden, 1988), for example by an open rearing method on an aphid species which is harmless to the crop (Bennison, 1992). The open rearing acts as a refuge for the natural enemies during periods of low aphid density in the crop. The availability of refuges can have a positive effect on the stability and equilibrium size of the pest population (Murdoch *et al*, 1995). Parasitoids seem to be more suitable for this method than predators for several reasons:

1. A parasitoid needs only one aphid for reproduction, while predators need considerably more aphids to develop successfully. Especially at low aphid densities on the banker plants, predators would have a disadvantage.
2. The active stages of parasitoids (the adults) are much more mobile than the active stages of predators (the larvae) and are thus able to search for aphids on a much larger area.

For many parasitoids the searching behaviour is very variable and can change through rearing history and previous experiences (Lewis *et al*, 1990). When this method is going to be used, studies are required on how host preference is influenced by the host species on which the parasitoids are reared, how host switching influences parasitoid behaviour and how learning and conditioning plays a role in host preference. Also studies on distribution and dispersal of the natural enemy through the glasshouse have to be performed. Application of the most promising natural enemy is studied in Chapter 6.

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Chapter 2

Life history of *Aphis gossypii*

2 Life history of *Aphis gossypii* Glover (Homoptera: Aphididae) on cucumber: influence of temperature, host plant and parasitism[1]

Abstract

Life table data for *Aphis gossypii* Glover (Homoptera: Aphididae), an important pest in glasshouse cucumber crops, were studied at 20, 25 and 30 °C on two cucumber cultivars (*Cucumis sativus* L.) in controlled climate cabinets. The development time on the cucumber cv. 'Sporu' ranged from 4.8 days at 20 °C to 3.2 days at 30 °C. The immature mortality was approximately 20% and did not differ among temperatures. Most mortality occurred during the first instar. The reproduction periods did not differ among temperatures. At 25 and 30 °C more nymphs were produced (65.9 and 69.8 nymphs/♀, respectively), than at 20 °C (59.9 nymphs/♀) because of a higher daily reproduction. The intrinsic rate of increase was greatest at 25 °C (r_m=0.556 day^{-1}). At 20 and 30 °C the intrinsic rate of increase was 0.426 and 0.510, respectively. On cv. 'Aramon', the development time of *A. gossypii* was approximately 20% longer at all temperatures than on cv. 'Sporu'. The immature mortality did not differ between the two cultivars. The intrinsic rate of increase on cv. 'Aramon' was 15% smaller than on cv. 'Sporu'. The use of cucumber cultivars partially resistant to aphids is discussed in relation to biological control of cotton aphid in glasshouses.

The development time and immature mortality on leaves of the middle and upper leaf layer of glasshouse grown cucumber plants (cv. 'Aramon') were comparable to the development in the controlled climate cabinets. On the lower leaves the immature mortality was much higher (approximately 82%) than on leaves of the middle (24.0%) and upper leaf layer (24.5%). The life-time fecundity was lowest on the leaves of the lower leaf layer (45.9, 70.5 and 70.1 nymphs/♀ on leaves of the lower, middle and upper leaf layer, respectively).

Aphids, successfully parasitized by *Aphidius colemani* Viereck (Hymenoptera: Braconidae), only reproduced when they were parasitized after the third instar. The life-time fecundity was 0.1 to 0.9 and 10.5 to 13.3 nymphs/♀ for aphids parasitized in the fourth instar or as adults, respectively. Reproduction of aphids that were stung but survived the attack was lower than for aphids not stung. Average longevity of these aphids was equal to the longevity of aphids not stung by *A. colemani*.

Introduction

Aphis gossypii Glover (Homoptera: Aphididae) is an important pest on various crops. Its first record as a pest was in cotton fields in 1854 in South Carolina, USA (Paddock, 1919). In Europe cotton aphid is an important pest on cucumber in glasshouses (Van Schelt *et al*, 1990; Bennison, 1992). On glasshouse cucumbers *A. gossypii* populations can increase at rates of 5.4, 8.8 and 6.5 times a week at average temperatures of 19.7, 25.0 and 26.0 °C, respectively (Wyatt, 1971).

Because cotton aphid has developed resistance to many commonly used insecticides (Kerns & Gaylor, 1992; Gubran *et al*, 1993), biological control with the parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae) and the predatory gall midge *Aphidoletes aphidimyza*

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Rondani (Diptera: Cecidomyiidae) is presently the only control method available for IPM programmes in glasshouses. However, biological control of cotton aphid in glasshouses is not always successful. Especially in the summer it is difficult to maintain good control of aphids.

Life table studies of *A. gossypii* have been done on several host plants (e.g., *Citrus unshiu* (Komazaki, 1982) and *Cucurbita pepo* (Aldyhim & Khalil, 1993)), but for cucumber (*Cucumis sativus* L.) detailed data are scarce and known on only two cultivars (Wyatt & Brown, 1977; Kocourek *et al*, 1994). Differences in host plant suitability of different melon cultivars for *A. gossypii* have been recorded (Kennedy & Kishaba, 1976; Shinoda & Tanaka, 1987) and might also occur among cucumber cultivars. Since partial resistance can enhance the effectiveness of natural enemies (Van Emden, 1986), it was thought desirable to study life history parameters of *A. gossypii* on more than one cucumber cultivar. For convenience we chose two cucumber cultivars which were already grown at the station: 'Sporu', an old cultivar, and 'Aramon', a more recent mildew-resistant cultivar. On both cultivars controlled climate cabinet experiments were done at three constant temperatures.

To find out how the life table studies in controlled climate cabinets relate to commercial cropping conditions, glasshouse experiments were also carried out. Here we studied development and reproduction at three different leaf layers in order to properly estimate aphid population development in the glasshouse.

The effect of parasitism by *A. colemani* on the biology of *A. gossypii* was examined at three temperatures. The importance of production of offspring by parasitized aphids, and the interaction between effectiveness of *A. colemani* and partial resistance to cotton aphid in cucumber cultivars will be discussed.

Material and Methods

Insect cultures

Aphis gossypii were collected from cucumber glasshouses in the Netherlands in 1990. At the Glasshouse Crops Research Station the aphids were cultured on cucumber (cvs. 'Sporu' and 'Aramon') under natural light and a minimum temperature of 18 °C.

The parasitoids used in these experiments were collected in 1989 from *A. gossypii* in Dutch cucumber glasshouses, where biological control was successful. From 1990 onwards the parasitoids were reared at the Glasshouse Crops Research Station in small glasshouse compartments under natural light and at a minimum temperature of 18 °C. *Aphis gossypii* was used as the host and cucumber (cvs. 'Sporu' and 'Aramon') as the host plant.

Experiment 1 - Life history of unparasitized Aphis gossypii *at three temperatures and in the glasshouse*

The life history of *A. gossypii* was studied at three different temperatures (20, 25 and 30 °C (± 1 °C)) in controlled climate cabinets with a photoperiod of L14:D10 and a constant relative humidity of 65% (± 5%). The development time and immature mortality were recorded on potted cucumber plants with five to six leaves (*Cucumis sativus* cvs. 'Sporu' and 'Aramon'). For each combination of cultivar and temperature, 50 wingless adults were put separately into a clip-on leaf cage (ϕ 2 cm) on the second or third cucumber leaf from the bottom. After one day all aphids except one young nymph per cage were removed. The 50 nymphs were followed in their development and the instar was recorded daily. After the nymphs had become adults their reproduction was recorded on cv. 'Sporu' only.

The glasshouse experiment was performed in a small glasshouse (17 m^2) with 26 cucumber plants (cv. 'Aramon'). The experiments were started when the plants were approximately eight weeks old and had reached a height of at least 2.5 meters. Aphids were placed on leaves at three different layers of the plant: the old lower leaves (first or second leaf from below), middle leaves (approximately the seventh leaf from below, 1.5 meters above the ground) and upper recently formed leaves. The same procedure as in the controlled climate cabinet experiments was followed. The average temperature during the experiment was 22.5 °C (range 17.8 - 36.0 °C). The few aphids that developed into winged individuals were omitted from the analysis.

Experiment 2 - Life history of parasitized aphids at three temperatures

The experiment was done in controlled climate cabinets at constant temperatures of 20, 25 and 30 °C (± 1 °C) and a L14:D10 photoperiod. The relative humidity was 65% (± 5%). Nymphs of different instars and young adults were exposed to one day old female parasitoids (*A. colemani*) in a small petri dish (ϕ 5.5 cm) with a cucumber leaf disc (cv. 'Sporu') on agar. Aphids, stung by a parasitoid, were removed until 25 stung aphids of each stage were available.

The mortality in the first two instars (27.1% (n=150)) was much higher than the natural mortality in experiment 1. Therefore, 25 more replicates were obtained for these instars. The higher mortality in the first two instars was probably due to handling of the aphids. In control experiments (in which the aphids were handled the same way, but were not exposed to a female parasitoid) the mortality was also high during the first two instars (28.2% (n=150)). The parasitized aphids were then transferred to the controlled climate cabinets and placed separately into small clip-on leaf cages (ϕ 2 cm) on potted cucumber plants (cv. 'Sporu'). The following data were recorded daily: the instar of the immature aphids, time until mummification, time until hatching of the parasitoid and number of offspring produced by the aphids.

Statistical analysis

Differences were tested by analysis of variance (ANOVA). If significant differences were detected, multiple comparisons were made using an LSD-procedure (α=0.05). Data on development times, adult reproduction and adult longevity were log-transformed to stabilize variances (Murdie, 1972). For comparison of mortality rates X^2-tests were used. Differences in r_m-values were tested for significance by estimating variances through the Jackknife technique (Meyer *et al*, 1986), followed by ANOVA. If significant differences were detected, multiple comparisons were made using an LSD-procedure (α=0.05).

Results

Experiment 1 - Life history of unparasitized Aphis gossypii *at three temperatures and in the glasshouse*

At 20, 25 and 30 °C the development times on cv. 'Sporu' were significantly different ($P<0.001$; ANOVA) (Table 1). For each instar a similar trend could be seen although differences were not always significant.

The life-time fecundity at 20 °C was significantly lower than the life-time fecundity at 30 °C. The life-time fecundity at 25 °C was intermediate (Table 1). The difference in life-time fecundity was caused by a higher daily reproduction at 30 °C (Table 1). The adult longevity was not significantly different among the temperatures (Table 1). This is also apparent from Figure 1b, since there are no clear differences in the survival curves. The reproductive period

was not significantly different among the temperatures (ANOVA) (Table 1). The intrinsic rate of increase was greatest at 25 °C (Table 1).The effect of temperature on the development and reproduction is presented in a simplified way in Figure 3a (after Lewontin (1965)).

The development times differed considerably between cultivars (Table 2). On cv. 'Sporu' development was significantly faster than on cv. 'Aramon' (27, 23 and 17% faster at 20, 25 and 30 °C, respectively) ($P<0.001$; ANOVA). No significant differences in immature mortality were present (X^2-test). The effect of plant cultivar on the development and reproduction at 20

Table 1
Life table parameters of *Aphis gossypii* at 20, 25 and 30 °C on potted cucumber plants (*Cucumis sativus* cv. 'Sporu'). Different letters between temperatures indicate a significant difference ($P<0.05$; LSD after ANOVA; X^2-test).

	Temperature		
	20 °C	25 °C	30 °C
	Development time (days (± s.e.; n))		
instar 1	1.7 (± 0.07; 42)[a]	1.0 (± 0.00; 45)[b]	0.9 (± 0.07; 42)[b]
instar 2	1.2 (± 0.07; 40)[a]	1.0 (± 0.03; 41)[b]	0.6 (± 0.04; 39)[c]
instar 3	0.8 (± 0.04; 40)[a]	0.7 (± 0.04; 40)[a]	0.8 (± 0.04; 38)[a]
instar 4	1.1 (± 0.06; 40)[a]	0.8 (± 0.04; 39)[b]	0.9 (± 0.05; 37)[b]
total	4.8 (± 0.07; 40)[a]	3.5 (± 0.08; 39)[b]	3.2 (± 0.07; 37)[c]
	Immature mortality (% (n))		
instar 1	14.3 (49)[a]	8.2 (49)[a]	14.3 (49)[a]
instar 2	4.8 (42)[a]	8.9 (45)[a]	7.1 (42)[a]
instar 3	0.0 (40)[a]	2.4 (41)[a]	2.6 (39)[a]
instar 4	0.0 (40)[a]	2.6 (40)[a]	2.6 (38)[a]
total	18.4 (49)[a]	20.6 (49)[a]	24.5 (49)[a]
	Adult life history (days (± s.e.; n))		
pre-repr. period	0.5 (± 0.09; 40)[a]	0.3 (± 0.08; 39)[a]	1.1 (± 0.08; 37)[b]
repr. period	11.7 (± 0.58; 40)[a]	11.5 (± 0.47; 39)[a]	10.4 (± 0.54; 37)[a]
post-repr. period	2.5 (± 0.45; 40)[a]	2.5 (± 0.56; 39)[a]	3.4 (± 0.59; 37)[a]
longevity	14.7 (± 0.90; 40)[a]	14.3 (± 0.80; 39)[a]	14.9 (± 0.99; 37)[a]
	Reproduction (nymphs/♀ (± s.e.; n))		
life-time fecundity	59.9 (± 2.47; 40)[a]	65.9 (± 2.28; 39)[ab]	69.8 (± 3.41; 37)[b]
daily repr.	5.3 (± 0.16; 40)[a]	5.9 (± 0.17; 39)[a]	6.7 (± 0.26; 37)[b]
Generation time (T) (days)	10.8	8.9	9.3
Net reproduction (R_0) (♀/♀)	49.9	53.0	52.7
r_m (1/day)	0.426 (± 0.009; 49)[a]	0.556 (± 0.013; 49)[b]	0.510 (± (0.013; 49)[c]

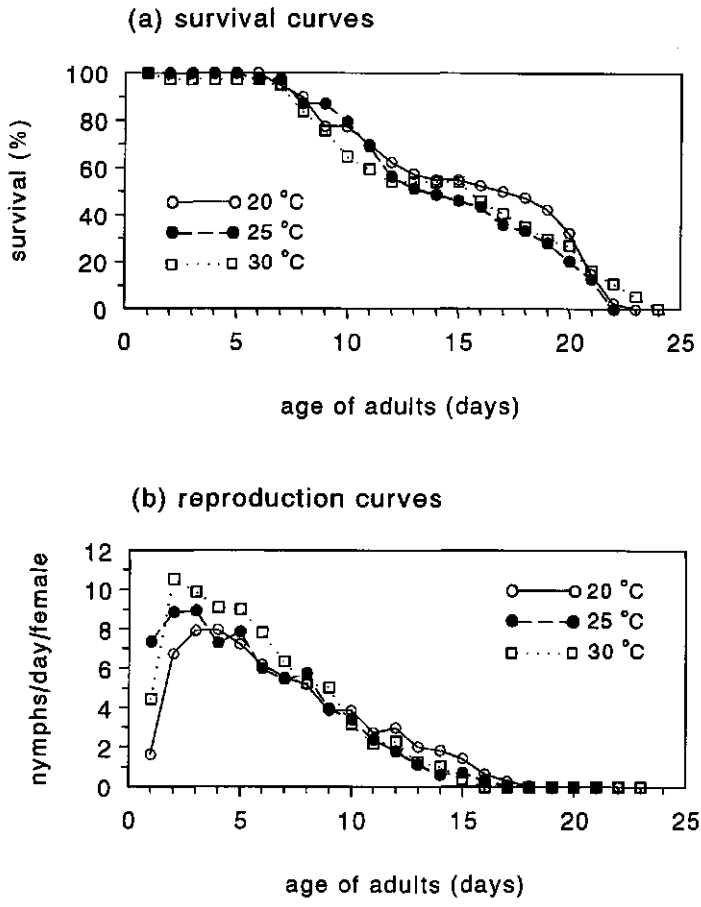

Figure 1
Survival (a) and reproduction (b) curves of adult *Aphis gossypii* on potted cucumber plants (cv. 'Sporu') at 20, 25 and 30 °C.

Table 2
Development of *Aphis gossypii* on potted cucumber plants (*Cucumis sativus* cvs. 'Aramon' and 'Sporu') at 20, 25 and 30 °C. Different letters between cultivars indicate a significant difference ($P<0.05$; LSD after ANOVA; X^2-test).

	DEVELOPMENT TIME (DAYS (± S.E.; N))		IMMATURE MORTALITY (% (N))	
Temp.	cv. 'Aramon'	cv. 'Sporu'	cv. 'Aramon'	cv. 'Sporu'
20 °C	6.6 (± 0.08; 37)[a]	4.8 (± 0.07; 40)[b]	26.0 (50)[a]	18.4 (49)[a]
25 °C	4.6 (± 0.09; 39)[a]	3.5 (± 0.08; 39)[b]	22.0 (50)[a]	20.6 (49)[a]
30 °C	3.8 (± 0.07; 32)[a]	3.2 (± 0.07; 37)[b]	36.0 (50)[a]	24.5 (49)[a]

°C is presented in a simplified way in Figure 3b (after Lewontin (1965)). In this figure the development data on cv. 'Aramon' are completed with reproduction data from cv. 'Sporu'.

In the glasshouse the development times of aphids on leaves at different layers were not significantly different (Table 3). The average duration of development from birth to adulthood (5.6 days at an average glasshouse temperature of 22.5 °C (range: 17.8 - 36.0 °C)) (Table 3), lies approximately between the development times at constant temperatures of 20 and 25 °C in the controlled climate cabinets on the same cultivar 'Aramon' (Table 2). The immature

Table 3
Life table parameters of *Aphis gossypii* on different leaf layers of glasshouse-grown cucumber plants (*Cucumis sativus* cv. 'Aramon'). Different letters between leaf layers indicate a significant difference ($P<0.05$; LSD after ANOVA; X^2-test). The average temperature in the glasshouses was 22.5 °C (range: 17.8 - 36.0 °C).

	LEAF LAYER		
	lower	middle	upper
	DEVELOPMENT TIME (DAYS (± S.E.; N))		
instar 1	1.3 (± 0.23; 27)[a]	1.7 (± 0.13; 45)[ab]	1.7 (± 0.13; 37)[b]
instar 2	1.7 (± 0.23; 18)[a]	1.3 (± 0.11; 42)[ab]	1.4 (± 0.10; 37)[b]
instar 3	1.4 (± 0.24; 12)[a]	1.3 (± 0.11; 40)[a]	1.4 (± 0.12; 37)[a]
instar 4	1.0 (± 0.00; 9)[a]	1.1 (± 0.09; 38)[a]	1.2 (± 0.10; 37)[a]
total	5.4 (± 0.24; 9)[a]	5.5 (± 0.12; 38)[a]	5.8 (± 0.11; 37)[a]
	IMMATURE MORTALITY (% (N))		
instar 1	46.0 (50)[a]	10.0 (50)[b]	24.5 (49)[b]
instar 2	33.3 (27)[a]	6.7 (45)[b]	0.0 (37)[b]
instar 3	33.3 (18)[a]	4.8 (42)[b]	0.0 (37)[b]
instar 4	25.0 (12)[a]	5.0 (40)[b]	0.0 (37)[b]
total	82.0 (50)[a]	24.0 (50)[b]	24.5 (49)[a]
	ADULT LIFE HISTORY (DAYS (± S.E.; N))		
pre-repr. period	1.4 (± 0.29; 9)[a]	1.3 (± 0.09; 38)[a]	1.5 (± 0.10; 37)[a]
repr. period	9.2 (± 1.01; 9)[a]	12.6 (± 0.88; 38)[a]	12.6 (± 0.58; 37)[a]
post-repr. period	1.1 (± 0.42; 9)[a]	2.8 (± 0.73; 38)[a]	3.6 (± 0.97; 37)[a]
longevity	11.8 (± 1.13; 9)[a]	16.7 (± 1.35; 38)[a]	17.8 (± 1.79; 37)[a]
	REPRODUCTION (NYMPHS/♀ (± S.E.; N))		
life-time fecundity	45.9 (± 6.85; 9)[a]	70.5 (± 4.07; 38)[b]	70.1 (± 4.17; 37)[b]
daily reproduction	4.7 (± 0.36; 9)[a]	5.8 (± 0.20; 38)[b]	5.8 (± 0.17; 37)[b]
Generation time (T) (days)	11.9	12.9	13.9
Net reproduction (R_0) (♀/♀)	8.4	49.4	52.9
r_m (1/day)	0.192 (± 0.031; 50)[a]	0.350 (± 0.010; 50)[b]	0.337 (± 0.009; 49)[b]

mortalities were, however, much higher at the lower leaf layer than at middle and top leaf layers (Table 3). On the lower leaf layer the immature mortality was much higher than in the controlled climate cabinets ($P<0.05$; X^2-test) whereas on the middle and upper leaf layers the immature mortality was equal to the immature mortality in the controlled climate cabinets (X^2-test). Again most mortality occurred in the first stage although on the lower leaf layer the mortality in later stages was also high (Table 3). The survival and reproduction of adult *A. gossypii* on leaves at different layers of the cucumber plants in glasshouses are given in Figure 2. The life-time fecundity at the lower leaf layer was significantly lower than the life-time fecundity at the

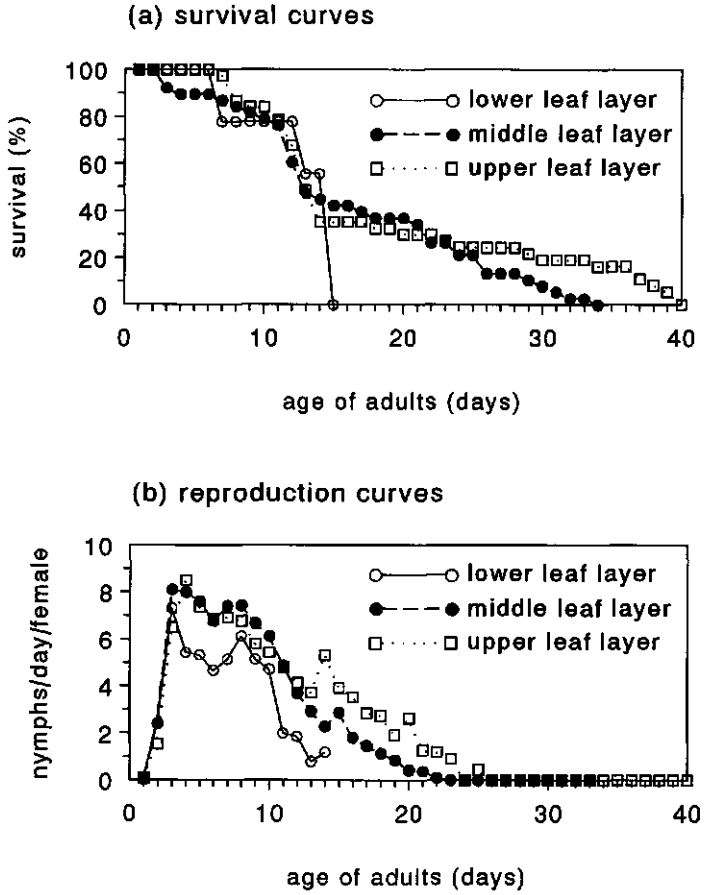

Figure 2
Survival (a) and reproduction (b) curves of adult *Aphis gossypii* on three leaf layers of glasshouse-grown cucumber plants (cv. 'Aramon').

middle and upper leaf layers (P=0.022; ANOVA) (Table 3). The differences are caused by a significantly lower daily reproduction on the lower leaves, in combination with a non-significant, shorter reproductive period (Table 3).

The r_m-values at the lower leaf layer were significantly lower than the r_m-values at the middle and upper leaf layers (P<0.001; ANOVA) (Table 3). The effect of the leaf layer on which the aphids feed is presented in a simplified way in Figure 3c (after Lewontin (1965)).

Experiment 2 - Biology of parasitized aphids at three temperatures

In Table 4 the death rate before mummification and the percentage of mummified aphids are shown for the three temperatures. The instar of the aphid did not significantly influence parasitization success (% mummies) or mortality during the mummy stage (X^2-test) and was omitted from the analysis.

Table 4
Reproduction and reproductive periods of aphids on potted cucumber plants (*Cucumis sativus* cv. 'Sporu') parasitized by *Aphidius colemani* in different instars at 20, 25 and 30 °C. Different letters indicate a significant difference between temperatures (P<0.05; LSD after ANOVA; X^2-test).

	TEMPERATURE		
	20 °C	25 °C	30 °C
dead before mummy (% (n))	25.1 (175)[a]	22.3 (175)[a]	22.9 (175)[a]
mummified (% (n))	78.6 (131)[a]	83.8 (136)[a]	85.2 (135)[a]
reproduction period of aphids parasitized successfully at different stages (days (± s.e.; n))			
instar 1 to 3	0.0	0.0	0.0
instar 4	0.3 (± 0.18; 20)[a]	0.1 (± 0.07; 21)[a]	0.9 (± 0.21; 20)[b]
adult	2.7 (± 0.18; 15)[a]	2.2 (± 0.14; 17)[b]	2.6 (± 0.26; 18)[a]
daily reproduction of aphids parasitized successfully at different stages (nymphs/♀ (± s.e.; n))			
instar 1 to 3	0	0	0
instar 4	1.9 (± 0.42; 2)[a]	6.0 (± 2.00; 2)[a]	1.8 (± 0.32; 8)[a]
adult	4.0 (± 0.39; 15)[a]	5.0 (± 0.28; 17)[ab]	5.5 (± 0.37; 18)[b]
reproduction of aphids parasitized successfully in different instars (nymphs/♀ (± s.e.; n))			
instar 1 to 3	0.0	0.0	0.0
instar 4	0.5 (± 0.37; 20)[a]	0.6 (± 0.42; 21)[a]	1.3 (± 0.33; 20)[a]
adult	10.5 (± 0.98; 15)[a]	10.6 (± 0.50; 17)[a]	13.3 (± 0.95; 18)[b]
r_m-values for aphids parasitized successfully in different instars (1/day (± s.e.; n))			
instar 1 to 3	0	0	0
instar 4	0.000 (± 0.000; 20)[a]	0.000 (± 0.000; 21)[a]	0.046 (± 0.053; 20)[b]
adult	0.340 (± 0.016; 15)[a]	0.445 (± 0.017; 17)[b]	0.507 (± 0.015; 18)[c]

Aphids, successfully parasitized in the first, second or third instar did not reproduce. When aphids were parasitized in the fourth instar less than 1.5 nymphs were produced and the reproduction period was less than one day (Table 4). Aphids successfully parasitized as young adults produced 10.5 to 13.3 nymphs over a period of approximately 2.5 days (Table 4). At 30 °C more nymphs were produced ($P<0.001$; ANOVA) during a longer period ($P<0.001$; ANOVA) than at 20 or 25 °C (Table 4). The daily reproduction of these aphids was lower than the daily reproduction of unparasitized aphids ($P<0.001$; ANOVA) (Table 1, Table 4). In Figure 3d the reproduction curves of parasitized aphids at 20 °C are given in a simplified way according to Lewontin (1965).

Although reproduction of aphids successfully parasitized as adult stopped within three days, the first days after parasitization the daily reproduction was almost equal to the daily reproduction of unparasitized aphids (Figure 3d). As a consequence the aphids parasitized as adults contributed nearly as much to the next generation as unparasitized aphids. This is shown by a slight reduction in the intrinsic rate of increase after parasitization (Table 4), which was significant at 20 and 25 °C.

Reproduction of aphids, that were stung, but did not mummify, was significantly lower than for the unparasitized aphids in the first experiment ($P<0.001$; ANOVA) (Table 5). There were no significant differences in lifespan or reproduction among temperatures (Table 5). Because only few observations were available for each aphid stage, the different stages were grouped together for each temperature. The reproduction period was as long as for unparasitized aphids. From Figure 3d it can be seen that the lower reproduction was caused by a lower daily fecundity compared with unparasitized aphids ($P=0.038$; ANOVA). The r_m-values were significantly reduced compared to unparasitized aphids ($P<0.001$; ANOVA).

Discussion

Under both controlled conditions and in the glasshouse most of the immature mortality occurred during the first instar. Only on leaves of the lower layer was mortality also high in older stages. Problems with settling of aphids might have been the main cause for the

Table 5
Reproduction and reproductive periods (avg (± s.e.; n)) of aphids stung by *Aphidius colemani* without development of a parasitoid larva at 20, 25 and 30 °C. Data were grouped over all aphid stages. Different letters indicate a significant difference between temperatures ($P<0.05$; LSD after ANOVA).

	Temperature		
	20 °C	25 °C	30 °C
pre-repr. per. (days)	1.1 (± 0.23; 20)[a]	0.6 (± 0.13; 16)[b]	1.0 (± 0.23; 14)[a]
repr. per. (days)	11.9 (± 0.56; 28)[a]	10.5 (± 0.54; 22)[a]	10.5 (± 0.64; 20)[a]
post-repr. per. (days)	2.8 (± 0.31; 28)[a]	3.4 (± 0.38; 22)[a]	3.0 (± 0.42; 20)[a]
longevity (days)	15.4 (± 0.67; 28)[a]	14.4 (± 0.71; 22)[a]	14.2 (± 0.78; 20)[a]
daily repr. (nymphs/♀)	4.4 (± 0.24; 28)[a]	4.9 (± 0.25; 22)[a]	4.8 (± 0.36; 20)[a]
repr. (nymphs/♀)	48.9 (± 2.93; 28)[a]	50.2 (± 2.94; 22)[a]	49.8 (± 3.86; 20)[a]
r_m (1/day)	0.371 (± 0.013; 28)[a]	0.479 (± 0.017; 22)[b]	0.472 (± 0.015; 20)[b]

immature mortality. In studies on immature development of other aphids (such as *Acyrthosiphon pisum* (Hutchison & Hogg, 1984) and *Eriosoma lanigerum* (Asante *et al*, 1991)), high mortalities were also observed in other instars, especially at temperatures above 25 °C. Cotton aphid seems to be very well adapted to temperatures above 25 °C.

The reproductive periods did not differ among temperatures, as was also found by Kocourek *et al* (1994) at similar temperatures. On *Cucurbita pepo*, the reproductive period at 30 °C was considerably shorter than at 20 and 25 °C (Aldyhim & Khalil, 1993). Daily and thus total reproduction increased with rising temperatures. The maximum intrinsic rate of increase of 0.556 at 25 °C, was higher than found by Wyatt & Brown (1977) on the cucumber cv. 'Butcher's disease resister' (0.447 at 24 °C), and higher than found by Kocourek *et al* (1994)

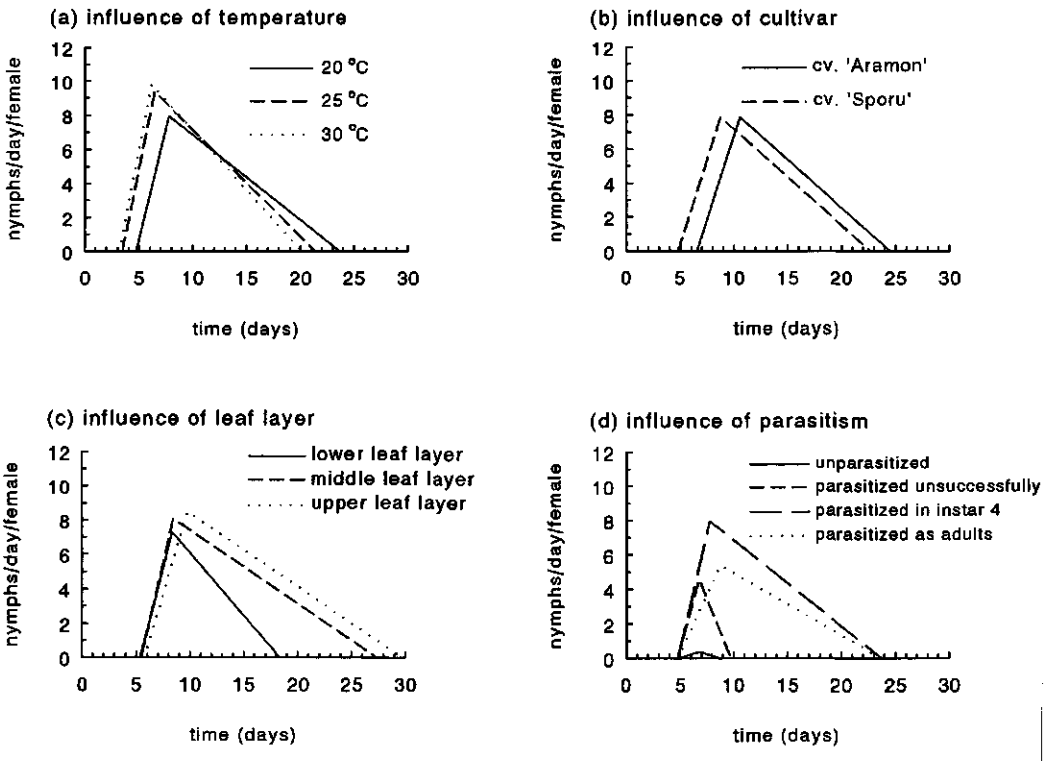

Figure 3
Influence of several factors on some life history parameters of *Aphis gossypii* (after Lewontin (1965)). Data used for the graphs are: day of first reproduction, day of the maximum daily reproduction and the last day of the reproductive period. (a) influence of temperature; (b) influence of different development times on two cucumber cultivars at 20 °C; (c) influence of plant leaf layer; (d) influence of parasitism at 20 °C.

on the cv. 'Sandra' (0.465 at 30 °C). Both on cv. 'Butcher's disease resister' and on cv. 'Sandra' the development times were longer than on cv. 'Sporu' in this study (Wyatt & Brown, 1977; Kocourek *et al*, 1994). They used the same temperatures as in the present study so the differences in r_m-values and development times can probably be attributed to the use of another cultivar.

There were no large differences between reproduction data on cv. 'Aramon' in the glasshouse (R_0=49.9 to 52.9 ♀/♀ at the suitable leaf layers) and cv. 'Sporu' in the controlled climate cabinets (R_0=49.9 to 53.0 ♀/♀). The main difference between the two cultivars seemed to be an increase in the development time on cv. 'Aramon'. At equal reproduction the longer development time would reduce the intrinsic rate of increase on cv. 'Aramon' by approximately 15% (0.339, 0.471 and 0.446 day^{-1} at 20, 25 and 30 °C, respectively). The weekly multiplication rate of a population at 25 °C was reduced from 49 times on cv. 'Sporu' to 27 times on cv. 'Aramon'. In melon cultivars resistance against *A. gossypii* is correlated with strong callose-deposition on the site of feeding (Shinoda, 1993). Both antibiosis and non-preference seem important mechanisms for resistance in melon (Yoshida & Iwanaga, 1991). The cause of the difference in suitability between the two cultivars used in the present research is not known and deserves more detailed study.

It is not possible to conclude why leaves of the lower layer are less suitable for aphids than leaves from the middle and top layer. The differences in reproduction suggest that the suitability of the plant sap is different in different leaf layers. On the other hand, aphids that complete development successfully on leaves of the lower layer have the same development time as aphids on the other leaf layers. This suggests that the suitability of the plant juices in different leaf layers is not different and that the differences in suitability of leaf layers are caused by morphological differences. The lower leaves seem to differ from other leaves because they are tougher and possibly more difficult for the young aphids to penetrate.

The influence of the high mortality on leaves of the lower layer on the population dynamics of the aphid in glasshouses is likely to be low. In commercial glasshouses the plants are in good condition and the proportion of lower leaves is very small compared to the more suitable middle and upper leaves.

Apart from the high immature mortality and lower reproduction at leaves of the lower layer of glasshouse-grown cucumber plants there are no differences in development and reproduction between the glasshouse and the controlled climate cabinets. It can be concluded that there is a good correlation between life table parameters of *A. gossypii* on cucumber plants in controlled climate cabinets and in glasshouses.

Reproduction of successfully parasitized aphids is low. Although aphids that are parasitized as adults could reproduce only for a couple of days, the r_m-values show that they are still able to contribute to the next aphid generation almost as much as unparasitized aphids. When the development time is short, total reproduction does not have a very large impact on population growth rates (Lewontin, 1965). In these cases the reproduction during the first days of adulthood is much more important than the total reproduction (Wyatt & White, 1977). For adult aphids reproduction ceased within three days after parasitization. In *A. pisum* parasitized as adults by *Aphidius smithi* it takes seven to eight days until embryogenesis ceases and no more offspring are produced (Campbell & Mackauer, 1975; Soldán & Starý, 1981). As a consequence more nymphs are produced by *A. pisum* than by *A. gossypii*. *Myzus persicae* parasitized as adults by *Aphidius matricariae* produce 9.2 nymphs in 3.9 days, whereas those parasitized as

fourth instar produce 5.8 nymphs (Rabasse & Shalaby, 1979).

A small portion of the aphids survived an attack by *A. colemani*. The reproduction period of these aphids did not differ from healthy aphids. The daily reproduction was reduced, but r_m-values were still high. It is impossible to say whether the smaller daily reproduction was caused by the parasitoid (through some substance injected by the parasitoid female or emanating from the egg), or by the costs of the immune defence reaction of the aphid. Also in *M. persicae* attacked by *A. colemani* a small portion of the aphids survived parasitization (Tardieux & Rabasse, 1988). Dissection revealed no sign of parasitization in these aphids but longevity and fecundity were slightly reduced in comparison with aphids not stung by *A. colemani* (Tardieux & Rabasse, 1988).

The importance of using resistant cultivars is not only the reduction of aphid population growth. Resistance in barley did slow down development of the grain aphid, *Schizaphis graminum*, but could not prevent the aphids from reaching damaging levels (Starks *et al*, 1972). However, in the presence of the parasitoid *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae) aphids did not reach damaging levels on resistant barley. No control could be obtained when a susceptible barley variety was used (Starks *et al*, 1972), indicating the importance of the interaction between host plant resistance and natural enemies for biological control. In Figure 4 the consequences of using a partially resistant cultivar are shown. Here we assume exponential growth of the aphid population and a weekly introduction of parasitoids,

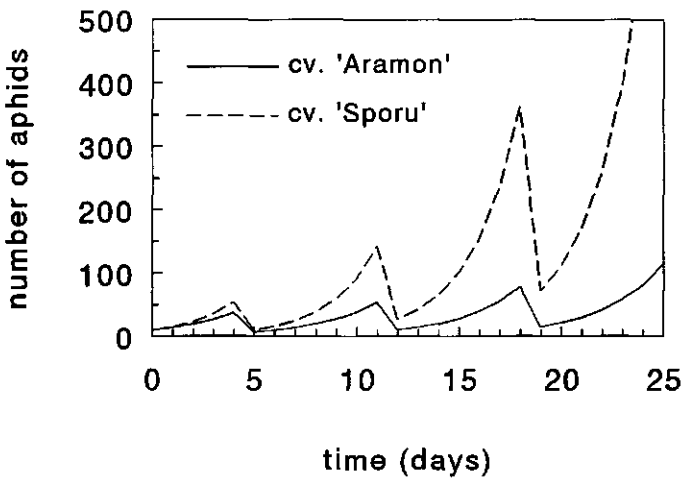

Figure 4
Model of population development of *Aphis gossypii* at 20 °C on a partially resistant (cv. 'Aramon') and a susceptible cucumber cultivar (cv. 'Sporu'), assuming that twenty percent of the aphids survives the weekly introductions of *Aphidius colemani*, and that the aphid population grows exponentially.

during which 80% of the aphids is parasitized. The remaining aphids start to grow exponentially immediately. Clearly there is a strong divergence between aphid populations on the susceptible and the partially resistant cultivar. On a partially resistant cultivar the parasitoids are able to keep the aphid population on a low level much longer. This is particularly important at the start of the season when weekly introductions of parasitoids are used to suppress population growth of immigrating aphids. Several weeks after the first aphid infestation the numerical response of the parasitoids will result in a large number of parasitoids and good control can be maintained.

Additionally, the prolonged development time on the partially resistant cultivar has consequences on the age distribution of the aphid population. The proportion of immatures will increase and more aphids will be parasitized as immatures. From a practical point of view this is advantageous since aphids, that are parasitized before the fourth instar will not reproduce any more. The higher proportion of immatures in the aphid population will also increase total parasitization rates because aphidiine parasitoids seem to show a slight preference for immature aphids over adults (Mackauer, 1973; Shirota *et al*, 1983; Liu Shu-Sheng *et al*, 1984).

The present research has shown that differences in suitability of cucumber cultivars for *A. gossypii* exist. These differences can help to make biological control of cotton aphid more effective. However, during selection for new cucumber cultivars not much attention is paid to suitability of the cultivar for cotton aphid. Since cotton aphid is still one of the biggest problems in European cucumber glasshouses and control does not always succeed, it might be advisable to look more deeply into the use of cucumber cultivars partially resistant to cotton aphid.

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Chapter 3

Evaluation of parasitoids

3 Evaluation of parasitoids

3.1 Evaluation of four aphidiine parasitoids for biological control of *Aphis gossypii* Glover (Homoptera: Aphididae)[1]

Abstract

Four aphidiine parasitoid species (Hymenoptera: Braconidae) were evaluated with respect to their potential to control *Aphis gossypii* Glover (Homoptera: Aphididae) in glasshouse cucumbers. In a laboratory experiment thirty cotton aphids were offered to individual females for two hours. *Aphidius matricariae* Haliday parasitized less than six percent of the aphids and was ruled out as potential biological control agent. *Ephedrus cerasicola* Starý and *Lysiphlebus testaceipes* Cresson parasitized 23 and 26 percent of the aphids, respectively. *Aphidius colemani* Viereck parasitized 72 to 80 percent of the aphids.

With the latter three species, experiments were performed in small glasshouses with cucumbers (*Cucumis sativus* L. cv. 'Aramon'). As in the laboratory test *A. colemani* performed best; significantly more colonies were found and the parasitization rates in the colonies were higher by *A. colemani* than by *E. cerasicola* and *L. testaceipes*.

Because of the good correspondence between laboratory and glasshouse experiments, it is suggested that bad performance of an aphid parasitoid species in a simple laboratory trial might be sufficient evidence to disregard this species for further tests.

Introduction

Several aphid species can be important pests in glasshouse crops including sweet pepper and cucumber. In the Netherlands, currently most problems occur with the cotton aphid (*Aphis gossypii* Glover (Homoptera: Aphididae)) in cucumber crops (van Schelt *et al*, 1990).

On a large area of Dutch glasshouses biological control of aphids is successful. The natural enemies used are the parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae) and the gall midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) (van Schelt, 1993). Most aphid species in glasshouses can, when needed, be controlled with selective aphicides. The cotton aphid, however, is highly resistant to selective insecticides (Furk & Hines, 1993) and use of broad spectrum pesticides inhibits the use of biological control methods against other pests. Therefore, biological control of cotton aphid in cucumber has to be developed and new natural enemies and introduction methods are under study. This paper will concentrate on the evaluation of four aphidiine parasitoid species.

On the basis of a literature study (van Steenis, 1992) several natural enemies were selected for study: *A. colemani* (two cultures), *Ephedrus cerasicola* Starý and *Lysiphlebus testaceipes* Cresson. In the first experiment the suitability of *A. gossypii* as host for these parasitoids was tested in the laboratory. *Aphidius matricariae* Haliday was added to the three species selected, although it is known that cotton aphid is not a good host for this species (Schlinger & Mackauer, 1963). Adding *A. matricariae* makes it possible to find out whether this test can show differences in host suitability at all.

One of the criteria for pre-introduction evaluation, as given by van Lenteren & Woets (1988),

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is the searching capacity of natural enemies. Searching capacity can be divided into efficiency in locating hosts within an aphid colony and efficiency in locating aphid colonies.

The efficiency in locating hosts within an aphid colony can be defined strictly by the instantaneous searching efficiency (a'), which has the dimension of number of hosts attacked per unit of searching time and unit of area (Hassell, 1982). It is related to the functional response and therefore its calculation and exact value depends on which type of functional response is used to describe the parasitoid-host interaction (Hassell, 1982). Functional responses and the corresponding searching efficiencies have been established in this way for many insects, including some aphid parasitoids (e.g., Dransfield, 1979; Mackauer, 1983; Kumar *et al*, 1988; Hughes *et al*, 1992).

Instantaneous searching efficiency only describes the number of hosts attacked within an aphid colony of a stated size and during a stated searching time. During evaluation of natural enemies not only searching efficiency within an aphid colony but also locating the colony itself should be incorporated in the searching capacity. Many papers have been written on the mechanisms by which Aphidiinae locate their hosts (e.g. Schuster & Starks, 1974; Bouchard & Cloutier, 1985). These results are, however, difficult to extrapolate to glasshouse conditions. Therefore, a glasshouse experiment was done with the most successful species to determine their searching capacity. Searching capacity was expressed as the rate at which aphid colonies at different distances were discovered and as parasitization rates in colonies found.

It is difficult to define searching capacity as a parameter that is valid for different species and under different circumstances. In this situation, however, we are dealing with closely related parasitoids, with similar searching behaviour and biology. Results for each species can therefore be compared relative to each other. Environmental circumstances do not differ when performing the experiments with different species simultaneously. The number of natural enemies searching, host species, host density and host plant species can easily be held constant in the experiments.

Materials and methods

Parasitoid cultures

The parasitoids tested were reared in small glasshouse compartments on different hosts and host plants as shown in Table 1. Except for *E. cerasicola*, all cultures were maintained on the same host plant and host aphid species as those from which the parasitoids were collected. Cultures have been maintained at the Glasshouse Crops Research Station under natural light and a minimum temperature of 20 °C since January 1991. *Aphidius colemani* cultures (one on *A. gossypii* and one on *M. persicae*) and *A. matricariae* were obtained from Koppert BV (the Netherlands), *E. cerasicola* was obtained from E.B. Hågvar (Norway) and *L. testaceipes* was obtained from Biocontrol Industries (Israel).

Experiment 1 - Host suitability

One female was released into a petri dish with a cucumber leaf disk (ϕ 5.7 cm) and 30 second instar cotton aphids. For each parasitoid species ten replicates were obtained. After the parasitoid had parasitized the first aphid, she was left in the petri dish for two hours. The aphids were followed in their development until the formation of mummies. Leaf disks were lying on a layer of agar and were replaced with fresh ones every three to four days. Once no mummies appeared anymore, parasitization rates were calculated.

Five to ten percent of the aphids died before mummification could have occurred and were not used in the analysis. Data were analyzed with binomial regression analysis (BRA) with Genstat 5 (Payne *et al*, 1987).

Experiment 2 - Searching capacity

The experiments on searching capacity were performed in 1992 and 1993 in six glasshouses of 17 m^2 with 26 cucumber plants (cv. 'Aramon') each. Experiments were started after the plants had reached a height of about three metres. *Aphidius matricariae* was not used in this experiment because of insufficient parasitism in the laboratory experiment. For *A. colemani* only the cotton aphid culture was used.

One day before the release of the parasitoids, two leaves each of three plants were infested with 20 adult *A. gossypii* in each glasshouse. The infested leaves were at a height of about 1.5 m. The infested plants were situated at different distances (0.5, 2.9 and 5.4 m) from the point where the parasitoids were to be released. Twenty-four hours later (day 0) the adult cotton aphids were removed from the leaves, leaving six colonies of 92 young cotton aphids on average (min.: 81, max.: 131) in each glasshouse. After the adult aphids were removed, ten mated female parasitoids were released in the corner of the glasshouse.

One, two, three and six days later from each leaf one quarter of the aphids was removed randomly. In the laboratory the removed aphids were put onto a cucumber leaf disk lying in a petri dish with agar (ϕ 5.7 cm). Leaf disks were replaced with fresh ones every three to five days. Development of the aphids was followed until formation of the mummy. Once no mummies appeared anymore, the parasitization rates were calculated. Five to ten percent of the aphids died before mummification could have occurred and were not used in the analysis. If at least one mummy developed in the sample the colony was considered to be found.

Because the glasshouses were usually left infested with a small amount of aphids after such an experiment, only one experiment could be performed in each glasshouse during one cropping period. In a first set of experiments in 1992 *A. colemani* was compared with *L. testaceipes* and in a second set of experiments in 1993 *A. colemani* was compared with *E. cerasicola*. In the final analysis all data will be presented together.

In total eight, five and seven replicates were obtained for *A. colemani*, *E. cerasicola* and *L. testaceipes*, respectively. The average glasshouse temperature was 21.6 °C, with a minimum of 17.8 °C and a maximum of 29.8 °C. Data were analyzed with binomial regression analysis (BRA) with Genstat 5 (Payne *et al*, 1987), at a significance level of 0.05.

Table 1
Rearing conditions and collection data of the aphid parasitoids. All cultures were started in 1991.

Parasitoid species	Rearing at the Glasshouse Crops Research Station	Collection data	
	Host aphid and host plant	Host aphid and host plant	Origin
Aphidius colemani-A	*A. gossypii*, cucumber	*A. gossypii*, cucumber	glasshouse, Netherlands
Aphidius colemani-M	*M. persicae*, sweet pepper	*M. persicae*, sweet pepper	glasshouse, Netherlands
Aphidius matricariae	*M. persicae*, sweet pepper	*M. persicae*, sweet pepper	glasshouse, Netherlands
Ephedrus cerasicola	*M. persicae*, sweet pepper	*M. persicae*, swedes	rearing, Norway
Lysiphlebus testaceipes	*A. gossypii*, cucumber	*A. gossypii*, cucumber	glasshouse, Israel

Results

Experiment 1 - Host suitability

Aphidius colemani parasitized more aphids than the other species ($P<0.05$; BRA) (Figure 1). There was no significant difference between the two cultures of *A. colemani* (BRA).

Although *A. matricariae* parasitized *A. gossypii* successfully, the parasitization rate of 6% was significantly lower than for all other species ($P<0.05$; BRA). *Ephedrus cerasicola* and *L. testaceipes* did parasitize *A. gossypii* successfully (about 20% of the aphids were parasitized) although the number of mummies found was significantly lower than for *A. colemani* ($P<0.05$; BRA).

Experiment 2 - Searching capacity

Aphidius colemani discovered significantly more colonies than the other two species and *E. cerasicola* found more colonies than *L. testaceipes* ($P<0.05$; BRA) (Figure 2).

The distance from the release point significantly influenced the percentage of colonies found by *A. colemani* ($P<0.05$; BRA). The colonies at 0.5 m were found more often than the colonies at 2.9 and 5.4 m (Figure 3). Parasitoids discovered most aphid colonies on the first day after release, with no significant increase in the number of discovered colonies on subsequent days (BRA) (Figure 3), apparently due to the high rates of finding on day 1 and 2. On the third day all colonies at 0.5 m were found. For the colonies at 2.9 and 5.4 m it took at least six days before the maximal percentage of colonies was found. At these distances not all colonies were discovered (75 and 62.5% at 2.9 and 5.4 m, respectively).

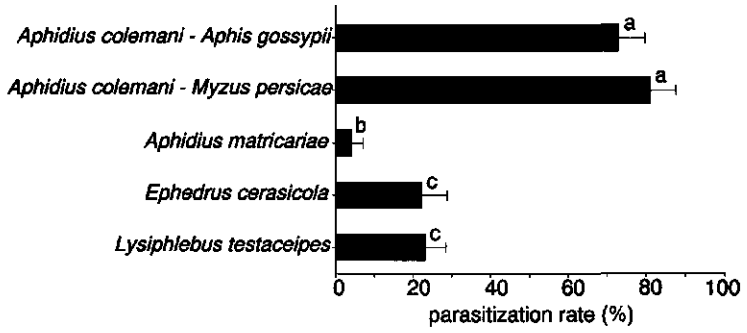

Figure 1
Parasitization rates of *Aphis gossypii* by several parasitoid species. Thirty aphids were offered in a small petri dish for two hours. Standard errors are given by bars, significant differences by different letters ($P<0.05$; binomial regression analysis).

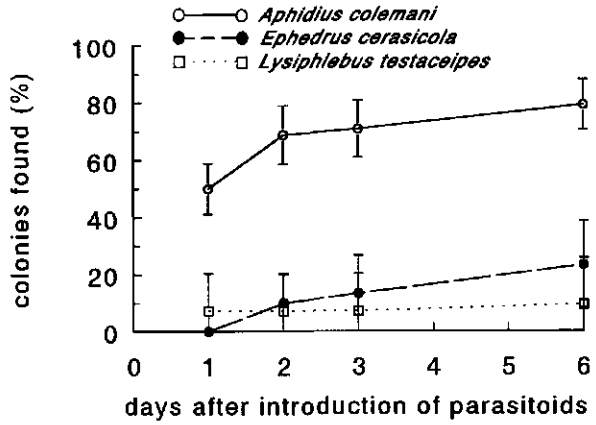

Figure 2
Percentage of colonies of *Aphis gossypii* found by several parasitoid species in small glasshouses. Ten parasitoids were released at day 0. Standard errors are given by bars. Differences in parasitization rates between species were significant ($P<0.05$; binomial regression analysis). No significant differences between the percentage of colonies found on successive days were present (binomial regression analysis).

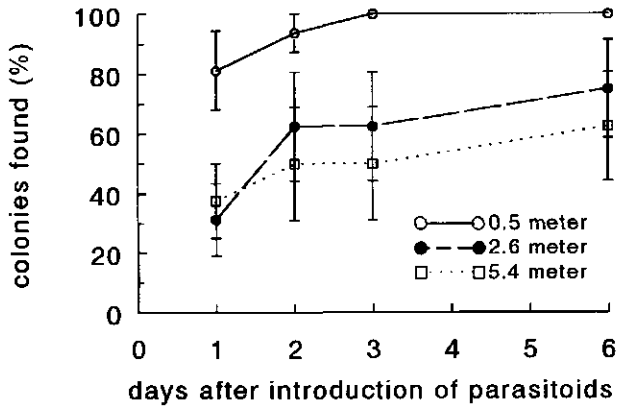

Figure 3
Influence of distance and time after release on the percentage of *Aphis gossypii*-colonies of found by *Aphidius colemani*. Ten parasitoids were released at day 0. Standard errors are given by the vertical bars. Colonies at 0.5 m were found significantly more often than colonies at 2.9 or 5.4 m ($P<0.05$; binomial regression analysis). No significant differences between the percentage of colonies found on successive days could be detected (binomial regression analysis).

Once a colony was discovered parasitization rates were constant and no influence of distance or time could be detected for any species (BRA). Again highly significant differences between species were present ($P<0.05$; BRA). *Aphidius colemani* parasitized 85% of the aphids in a colony once it was found. *Ephedrus cerasicola* and *L. testaceipes* parasitized only about 20 and 45%, respectively (Figure 4). The parasitization rate by *L. testaceipes* was significantly higher in the glasshouse than in the laboratory ($P<0.05$; BRA).

Discussion

Although *A. gossypii* can be parasitized successfully by all four parasitoid species (*A. colemani*: Starý (1975), Tardieux & Rabasse (1986); *A. matricariae*: Starý (1966, 1976, 1979); *E. cerasicola*: E.B. Hågvar (pers. comm.); *L. testaceipes*: Schlinger & Hall (1960), Carver (1984)), large differences in parasitization rates were found. With this experimental set-up it is not directly clear whether these differences are caused by differences in host acceptance sensu Vinson (1976) (i.e., motivation of the female parasitoid to deposit an egg), or host suitability in the strict sense (i.e., survival of the egg to adulthood (here: survival until formation of the mummy)). However, for *A. colemani* and *L. testaceipes* pre-adult mortalities are not very different (14.1 and 9.5% at 20 °C for *A. colemani* and *L. testaceipes*, respectively) (van Steenis, 1993, 1994). Thus, host acceptance seems to play an important role in determining

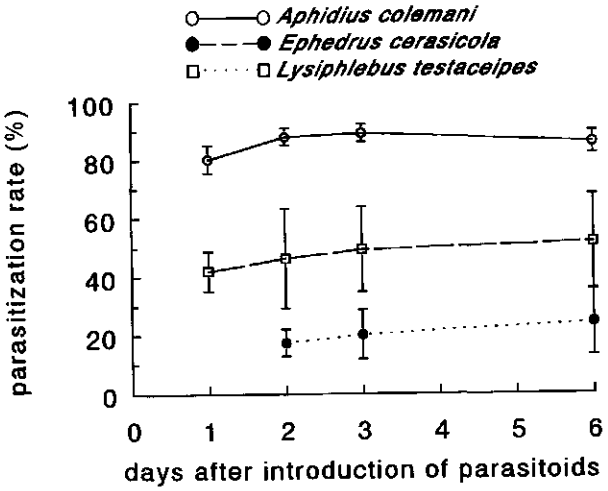

Figure 4
Parasitization rates of colonies of *Aphis gossypii* found by one or more parasitoid(s) in small cucumber glasshouses. Ten parasitoids were released at day 0. Standard errors are given by the vertical bars. Among the species differences in parasitization rates were significant ($P<0.05$; binomial regression analysis). No significant differences in parasitization rates on successive days were present (binomial regression analysis).

parasitization rates.

The laboratory experiment showed that *A. matricariae* is not useful for control of cotton aphid, which is confirmed by records from Schlinger & Mackauer (1963). They rarely found *A. matricariae* on *A. gossypii* in the field. *Ephedrus cerasicola* and *L. testaceipes* did parasitize cotton aphid in the laboratory and glasshouse experiments, but the parasitization rates are probably too low to give adequate control. Also, these parasitoid species found significantly fewer colonies than *A. colemani*. *Aphidius colemani* therefore seems to be the best parasitoid to use for control of cotton aphid.

It is striking that already at a distance of 2.9 m fewer colonies were found by *A. colemani*, than were found within 0.5 m of the release point. Possibly part of the parasitoids was arrested on the first colony that they encountered, which is likely to be the closest colony. A strong arrestment response caused by the presence of honeydew and gathering of parasitoids on infested plants has been shown for several aphid parasitoids (e.g., Hågvar & Hofsvang, 1987; Budenberg, 1990). Because of the small size of the glasshouses it is difficult to draw conclusions on the number of introduction sites necessary in a commercial glasshouse. However, it seems advisable to introduce at least part of the parasitoids as close to aphid colonies as possible.

Suitability of an aphid species as host can differ for different strains of the same parasitoid species (e.g., Powell & Wright, 1988). In the present study no differences were found between two cultures of *A. colemani*, although the parasitoids have been reared on different aphid species for at least 1.5 years.

The large reproductive capacity of aphidiine parasitoids and the short life span of females, make it likely that parasitoid searching behaviour will be based on time limitation rather than on egg limitation (Mackauer *et al*, 1992). In the beginning of the cropping period and when aphid control is successful, the environment will be relatively stable with low aphid densities. In these environments searching capacity is the most important criterion for maintaining successful control (Huffaker *et al*, 1977). For these reasons searching capacity which is realized under circumstances in which the parasitoids will be used is a very important feature of a successful natural enemy and research on searching capacity should therefore be included in evaluation of natural enemies. The present experiments show the importance of searching capacity under glasshouse conditions, where, once an aphid colony was found, parasitization rates were high but did not increase in time.

The sequence in parasitization rates in colonies found by the three species in the glasshouse corresponded very well with the sequence of parasitization rates found in the laboratory setup. The only difference was the parasitization rate in colonies found by *L. testaceipes* in glasshouses, which was higher than in the laboratory (45 and 26%, respectively). Maybe the fact that more than one parasitoid might have visited the glasshouse colonies can account for this. The strong correspondence between the glasshouse and the laboratory experiments implies that species with low parasitization rates in small scale laboratory experiments can be disregarded for further tests. For species giving high parasitization rates in the laboratory, experiments on searching capacity should be performed to identify the most promising natural enemy species.

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3.2 Evaluation of *Aphelinus varipes* Förster (Hymenoptera: Aphelinidae), as a biological control agent for the cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae)[1]

Abstract

The aphelinid parasitoid *Aphelinus varipes* Förster (Hymenoptera: Aphelinidae) was evaluated with respect to its use for biological control of *Aphis gossypii* Glover (Homoptera: Aphididae). First and second instar cotton aphids were most suitable for parasitization. Ovipositions, with a duration of 50 to 70 seconds, resulted in a parasitization rate of 90%. A maximum of approximately 60 aphids was parasitized by one female per day. Additionally five to ten aphids were killed for host feeding daily.

Glasshouse observations showed that introductions of *A. varipes* alone will not be sufficient to control cotton aphid. Best aphid control was obtained in the glasshouses where *Aphidius colemani* Viereck (Hymenoptera: Braconidae) and *A. varipes* were introduced simultaneously. In these glasshouses part of the aphids were killed immediately by host feeding by *A. varipes*. The remaining aphids were parasitized and the aphid population was kept on a very low level throughout the experiment. In glasshouses were only *A. colemani* was introduced the aphid levels during the first weeks were slightly higher than in the glasshouses with both parasitoid species, maybe because the direct effect of host feeding was lacking. Through the strong reproductive numerical response of *A. colemani* total control of the aphids was obtained in the '*A. colemani*'-glasshouses in several weeks.

Mummies collected from the glasshouses showed that hyperparasitism of *A. colemani*-mummies occurred frequently, whereas hyperparasitism of *A. varipes*-mummies was not detected.

Introduction of aphids after several weeks of low aphid (and thus low parasitoid) density showed that both parasitoid species survived this period. In glasshouses where *A. varipes* was introduced together with *A. colemani*, parasitization rates were much higher than in the glasshouses where only *A. colemani* was introduced. It is concluded that because of the ability to survive periods of low aphid density and the low rate of hyperparasitism, *A. varipes* can be very useful in combination with *A. colemani*.

Introduction

In glasshouse cucumber crops the cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), is controlled with natural enemies on a large scale (van Schelt, 1993). Evaluation of four aphidiine parasitoids revealed that *Aphidius colemani* Viereck (Hymenoptera: Braconidae) was the best species for control of *A. gossypii* (van Steenis, 1995a). Still, aphid control is not always reliable. Especially in summer problems can arise, probably because the parasitoids are more negatively influenced by the high temperatures than *A. gossypii*. R_m-values at 20 °C do not differ much between *A. colemani* and *A. gossypii* but at 25 °C the population growth of *A. gossypii* is larger than the population growth of *A. colemani* (van Steenis, 1993; van Steenis & El-Khawass, 1995b).

In commercial glasshouses preventive introductions of *A. colemani* are used at a rate of 0.1

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parasitoids/m²/week as long as no aphids are present (van Schelt, 1993). At glasshouse temperatures the average life span of *A. colemani* is however only four to five days (van Steenis, 1993). As a consequence the parasitoid density will decrease during the week. If aphids enter a glasshouse at a period of low parasitoid density, the aphid colonies (which can multiply about 50 times per week (van Steenis & El-Khawass, 1995b)) can grow to such a level that rapid control can not be obtained anymore.

Aphidius colemani is an efficient searcher and has a large numerical increase (van Steenis, 1993; van Steenis & El-Khawass, 1995a). Efficiently searching natural enemies are able to eliminate local pest populations but will survive on a larger scale because of the presence of hosts in other places (Murdoch *et al*, 1985). As a consequence highly fluctuating parasitoid and host population can be found on a small scale, whereas on a larger scale a more or less stable interaction will be present. The wave-like interaction between aphids and natural enemies during biological control of aphids indicates that the size of glasshouses is too small to result in a stable and low equilibrium aphid population (Ramakers & Rabasse, 1995). After successful suppression of the pest, aphid levels are very low and not many parasitoids and predators will survive, making it possible for newly entered aphids to increase rapidly (Ramakers & Rabasse, 1995). During the absence of the natural enemies the aphids are able to multiply to such levels that the next generation of natural enemies is too late to establish efficient control.

In summary we can say that even though *A. colemani* is an efficient control agent, control is not always satisfactory because of too high peak abundances of *A. gossypii*. The use of another natural enemy or a combination of natural enemies could result in a different interaction between the aphid and the natural enemies, and possibly in improved biological control (Messenger *et al*, 1976). In some cases the joint operation of two or more natural enemies was even essential for obtaining sufficient control (Murdoch *et al*, 1985). During a multiple introduction the introduced species will compete with one another, both intrinsically (direct competition inside the host) and extrinsically (indirect competition for the same resource). Depending on the outcome of the competition releases of two parasitoid species might result in better, equal or worse control (Huffaker *et al*, 1976).

One of the candidates to be used in addition to *A. colemani* is the parasitoid *Aphelinus varipes* Förster (Hymenoptera: Aphelinidae), which was collected in cotton fields in Cameroon. Species of this genus have a longer life span than aphidiine parasitoids (Force & Messenger, 1965) and might therefore be present in higher densities than *A. colemani* during periods when few aphids are present. Additionally, aphelinids are less susceptible than aphidiine parasitoids to high temperatures (Force & Messenger, 1964a; Bernal & González, 1993), which might of importance during the summer months. Using an aphelinid parasitoid might, therefore, result in higher rates of parasitism during periods when *A. colemani* is not able to give reliable control.

The effect of interference between two parasitoid species foraging for the same host is difficult to predict. Nevertheless several observations might be of value. First of all, it was shown that aphelinid and aphidiine parasitoids discriminate between unparasitized aphids and aphids parasitized by either species (Bai & Mackauer, 1991). Further, the suitability of young aphid stages for *Aphelinus*-species is much higher than the suitability of older aphid stages (Kuo-Sell & Kreisfeld, 1987; Starý, 1988a; Gerling *et al*, 1990; van Steenis, 1995b), whereas the suitability of different aphid stages for aphidiine parasitoids is less pronounced (Rabasse & Wyatt, 1985; Starý, 1988b). Interference will occur but due to the discrimination and differences in suitability of aphid stages, it does not seem likely that one species will totally

replace the other during one growing season.

This paper will concentrate on a comparison between *A. colemani* and *A. varipes*. Laboratory evaluation of natural enemies can be performed with species with similar biology (van Steenis, 1995a). However, aphidiine and aphelinid parasitoids have a very different reproduction strategy. Aphidiine parasitoids have a high daily reproduction over a short reproduction period (Starý, 1988b), whereas aphelinid parasitoids have a lower daily reproduction over a longer period (Bai & Mackauer, 1990b). Because of these differences in parasitization strategy, differences in parasitization rates in the laboratory will be difficult to interpret. Further, field releases of aphelinid parasitoids (*Aphelinus abdominalis* and *A. varipes*) against cereal aphids failed completely, despite high parasitization rates in the laboratory (Höller & Haardt, 1993; Hughes *et al*, 1994). Therefore, the best test available would be a glasshouse test in which the parasitoids are compared.

Nevertheless, it is important to test the suitability of *A. gossypii* as host for *A. varipes* before glasshouse releases are made. Large differences in preference for and suitability of certain aphid species do exist among *Aphelinus*-species (Wilbert, 1964; Manglitz & Schalk, 1970; Jackson & Eikenbary, 1971; Raney *et al*, 1971; Carver & Woolcock, 1985; Kuo-Sell & Kreisfeld, 1987; Lajeunesse & Johnson, 1992). These preferences and suitabilities can change within several generations after there has been a transfer of hosts (Michel, 1971, 1973; Hughes *et al*, 1994). Also among different lines of one species the suitability of a certain host may differ (Haardt & Höller, 1992). The suitability of and preference for different aphid instars and adult aphids and the total daily fecundity and host feedings was determined as a measure of overall host suitability. Thereafter glasshouse experiments were done.

Material and Methods

Insect cultures

Aphis gossypii were collected from cucumber glasshouses in the Netherlands in 1990. At the Glasshouse Crops Research Station the aphids were cultured on cucumber (cvs. 'Sporu' and 'Aramon') under natural light and a minimum temperature of 18 °C.

Aphelinus varipes-mummies were collected from *A. gossypii* in cotton fields in Maroua, Cameroon. From October 1992 onwards the parasitoids were reared at the Glasshouse Crops Research Station in small glasshouse compartments under natural light and at a minimum temperature of 18 °C. *Aphis gossypii* was used as the host and cucumber (cvs. 'Sporu' and 'Aramon') as the host plant.

Experiment 1 - Oviposition behaviour

Cucumber leaf disks (Ø 5.7 cm) lying on a layer of agar were used as experimental arena. Ten aphids of the same stage were put on the leaf disk. After 45 minutes these aphids had settled and one *A. varipes*-female was introduced into the petri dish. The parasitoids had no oviposition experience and had an age of 24 to 48 hours. The female was observed continuously and the duration of each contact, oviposition and host feeding was recorded. After an aphid was stung and the parasitoid moved away from it, the aphid was removed and kept separately on a cucumber leaf disk in a petri dish with agar. The observation continued until all aphids were stung, until the parasitoid left the leaf or until it had not moved for ten minutes. This procedure was repeated with six parasitoids for each aphid stage: four immature stages and the wingless adults.

The parasitized aphids were kept on the cucumber leaf disks at a constant temperature of 25 °C, a constant relative humidity of 65% and a photoperiod of 16L:8D. The aphids were dissected after four days to check for the presence of parasitoid larvae.

Parasitization rates and host instar preferences were compared with binomial regression analysis (BRA) in Genstat 5 (Payne *et al*, 1987) at a significance level of 0.05. After a logarithmical transformation to stabilize variances (Murdie, 1972) the duration of the parasitization process was compared with Analysis of variance (ANOVA) at a significance level of 0.05. If a significant difference was detected multiple comparisons were made using an LSD-procedure ($\alpha = 0.05$).

Experiment 2 - Daily reproduction and host feeding

Since experiment 1 showed that second instar cotton aphids were the most suitable for parasitization, the maximum daily reproduction and host feeding at several aphid densities was determined by offering individual female parasitoids second instar aphids. Aphids were offered in a petri dish with a cucumber leaf disk (Ø 5.7 cm) for 24 hours to unexperienced mated females at a density of 1, 2, 4, 6, 8, 10, 20, 30, 40, 50, 60 and 80 aphids. The parasitoids had an age of 24 to 48 hours. The leaf disk with the aphids and one parasitoid was kept at a constant temperature of 25 °C, a constant relative humidity of 65% and a photoperiod of 16L:8D. At each density five observations were made. After 24 hours the parasitoid was removed and the number of host feedings was counted. The remaining aphids were kept at a constant temperature of 25 °C, a constant relative humidity of 65% and a photoperiod of 16L:8D. After three to five days the aphids were dissected under a stereo microscope and the number of parasitized aphids was determined.

In a control experiment mortality of aphids which were not exposed to parasitoids was less than one percent and was therefore neglected in the analysis.

An exponential equation of the form $y = a - b * r^X$ was used to describe the daily number of aphids killed for host feeding or parasitization. The equation was fitted to the data with linear regression in Genstat 5 (Payne *et al*, 1987).

Experiment 3 - Glasshouse evaluation

The glasshouse experiments were performed in six glasshouse compartments of 17 m² with 26 cucumber plants (cv. 'Flamingo'). The cucumber plants were planted on 6 September 1994. On 27 September 1994 in each glasshouse three aphid colonies were established by placing five wingless aphids on one leaf (approximately 1.5 m above the ground). The colonies were sited at 0, 2.6 and 5.4 m from the releasing point of the parasitoids. One day later the weekly

Table 1
Rates of introduction of parasitoids in experiment 3.

glasshouse	*Aphidius colemani* per week (50% ♀)	*Aphelinus varipes* per week (50% ♀)
1+2	10	
3+4	10	20
5+6		20

introductions of parasitoids started according to the scheme in Table 1. On average the colonies had a size of 49 aphids (min.: 32; max: 68). After five weeks no parasitoids were introduced anymore because large numbers of parasitoids were present in the glasshouses.

On each colony the number of winged, wingless and immature aphids was recorded biweekly together with the number of mummies (*A. colemani* and *A. varipes*), the number of emerged mummies (*A. colemani* and *A. varipes*) and the number of aphids killed by host feeding. Killed aphids and emerged mummies were removed.

Six weeks after the introduction of the aphids, mummies of both parasitoid species were collected from the glasshouse to determine the rate of hyperparasitism. At the end of the experiment (after no parasitoids had been released for three weeks) three new aphid colonies were established in each glasshouse. After five days the colonies were taken into the laboratory after which four days later the aphids were dissected to determine parasitization rates by either parasitoid species.

Aphid densities in glasshouses were compared with Analysis of variance (ANOVA) at a significance level of 0.05. If a significant difference was found multiple comparisons were made using an LSD-procedure ($\alpha = 0.05$). Before analysis the data were transformed to square root values (Murdie, 1972). Parasitization rates and the rate of host feeding in glasshouses were compared with binomial regression analysis (BRA) in Genstat 5 (Payne *et al*, 1987).

Results

Experiment 1 - Oviposition behaviour

The average time the parasitoid spent investigating the aphid before parasitization was 15.7 seconds and did not differ among aphid stages ($P = 0.14$; ANOVA). The average duration of a sting which resulted in successful parasitism was 71.0 seconds and did not differ among aphid stages ($P = 0.42$; Anova). *Aphelinus varipes* parasitized second instar aphids most frequently ($P < 0.05$; BRA) and parasitized adult aphids significantly less often than all immature stages ($P < 0.05$; BRA) (Figure 1). Eighty percent of the second instar aphids encountered, were accepted for oviposition. Adult aphids were attacked on 20% of the encounters (Figure 1). Seventy percent of the attacks in first and second instar aphids resulted in successful parasitism, for the other stages approximately 45% of the attacks resulted in a larva (Figure 1). Successful parasitism was significantly higher in first instar aphids than in third instar aphids and adults ($P < 0.05$; BRA) (Figure 1).

Most parasitizations in second instar aphids took between 20 and 80 seconds (Figure 2). When the ovipositor was inserted for less than 20 seconds no larva was found at dissection. Between 40 and 120 seconds 70 to 90% of the attacks was successful (Figure 2). Fourteen attacks resulted in host feeding and were not used in the analysis. Before host feeding the ovipositor was inserted several times with an average duration of 395 seconds (s.e. = 26.04).

Experiment 2 - Daily reproduction and host feeding

The number of host feedings was fairly constant at the different aphid densities and could be described by the exponential equation $y = 10.9\text{-}9.3*0.9864^X$ ($r^2 = 86.9$; $F = 37.47$; $P < 0.001$) (Figure 3a). At a density above six aphids per leaf disk four to eight aphids were killed for host feeding daily. The regression equation predicts a maximum of 10.9 aphids killed for host feeding daily. At a density of ten aphids or less all aphids were killed for host feeding and no parasitization occurred (Figure 3b). The daily number of aphids parasitized by one *A. varipes*

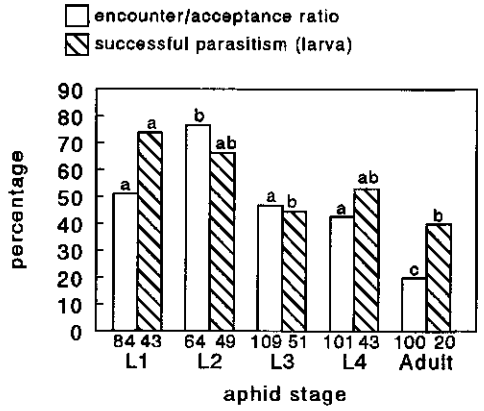

Figure 1
The results of attacks of different aphid instars and adults by female *Aphelinus varipes*. Different letters between the bars indicate a significant difference between aphid stages ($P < 0.05$; binomial regression analysis). Below each bar the number of observations is given.

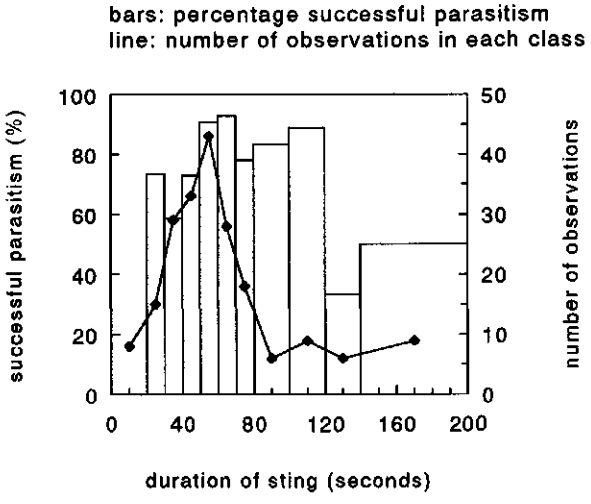

Figure 2
Relation between the duration of the attack by *Aphelinus varipes* and the parasitization success.

female could be described by the equation $y = 82.7 - 84.3 * 0.9892^X$ ($r^2 = 98.0$; $F = 267.0$; $P < 0.001$) (Figure 3a). The maximum number of parasitizations (approximately 45 aphids/day) was reached when more than 60 aphids were present on the leaf disk (Figure 3a). According to the regression equation a maximum of 82.7 aphids can be parasitized daily.

Experiment 3 - Glasshouse evaluation

One week after introduction of the parasitoids the first differences among the treatments started to become clear. In the glasshouses where both parasitoid species were introduced the number of aphids declined most fast (Figure 4). From day 15 to day 26 the number of aphids in

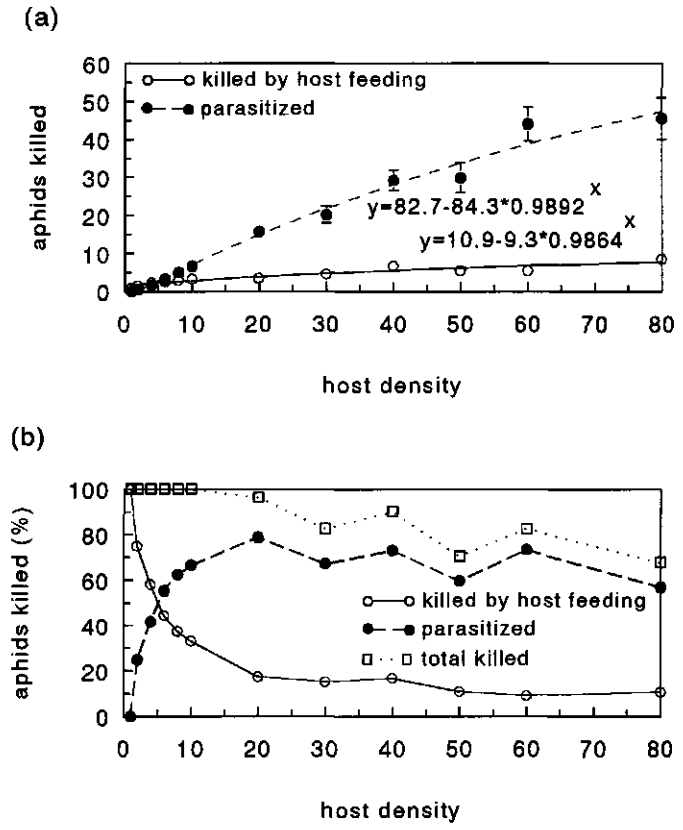

Figure 3
Daily parasitization and host feeding by *Aphelinus varipes* females at different aphid densities. (a) absolute number of aphids killed; (b) proportion of the offered aphids that was killed.

these glasshouses was significantly lower than in the glasshouses where only one parasitoid species was introduced ($P<0.05$; LSD after ANOVA). From day 26 onwards no significant difference was present between the glasshouses where both parasitoids species were introduced and the glasshouses where only *A. colemani* was introduced (LSD after ANOVA). The host feeding during the first weeks reduced the number of aphids considerably and mummies of both parasitoid species could be found one week after the first introduction of parasitoids (Figure 5b). The parasitization rate by *A. colemani* was significantly lower in the glasshouses where both parasitoid species were released than in the glasshouses where only *A. colemani* was introduced ($P<0.05$; BRA). The parasitization rate by *A. varipes* did not differ between the glasshouses where both species were introduced and the glasshouses where only *A. varipes* was introduced ($P<0.05$; BRA) (Figure 5). The total parasitization rate reached approximately 100% after 40 days (Figure 5b).

After 23 days a sudden rise of the number of aphids could be observed in the glasshouses where only *A. varipes* was introduced (Figure 4). From day 29 onwards the number of aphids in these glasshouses was significantly higher than in the other glasshouses ($P<0.05$; LSD after ANOVA). After 38 days no observations were made in these glasshouses anymore. The plants were in a bad condition and many of them died because of the high aphid densities. In glasshouses where only *A. varipes* was introduced the first mummies appeared after eight days (Figure 5c). Additionally a considerable part of the aphids was killed by host feeding during the first week after introduction of the parasitoids. The parasitization rates stayed below 40%.

With releases of *A. colemani* the first parasitized aphids appeared after 11 days (Figure 5a). Thereafter a rise of parasitization rates could be seen until all aphids were parasitized (Figure

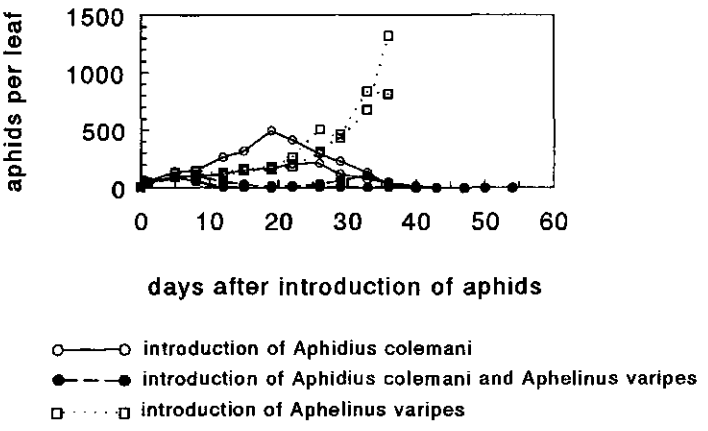

Figure 4
Development of aphid populations after introduction of parasitoids. Aphids were introduced on day 1. From day 2 onwards parasitoids were released weekly during five weeks. From day 16 to 25 the aphid population in the glasshouses where both *Aphelinus varipes* and *Aphidius colemani* were released was significantly lower than in the other glasshouses ($P<0.001$; ANOVA).

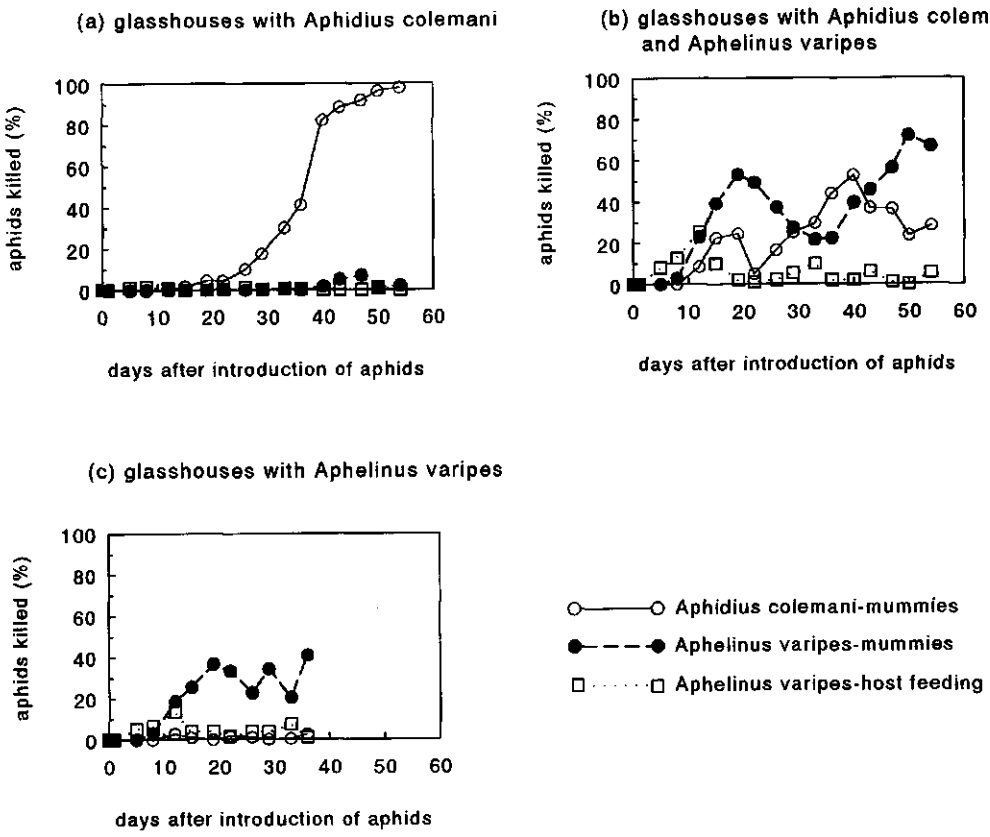

Figure 5
Percentage of aphids killed by parasitism (mummies of *Aphidius colemani* or *Aphelinus varipes*) and by host feeding. Parasitization by *A. colemani* was significantly lower in the glasshouses where also *Aphelinus varipes* was introduced ($P<0.05$; binomial regression analysis). Parasitization rates by *A. varipes* did not differ significantly between the glasshouses (binomial regression analysis).

5a). A few aphelinid mummies were also observed in these glasshouses.

Hyperparasitoids were observed during the entire experiment but did not seem to interfere with aphid control. Mummies collected from the glasshouses showed that *A. colemani* was parasitized by *Dendrocerus aphidum*, *Alloxysta sp.* and *Asaphes sp.*. Mummies of *A. varipes* did not show any sign of hyperparasitism, although approximately 30% of the parasitoids had died during the mummy stage. Very few *A. colemani* died inside the mummy.

The second aphid introduction showed that both parasitoid species were still present in the glasshouses. In the glasshouses where both parasitoids were released 10 to 50% of the aphids were killed for host feeding within five days (Table 2). In these glasshouses more aphids died than in the glasshouses where only *A. colemani* was introduced ($P<0.05$; BRA). Although more aphids seemed to be parasitized by *A. colemani* in the glasshouses where both parasitoid species were introduced, no significant difference could be detected (BRA). The parasitization rate by *A. varipes* and the total parasitization rate was significantly larger in the glasshouses where both parasitoid species were introduced ($P<0.05$; BRA).

Discussion

Experiment 1 - Oviposition behaviour

All aphid instars and adults are accepted and suitable for the development of *A. varipes* but the first and second instar aphids are more easily parasitized. This is in contrast with a general trend that parasitoids feed on earlier host stages and oviposit in older stages. With this strategy handling time through host feeding and wastage of progeny through other mortality factors than

Table 2
Parasitization rates in cotton aphid colonies after the second aphid introduction. Aphid colonies were established after successful control was obtained and no parasitoids had been introduced for three weeks. In the glasshouses where *Aphidius colemani* and *Aphelinus varipes* were released, significantly more aphids were killed for host feeding and significantly more aphids were parasitized by *A. varipes* ($P<0.05$; BRA) than in glasshouses where only *A. colemani* was released. Parasitization by *A. colemani* did not differ between the glasshouses (BRA). The total parasitization rate was significantly higher in the glasshouses where both parasitoid species were introduced ($P<0.05$; BRA).

released parasitoid species	colony size	aphids killed for host feeding (%)	aphids parasitized by *A. colemani* (%)	aphids parasitized by *A. varipes* (%)	aphids parasitized by either parasitoid species (%)
Aphidius colemani	23	0.0	0.0	0.0	0.0
	19	0.0	0.0	0.0	0.0
	34	0.0	79.4	0.0	79.4
	18	5.6	0.0	0.0	0.0
	14	0.0	57.1	14.3	71.4
Aphidius colemani + *Aphelinus varipes*	29	10.3	100.0	0.0	100.0
	18	11.1	75.0	25.0	100.0
	16	12.5	0.0	70.0	70.0
	19	21.1	100.0	0.0	100.0
	29	48.3	73.3	26.7	100.0
	20	25.0	100.0	0.0	100.0

host feeding is reduced (Kidd & Jervis, 1991). Higher parasitization rates in young aphids were also found for other aphelinid species (Starý, 1988a). Though host age acceptance and host age suitability are in many cases correlated (Godfray, 1994), this is probably not the case with *A. varipes*. The survival of *A. asychis* from larva to adult is not influenced by the age of the parasitized aphid (Cate *et al*, 1977). Instead, the differences in parasitization rates among aphid instars are caused by the stronger defence reactions of older instars which makes successful parasitization more difficult (Wilbert, 1964; Force & Messenger, 1965; Cate *et al*, 1977; Kuo-Sell & Kreisfeld, 1987; Gerling *et al*, 1990).

For *A. colemani* only winged adult *Pentalonia nigronervosa* were attacked less frequently but among the other aphid stages no differences in preference or suitability were detected (Völkl *et al*, 1990). In some studies with aphidiine parasitoids younger instars were parasitized more frequently although this difference was less pronounced than for *A. varipes* (Fox *et al*, 1967; Mackauer, 1973; Weisser, 1994). In other studies it was shown *Aphidius sonchi* preferred larger (second and third instar) apterous nymphs (Liu Shu-Sheng *et al*, 1984).

A short insertion of the ovipositor (less than 20 seconds) never resulted in deposition of an egg. Also when the ovipositor was inserted for more than 120 seconds less larvae were found. This might be because long insertions often precede host feeding. In aphids which are used for host feeding no eggs are deposited (Wilbert, 1964; Esmaili & Wilde, 1972; Hamilton, 1973; Boyle & Barrows, 1978; Bai & Mackauer, 1990b). Also detailed behavioural observations showed that *Encarsia formosa* does not feed on parasitized hosts and that the parasitoid does not oviposit in hosts killed for host feeding (van Lenteren *et al*, 1980). The long insertions of the ovipositor are probably attempts for host feeding which somehow failed. Aphids which are used for host feeding are paralyzed and even if the aphids are removed before the actual host feeding starts these aphids will die (Cate *et al*, 1977; Bai & Mackauer, 1990b).

Oviposition with a duration between 50 and 70 seconds will results in successful parasitization in 90% of the cases. For *Aphelinus asychis*, the ovipositor has to be inserted for 60 (Wilbert, 1964; Hamilton, 1973; Boyle & Barrows, 1978) to 80 seconds (Bai & Mackauer, 1990a) for parasitization to be successful. In the present study also shorter ovipositions (between 20 and 50 seconds) were most of the times successful.

Experiment 2 - Daily reproduction and host feeding

At low host densities most of the aphids are killed for host feeding and only very few aphids are parasitized. At densities of more than 10 to 20 aphids the number of aphids killed for host feeding stayed almost constant. These observations can be contributed to the fact that starved females first feed on aphids before they start to parasitize aphids (Bai & Mackauer, 1990b). When hosts are rare a large fraction of the encountered hosts is used for host feeding. The fraction of hosts used for oviposition rose with increasing aphid density and no direct relation between the number of host feedings and parasitizations (as was suggested by Hamilton (1973)) was found. Instead a basic amount of host feeding is necessary to satisfy the basic nutritional and reproductive requirements of the female parasitoid (Bai & Mackauer, 1990b). The observations agree with the model for synovigenic species with anhydropic eggs as suggested by Jervis & Kidd (1986). These species are in general long-lived, produce large eggs that contain nutrients for embryonic development and have only few mature eggs available at one time.

Since at low aphid densities all aphids were killed for host feeding, this could cause problems

in glasshouses during periods of low aphid infestation. Very few aphids will be parasitized and the next parasitoid generation will be very small (Flanders, 1953).

Compared with other *Aphelinus*-species the maximum number of aphids killed for host feeding daily is very high. In studies with *A. asychis* only one to two aphids were killed daily (Cate *et al*, 1973, 1977; Bai & Mackauer, 1990b). Maybe this difference can be partly contributed to the fact that second instar cotton aphids are small and feeding requirements vary in relation to aphid size (Cate *et al*, 1973, 1977). Additionally, the parasitoids used in the experiments had not been in contact with aphids for on average 12 hours. Especially these starved females will first feed on aphids before they start to parasitize aphids (Bai & Mackauer, 1990b). Aphids which are killed for intended host feeding are first paralyzed and usually die, even when host feeding is interrupted (Cate *et al*, 1977; Bai & Mackauer, 1990b). Therefore, it is possible that part of the dead aphids has not been used for actual host feeding.

Also the number of aphids parasitized daily by a female *A. varipes* is much higher than was found for *A. asychis*. *Aphelinus varipes* parasitized a maximum of approximately 60 aphids daily. For *A. asychis* a maximum of 8 to 16 parasitized aphids per day was found (Cate *et al*, 1973, 1977; Kuo, 1986; Bai & Mackauer, 1990b). In these studies less aphids were offered which might partly explain the lower daily reproduction in comparison with *A. varipes* in the present study. Also *A. semiflavus* and *A. abdominalis* parasitoids have a lower maximum daily reproduction (Force & Messenger, 1964b; Mackauer, 1982; Höller & Haardt, 1993). At low densities the number of eggs deposited is likely to be higher than the number of parasitized aphids because of the occurrence of superparasitism (Bai & Mackauer, 1990b).

In the laboratory experiments it was shown that *A. gossypii* is a good host for *A. varipes* and that many aphids were killed daily, either for oviposition or for host feeding. Performance of glasshouse experiments in which introduction of *A. varipes* can be compared with introduction of *A. colemani* seemed, therefore, justified.

Experiment 3 - Glasshouse evaluation

In glasshouses where only *A. colemani* was introduced aphid control was successful. In one glasshouse control was obtained immediately. In the other glasshouse it took several weeks before control was successful because one colony was not found immediately. The number of aphids in this colony only started to decline when the first offspring of the introduced parasitoids emerged in the glasshouse.

In the glasshouses where *A. varipes* was introduced, many dead aphids were found because of host feeding. This gives a quicker reduction because parasitized aphids can still produce some offspring (van Steenis & El-Khawass, 1995b). Compared to the maximum daily host feeding in the laboratory the number of aphids killed for host feeding is very low. *Aphelinus*-species spread relatively slow through glasshouses (Wyatt, 1970) and probably not all parasitoids found the aphid colonies immediately. If a parasitoid encounters a colony, which has already been visited by another female, many parasitized aphids will be present. Discrimination of parasitized aphids will then result in a low rate of oviposition (Starý, 1988a) and probably also a low rate of host feeding.

Even though introduction of *A. varipes* gave a high mortality through host feeding, the aphids could escape the parasitization pressure after three weeks. This might be partly explained by the fact that *A. varipes* showed a preference for younger aphids. As a consequence part of the adult aphids will not be parasitized and aphid colonies can keep growing. Also the numerical

response of the parasitoids was probably insufficient to give continuous aphid control. For *A. sp. aff. flavipes* population growth was insufficient to control *A. gossypii* on cucumber (Wyatt, 1969; Lyon, 1976). Only at high initial parasitoid:host ratio's reliable control of *A. gossypii* was obtained (Wyatt, 1971). *Aphelinus abdominalis* gave successful control of *M. euphorbiae* in glasshouses (Rabasse *et al*, 1989; Haardt & Höller, 1992), but population development of this aphid is slower than for *A. gossypii* (Barlow, 1962; Wyatt & Brown, 1977; van Steenis & El-Khawass, 1995b). The numerical response of *A. colemani* is stronger than of *A. varipes* because of the shorter development time and the larger daily reproduction of aphidiine parasitoids (Starý, 1988a, 1988b; van Steenis, 1992). Also *Aphelinus mali* does not depress *A. gossypii* populations as fast as the aphidiine parasitoid *Trioxys indicus* (Shi Da-san, 1985). In the presence of the aphidiine parasitoid *T. indicus* the increase rate of *A. mali* was decreased with 73.7% (Shi Da-san, 1985).

When both parasitoids were released together the depression of the aphid population was quickest. *Aphelinus varipes* killed a large amount of aphids for host feeding and the successive parasitization by both parasitoid species gave sufficient control. Although in another *Aphidius-Aphelinus* system *Aphidius*-larvae are superior competitors inside the aphid compared to *Aphelinus*-larvae (Force & Messenger, 1965; Bai & Mackauer, 1990b), the species can coexist in the glasshouse, maybe because *Aphelinus*- and *Aphidius*-species recognize aphids parasitized by the other species (Bai & Mackauer, 1991). Also the higher parasitization rates by *A. varipes* in young aphid instars and the lack of a clear preference by *A. colemani* reduces the interference between both parasitoid species. Despite the superior competitive ability of *Aphidius*-species and the host discrimination, parasitization rates by *A. colemani* were lower in the glasshouses where both parasitoid species were introduced.

Hyperparasitoids were observed in all glasshouses but did not prevent successful aphid control. This is confirmed by field and modelling studies, which showed that the impact of hyperparasitism on the meta population level is probably low because of the low fecundity and long development time (van den Bosch *et al*, 1979; Mackauer & Völkl, 1993). Theoretical studies indicate that in some situations hyperparasitoids may even enhance the stability of the aphid-parasitoid interaction (May & Hassell, 1981; Hassell & Waage, 1984; Sullivan, 1988). Nevertheless, the occurrence of hyperparasitoids will always raise the pest level (May & Hassell, 1981; Hassell & Waage, 1984). In the confined area of glasshouses, accumulation of hyperparasitoids at the end of the season because of their high longevity (Brodeur & McNeil, 1995) makes it possible that aphid levels will increase. *Aphelinus varipes* (which was not parasitized by hyperparasitoids) might help to make aphid control more reliable. Since many species of hyperparasitoids have been observed on several other *Aphelinus*-species (Schlinger & Hall, 1959; Hamilton, 1973; Stechmann & Völkl, 1990; Carver, 1992) it is unlikely that hyperparasitism will never occur in glasshouses.

The high mortality of the *Aphelinus*-mummies in the glasshouse is difficult to explain. Hamilton (1973) suggested that Anthocorids were responsible for the high mortality of *Aphelinus flavus*-mummies in the field. In our experiments no anthocorids or other predators have been introduced or observed. Maybe unsuccessful parasitism by hyperparasitoids was responsible for the high mortality rate.

The second aphid introduction showed that both species had survived several weeks of absence of aphids. Introducing *A. varipes* resulted in higher parasitization rates in the new aphid colonies, despite lower aphid and thus lower parasitoid levels in these glasshouses.

It can be concluded that *A. varipes* is useful for biological aphid control programmes. *A. gossypii* is a suitable host and many aphids can be killed and parasitized daily. When both *A. colemani* and *A. varipes* are introduced, the absence of hyperparasitoids and the habit of host feeding by *A. varipes* results in better aphid control when *A. colemani* is introduced alone.

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Chapter 4

Life histories of selected parasitoids

4 Life histories of selected parasitoids

4.1 Intrinsic rate of increase of *Aphidius colemani* Viereck (Hymenoptera: Braconidae), a parasitoid of *Aphis gossypii* Glover (Homoptera: Aphididae), at different temperatures[1]

Abstract

Increasing problems with chemical control of the cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), in vegetable crops necessitate development of a biological control programme. An endoparasitoid of *A. gossypii*, *Aphidius colemani* Viereck (Hymenoptera: Braconidae), is one of the candidate control agents. Data on longevity, reproduction and development of *A. colemani* with *A. gossypii* as host are presented. The parasitoid has a fecundity of 302 eggs per female at 20 °C and 388 eggs per female at 25 °C, a development period of 12.7 days at 20 °C and 10.0 days at 25 °C and an immature mortality of 14.1% at 20 °C and 27.8% at 25 °C. The intrinsic rate of increase of the parasitoid is both at 20 and at 25 °C comparable to the intrinsic rate of increase of the cotton aphid. *Aphidius colemani* seems, therefore, a promising candidate for biological control of *A. gossypii*.

Introduction

The cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), is an important problem in glasshouse crops, especially in cucumber and melon, although its occurrence in other crops is increasing. Population growth of cotton aphid is very fast: without control measures a total collapse of a cucumber crop can follow within five weeks after introduction of a few aphids (Scopes & Biggerstaff, 1976).

In the biological control programmes developed for glasshouse crops, aphids are usually controlled by the parasitoid *Aphidius matricariae* Haliday (Hymenoptera: Braconidae) and the gall midge *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae). Additional control can be obtained with the selective aphicide pirimicarb.

In case of *A. gossypii*, however, biological control often fails. Furthermore, *A. gossypii* has developed resistance against pirimicarb (Furk *et al*, 1980; van Schelt *et al*, 1990). For maintaining the possibility of biological control of other pests in the same crop, which is quite generally applied nowadays, a biological control programme for cotton aphid has to be developed as well.

Aphidius colemani is one of the candidates for use in biological control of cotton aphid. *Aphidius colemani* has proved to be an efficient biological control agent of *Myzus persicae* Sulzer (Homoptera: Aphididae) on chili and egg-plant, both grown in glasshouses (Easwaramoorthy *et al*, 1976). In this paper the biology of *A. colemani* with *A. gossypii* as host and cucumber as host plant is described.

Material and methods

Insect cultures

Aphis gossypii were collected from cucumber glasshouses in the Netherlands in 1990. At the

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Glasshouse Crops Research Station the aphids were cultured on cucumber (cvs. 'Sporu' and 'Sortena') under natural light and a minimum temperature of 18 °C.

Aphidius colemani is a solitary aphid endoparasitoid, originating from Asian regions (Starý, 1975). Nowadays it has spread over many regions including South America, Africa and Australia (Starý, 1975). Many hosts are known, but they seem to be restricted to the Aphididae, including *A. gossypii* (Starý, 1975). The parasitoids used in the experiments were obtained from Koppert BV in January 1991. The stock has been collected from *A. gossypii* in glasshouses and has subsequently been reared with *A. gossypii* as host. At the Glasshouse Crops Research Station they were also reared with *A. gossypii* as host. The culture was kept in a small glasshouse compartment without artificial light. The minimum temperature was 20 °C, maximum temperatures depended on weather conditions and did not exceed 36 °C. Relative humidity varied between 50% under warm weather conditions and 90% under cold weather when almost no ventilation was necessary.

Experiment 1 - Longevity and reproduction of adults

At the start of the experiment, the females had an age of 0 to 24 hours. During this period males and females were confined together. To standardize the size of the parasitoids, they were collected from aphids which were parasitized at an age of 2 days (approximately second nymphal stage). The experiment was carried out at 20 (± 0.3) and 25 (± 0.3) °C with 15 wasps at each temperature. During both experiments a light-dark regime of 16L:8D and a relative humidity of 60% (± 5%) was maintained.

During the life time of the female every day a cucumber leaf (cv. 'Sortena') with unparasitized cotton aphids of two days old was offered. The leaves were still attached to the plant and plants were used once only. The aphids used in the experiments were reared at a temperature of 25 °C. The number of cotton aphids offered daily to an individual female was 200 at day one and two, 150 at day three and four and 100 from day five to day 13.

The cotton aphids and one wasp were kept in a cylindrical with a length of 24 cm and a diameter of 12 cm which could contain the entire lower leaf of the cucumber plant. Three (at 25 °C) or four days (at 20 °C) after the wasp had parasitized, the leaf was frozen together with the aphids. Later on, the aphids were dissected in a drop of water with detergent under a stereo microscope, to check for the presence of larvae. At this stage it is still possible to recognize supernumerary larvae or eggs. Mortality of the eggs during the first days of development is neglected, because it is difficult to recognize dead eggs under the stereo microscope. Circumstantial evidence indicates that the bias introduced by the negligence of egg mortality is small, since Hågvar & Hofsvang (1986) showed for another aphidiine parasitoid, *Ephedrus cerasicola* Starý, that mortality from eggs deposited in young aphids was at most three percent.

Table 1
Temperatures (°C ± s.d.; n) inside the leaf cages with the adult wasps used in experiment 1.

room temperature	lights on (16 h)	lights off (8 h)	average daily temperature
20 °C	22.0 (± 0.50; n=34)	20.0 (± 0.08; n=28)	21.3
25 °C	28.3 (± 0.71; n=38)	25.0 (± 0.16; n=29)	27.2

The temperature inside the leaf cage differed from the air temperature of the climate room due to the radiation of the lamps. The exact temperatures inside (below the leaf) and outside the cages (air temperature) are given in Table 1. Over a 24 hour period the average temperatures were 21.3 and 27.2 °C.

With the method described above at least 90% of the offered aphids could be recollected on each leaf at the time of dissection. The data on reproduction were corrected for missing aphids, assuming that parasitized and unparasitized aphids had the same chance of disappearing, since Brodeur & McNeil (1989) showed that changes in behaviour of parasitized aphids only start to become clear 24 to 36 hours before mummification (Brodeur & McNeil, 1989).

To obtain a more accurate estimate of the mortality rates of the female adults, the procedure was repeated for five more wasps at each temperature without dissection of the aphids.

Experiment 2 - Larval development and immature mortality

Female wasps were allowed to parasitize 20 cotton aphids of two days old (approximately second nymphal stage). To prevent superparasitism, the parasitization process was observed and every aphid which was parasitized was removed. The females had an age of at most 48 hours and had been confined with males during at least 12 hours before the experiment. Females were also allowed to parasitize a small number of cotton aphids before the experiment.

After three (at 25 °C) or four days (at 20 °C), ten aphids were dissected to determine the exact number of parasitized aphids. Mortality before dissection was again neglected. The portion of unparasitized aphids was used to correct the data on immature mortality. The remaining aphids were individually put into clip-on leaf cages on cucumber leaves (cv. 'Sortena') and followed in their development. Formation of the mummy and hatching of the adults were recorded together with the sex of the adults. Females which produced only male progeny and apparently had not mated were disregarded. Experimentation continued until data from 10 mated females were obtained.

Calculation of the intrinsic rate of increase

With the data from the reproduction and the development experiments, the intrinsic rate of increase was calculated according to the method of Birch (1948). For this Equation [1] was solved iteratively:

$$\sum_{X=0}^{\infty} e^{r*x} * l_x * m_x = 1 \qquad [1]$$

in which x = age in days (including immature stages), r = intrinsic rate of increase, l_x = age specific survival (including immature mortality) and m_x = age specific number of female offspring.

Data analysis

Differences between the mean values of two populations were tested for significance with the Mann-Whitney U-test. For determination of differences in immature mortalities the G-test was used. All tests were performed at a significance level of 0.05.

Results

Experiment 1 - Longevity and reproduction of adults

Wasps that escaped from the leaf cages during the experiment (two at 20 °C and one at 25 °C) were omitted from the analysis. Thus the number of wasps used for determination of the reproductive capacity was 13 and 14 at 20 and 25 °C, respectively. The survival at 20 °C was higher than at 25 °C (Figure 1a). The average life-span was significantly longer at 20 °C ($P<0.05$; Mann-Whitney U-test), being 5.8 days (s.e. = 0.61) at 20 °C and 4.4 days (s.e. = 0.41) at 25 °C.

Data on the reproduction of *A. colemani* are given in Table 2. Superparasitism was higher at 25 °C (3.21%) than at 20 °C (0.65%). Most of the superparasitism occurred during the first day. At this stage the urge to deposit eggs is high relative to the number of aphids offered. The daily egg-production seemed to be lower at 20 °C than at 25 °C (Figure 1b), but there was no significant difference between the total fecundity of the wasps at the two temperatures (301.5 eggs/female (s.e. = 42.6) at 20 °C and 388.1 eggs/female (s.e. = 28.5) at 25 °C).

Table 2
Daily fecundity of *Aphidius colemani* at 20 °C and 25 °C (mean (s.e.)).

age of wasp	n	number of aphids offered	number of aphids not parasitized	number of aphids parasitized once	number of superparasitized aphids			total number of eggs produced[1]
					2 larvae	3 larvae	4 larvae	
20 °C								
1	14	200	51.7 (9.7)	144.6 (10.0)	1.1 (0.4)	0.1 (0.1)	0.0	149.7
2	14	200	103.6 (15.3)	88.6 (16.0)	0.6 (0.3)	0.0	0.0	92.0
3	13	150	107.2 (11.8)	43.2 (12.1)	0.0	0.0	0.0	43.4
4	12	150	130.7 (8.8)	19.2 (8.8)	0.0	0.0	0.0	19.3
5	8	100	95.5 (2.4)	4.6 (1.9)	0.1 (0.1)	0.0	0.0	5.0
6	3	100	99.0 (1.0)	0.7 (0.7)	0.0	0.0	0.0	0.7
7	1	100	100.0	0.0	0.0	0.0	0.0	0.0
8	1	100	98.0	0.0	0.0	0.0	0.0	0.0
25 °C								
1	13	200	35.3 (4.4)	145.4 (5.3)	7.6 (1.9)	0.5 (0.3)	0.1 (0.1)	171.1
2	13	200	63.2 (11.9)	121.9 (12.7)	0.1 (0.1)	0.0	0.0	134.5
3	13	150	85.8 (13.7)	53.5 (13.1)	0.7 (0.3)	0.0	0.0	58.9
4	8	150	115.5 (8.3)	28.4 (8.3)	0.1 (0.1)	0.1 (0.1)	0.0	30.5
5	4	100	90.3 (5.3)	3.3 (1.7)	0.0	0.0	0.0	3.5
6	3	100	71.1 (17.9)	18.0 (17.6)	1.0	0.0	0.0	21.1
7	1	100	85.0	11.0	1.0	1.0	0.0	16.3

1 after correction for missing aphids

Experiment 2 - Larval development and immature mortality

At 20 °C, ten percent of the aphids did not contain a larva a the time of dissection, at 25 °C only three percent of the aphids did not contain a larva at the time of dissection. No superparasitized aphids were found.

The development of the larvae was significantly faster at 25 °C (12.7 days at 20 °C and 10.0 days at 25 °C for females) (Table 3). At both temperatures no significant differences existed between the development times for males and females.

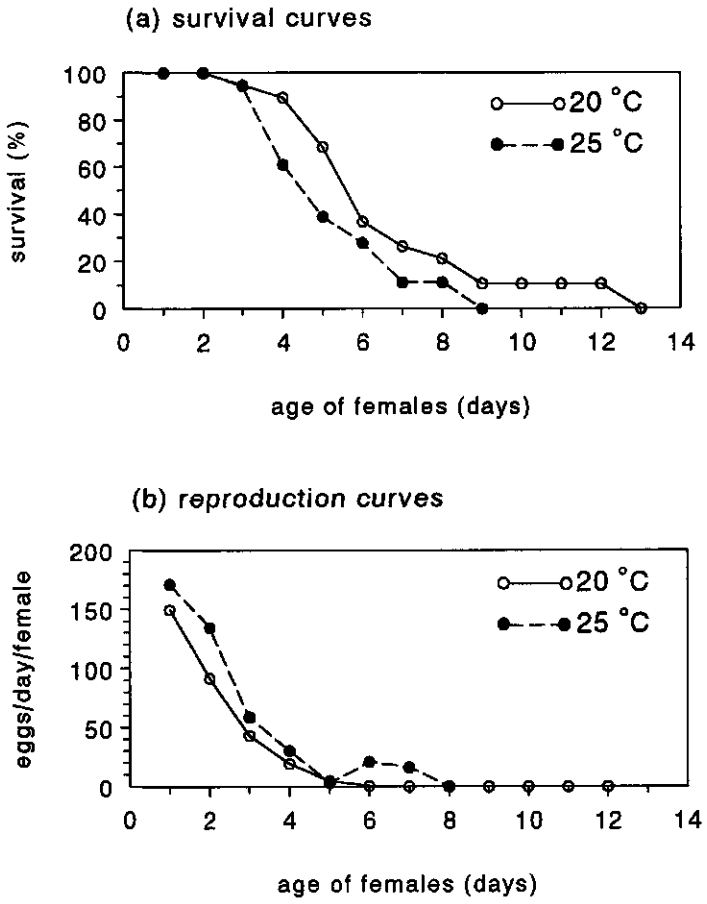

Figure 1

Survival (a) and reproduction (b) curves of adult *Aphidius colemani* females as a function of age. The life-span was significantly longer at 20 °C ($P<0.05$; Mann-Whitney U-test) and the life-time fecundity was significantly higher at 25 °C ($P<0.05$; Mann-Whitney U-test).

Table 3
Development and immature mortality of *Aphidius colemani* with *Aphis gossypii* as host at different temperatures.

	20 °C	25 °C
aphids without larvae at time of dissection (%)	9.9 (n=91)[a]	2.6 (n=78)[a]
larval mortality (%)*	12.8 (n=76)[a]	22.8 (n=79)[a]
mortality during mummy (%)	1.5 (n=66)[a]	6.6 (n=61)[b]
total immature mortality (%)	14.1 (n=76)[a]	27.8 (n=79)[b]
development period (days (± s.e.; n))		
males	12.6 (± 0.15; n=36)[a]	9.6 (± 0.14; n=29)[b]
females	12.7 (± 0.21; n=29)[a]	10.0 (± 0.13; n=28)[b]

* After correction for unparasitized aphids
Different letters indicate a significant difference between the temperatures ($P<0.05$; Mann-Whitney U-test; G-test)

Table 4
Intrinsic rate of increase of *Aphidius colemani* and *Aphis gossypii*.

Aphidius colemani (this study)								*Aphis gossypii* (Wyatt & Brown, 1977)	
20 °C				25 °C				18 °C	24 °C
x	l_x	m_x	r_m	x	l_x	m_x	r_m	r_m	r_m
13.7	0.859	89.84	0.352	11.0	0.722	102.68	0.438	0.38-0.44	0.37-0.45
14.7	0.859	55.22		12.0	0.722	80.67			
15.7	0.814	26.01		13.0	0.682	35.56			
16.7	0.769	11.59		14.0	0.441	18.29			
17.7	0.588	2.97		15.0	0.281	2.08			
18.7	0.317	0.40		16.0	0.201	12.64			
19.7	0.226	0.00		17.0	0.080	9.79			
20.7	0.181	0.00		18.0	0.080	0.00			
21.7	0.091	0.00		19.0	0.000				
22.7	0.091	0.00							
23.7	0.091	0.00							
24.7	0.091	0.00							
25.7	0.000								

x = age in days (including immature stages); l_x = age specific survival (including immature stages; m_x = age specific number of female offspring; r_m = intrinsic rate of increase.

The immature mortality was low. The mortality within the mummified aphids was 1.5% at 20 °C and 6.6% at 25 °C (Table 3). At 25 °C the total immature mortality was significantly higher than at 20 °C ($P<0.05$; G-test).

The data for calculation of the intrinsic rate of increase are given in Table 4. The sex ratio is set to be 60% females, according to Giri *et al* (1982), Mackauer (1976) and Shalaby & Rabasse (1979). In the experiments presented in this paper the percentage of females was much lower even though the female wasps had been confined with males for several hours.

Discussion

The life-time fecundity found in this study (302 eggs per female at 20 °C) is much larger than found by Hofsvang & Hågvar (1975b) at 21 °C with *M. persicae* as host (46 mummies per female). They did find a similar pattern in egg production; 88% of the mummies was produced during the first two oviposition days. Due to the surplus of aphids offered, superparasitism was rare. The lifespan found by Hofsvang & Hågvar (1975b) at 21 °C is similar to the lifespan of females in this study at 20 °C (5.6 and 5.8 days, respectively). If the wasps do not have access to aphids but are fed with honey and water, lifespan increases to 12.7 days at 21 °C and 7.4 days at 24 °C (Hofsvang & Hågvar, 1975a). A shorter lifespan when aphids are offered instead of only honey has also been observed in other members of the Aphidiinae (Wiąckowski, 1962; Pandey *et al*, 1984). Increased activity and oviposition, because of the presence of hosts, with a consequent decrease of the supply of energy might be responsible for the shorter lifespan (Wiąckowski, 1962).

The development times are faster than found by Hofsvang & Hågvar (1975a) at a temperature of 21 °C (15.6 days) and 24 °C (12.4 days) with *M. persicae* as host. Development is also faster than described by Völkl *et al* (1990) at a temperature of 21 °C (14.2 days for females) and 24 °C (13.7 days for females) with *Pentalonia nigronervosa* as host. Whether these difference are due to the experimental setup or to the different host species is unknown.

The immature mortality was low and similar to data obtained by Giri *et al* (1982) and 't Hart *et al* (1978) for *A. matricariae* with *M. persicae* as host. They found the immature mortality to be about 20%. The mortality within mummified aphids was lower than mummy mortality found by Hofsvang & Hågvar (1975b) (17% at 21 °C).

The intrinsic rate of increase was, at both temperatures, of the same magnitude as or even larger than the intrinsic rate of increase of cotton aphid on cucumber (Wyatt & Brown, 1977) (Table 4).

Aphidius colemani is known to parasitize many aphid species (Starý, 1975). This study showed *A. gossypii* to be a suitable host for *A. colemani*. Following the guidelines for pre-introductory evaluation as presented by van Lenteren & Woets (1988), *A. colemani* might be a good biological control agent because:

- *A. colemani* does develop in *A. gossypii*
- *A. colemani* does not interfere with other biological control methods
- *A. colemani* is relatively easy to rear
- the intrinsic rate of increase of *A. colemani* has the same magnitude as the intrinsic rate of increase of *A. gossypii* on cucumber.

It seems therefore justified to continue research on *A. colemani*, although r_m-values of cotton aphid under the same conditions as the experiments on *A. colemani* were performed, still have

to be determined. The next experiments will be aimed to assess the suitability of *A. colemani* as a biological control agent of *A. gossypii* in a cucumber crop. The main problem that is faced when *A. colemani* is used in a biological control programme is the short lifespan and the even shorter period of intensive egg laying. If the intervals between the introductions are too large, the cotton aphid population might be able to multiply to such levels that control can not be obtained at the moment of the next introduction. This implies that the method of introduction has to be adapted in such a way that a continuous presence of female parasitoids can be assured.

Another factor that deserves more attention is the influence of the origin of the parasitoid stock on the performance on *A. gossypii*. Powell & Wright (1988) for example showed a partly genetical difference in host preference and host suitability between different strains of *Aphidius ervi* and *A. rhopalosiphi* which were collected from different aphid species and subsequently reared on the same aphid species they were collected from. Accordingly, it can be questioned whether parasitoids collected from or reared on another aphid species will still be as successful in parasitizing *A. gossypii* as those reared on *A. gossypii*. This will be a topic of future research.

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4.2 Intrinsic rate of increase of *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae), a parasitoid of *Aphis gossypii* Glover (Homoptera: Aphididae), at different temperatures[1]

Abstract

Lysiphlebus testaceipes Cresson (Hymenoptera: Braconidae) is one of the candidates for use in a programme for biological control of cotton aphid, *Aphis gossypii* Glover. Longevity, reproduction, development and intrinsic rate of increase of *L. testaceipes* were determined in the laboratory at two different temperatures with cotton aphids as host.

The average fecundity of one parasitoid was 128.2 eggs at 20 °C and 180.0 eggs at 25 °C. The immature mortality was 9.5 and 29.6 % at 20 and 25 °C, respectively. Development from egg to female adult was completed in 12.9 days at 20 °C and 9.5 days at 25 °C. The lifespan of the females was very short (2.7 and 2.6 days at 20 and 25 °C, respectively). At 20 °C the r_m-value of *L. testaceipes* was slightly lower than for cotton aphid. At 25 °C the r_m-values of *L. testaceipes* and *A. gossypii* were equal.

Lysiphlebus testaceipes might be a suitable natural enemy although r_m-values are probably too low to be able to overtake an established aphid population.

Introduction

Cotton aphid is an important problem in glasshouse crops, especially in cucumber and melon (van Schelt *et al*, 1990). Population growth of this aphid is very fast. On glasshouse grown cucumber, cotton aphid populations can increase 10 times a week, under favourable conditions even an increase of 22.7 times a week has been observed (Scopes & Biggerstaff, 1976).

In the Netherlands the parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae) and the predatory gall midge *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) are used for cotton aphid control, but are not always successful. Chemical control of cotton aphid is difficult to combine with biological control of other glasshouse pests, because cotton aphid has developed resistance against pirimicarb, the only selective aphicide available (Furk *et al*, 1980; van Schelt *et al*, 1990). For maintaining the possibility of biological control of other pests it is therefore necessary to develop a biological control programme for cotton aphid.

One of the candidates for use in biological control of cotton aphid is the aphid parasitoid *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae). This parasitoid is probably native to North and Central America (Mackauer & Starý, 1967). In the beginning of this century *L. testaceipes* was reported as biological control agent against the greenbug, *Schizaphis graminum* (Rondani) in the midwestern United States (Kelly, 1917) and as the most abundant parasitoid on *A. gossypii* in Texas (Paddock, 1919). Its host range includes most Aphidinae, *Myzus-Brachycaudus spp.* and *Macrosiphum* and related genera (Mackauer & Starý, 1967). *Lysiphlebus testaceipes* is introduced for control of aphids in many areas, e.g. in Australia (Carver, 1984) and the Mediterranean area (Starý *et al*, 1988).

One of the criteria used in pre-introduction evaluation of natural enemies is that the population growth rate of the control agent should at least equal the population growth rate of the pest (van Lenteren & Woets, 1988). In this paper r_m-values of *L. testaceipes* will be

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estimated and compared with r_m-values of *A. gossypii*.

Materials and methods

The parasitoid culture

The parasitoids used in this experiment were obtained from Biological Control Industries, Israel in January 1991. At the Glasshouse Crops Research Station they were reared with *A. gossypii* as host. The culture was in a small glasshouse compartment without artificial light. The minimum temperature was 20 °C, the maximum temperature depended on weather conditions but was usually under 30 °C and never exceeded 36 °C. Relative humidity varied between 50 and 90%.

Experiment 1 - Longevity and reproduction of adults

At the start of the experiment the females had an age of 0 to 24 hours. Males and females were confined together, and had access to some cotton aphids. To standardize the size of the female parasitoids, they were collected from second instar cotton aphids which were parasitized by *L. testaceipes* in the laboratory.

The experiments were performed in climate chambers with an air temperature of 20 °C (± 0.2) and 25 °C (± 0.2). The number of wasps studied was 15 at 20 °C and 16 at 25 °C. During both experiments a light-dark regime of 16L:8D was maintained.
During the lifetime of a female every day a cucumber leaf (cv. 'Sortena') with unparasitized cotton aphids of two days old (nymphs of the second and third stage) was offered. The leaves were still attached to the plant and plants were used only once. The aphids were reared in the laboratory at 25 °C. Because in preliminary experiments it was shown that the number of aphids parasitized daily declined fastly with increasing age of the parasitoid, the number of cotton aphids offered daily to an individual female declined from 200 at day one and two, to 150 at day three and four and 100 from day five to day eight. The cotton aphids and the wasp were secured from the surroundings by a cylindrical leaf cage which was placed around the leaf. Escape of the parasitoids was prevented with a piece of gauze surrounding the leaf stalk.

The temperature inside the leaf cages differed from the temperature of the climate room when the lights were on. The exact temperatures during the experiments inside and outside the cages are given in Table 1.

Three (at 25 °C) or four (at 20 °C) days after the wasp had parasitized the aphids, the leaf with the aphids on it was put into a freezer. Later on the aphids were dissected in a drop of water with detergent under a stereomicroscope to check for the presence of parasitoid larvae. At this stage it is still possible to recognize supernumerary larvae or eggs. Mortality during the first days of development is negligible, as shown by Hågvar & Hofsvang (1986) for another aphid parasitoid.

Table 1
Temperatures (°C ± s.d.; n) inside the leaf cages with the adults wasps used in experiment 1.

room temperature	lights on (16 h)	lights off (8 h)	average daily temperature
20 °C	22.1 (± 0.37; n=32)	20.0 (± 0.25; n=26)	21.4
25 °C	27.9 (± 0.57; n=29)	25.0 (± 0.16; n=22)	26.9

With the method described above at least 88 percent of the aphids offered could be recovered at the time of dissection. Because the time from parasitization to freezing of the aphids was very short, the data on reproduction were corrected for missing aphids, assuming that parasitized and unparasitized aphids had the same chance of disappearing.

Experiment 2 - Larval development and immature mortality

For this experiment ten experienced mated female wasps were each allowed to parasitize 20 cotton aphids with an age of two days. The females had an age of at most 48 hours.

After three (at 25 °C) or four (at 20 °C) days, half of the aphids were dissected to determine the proportion of parasitized aphids. Mortality before this moment was again neglected. The proportion of unparasitized aphids was used to correct the data on immature mortality. The remaining aphids were individually put into clip-on leaf cages on cucumber leaves (cv. 'Sortena') and followed in their development. Formation of the mummy and hatching of the adults were recorded together with the sex of the adults.

Calculation of the intrinsic rate of increase

With the data from the reproduction and the development experiments, the intrinsic rate of increase was calculated according to the method of Birch (1948). For this Equation [1] was solved iteratively:

$$\sum_{X=0}^{\infty} e^{r*x} * l_x * m_x = 1 \qquad [1]$$

in which x = age in days (including immature stages), r = intrinsic rate of increase, l_x = age specific survival (including immature mortality) and m_x = age specific number of female offspring.

Data analysis

Differences between the total number of eggs produced and the life span of the parasitoids were tested for significance with the Mann-Whitney U-test at a significance level of 0.05. For determination of differences in immature mortalities the G-test was used.

Results

Experiment 1 - Longevity and reproduction of adults

Survival rates at 20 and 25 °C were quite similar (Figure 1a) and there was no significant difference in the average life spans (P = 0.90; Mann-Whitney U-test) (2.73 days (s.e. = 0.38; n = 15) at 20 °C and 2.56 days (s.e. = 0.22; n = 16) at 25 °C).

Data on the age specific reproduction of *L. testaceipes* are given in Table 2. Superparasitism was rare in the experiment, due to the surplus of aphids offered. Superparasitism was 1.34% at 25 °C and 0.84% at 20 °C. There was no significant difference in total fecundity at 20 °C and at 25 °C (Figure 1b), (128.2 eggs/female (s.e. = 20.8; n = 15) at 20 °C and 180.0 eggs/female (s.e. = 18.4; n = 16) at 25 °C) (Mann-Whitney U-test).

Experiment 2: larval development and immature mortality

A large quantity of the aphids in this experiment was parasitized: at 20 °C 9.9% of the aphids did not contain a larva, while at 25 °C almost 19.7% of the aphids did not contain a larva (Table 3).

The development of the larvae was significantly faster at 25 °C ($P<0.05$; Mann-Whitney U-test). At both temperatures development of the males was significantly faster than development of the females ($P<0.05$; Mann-Whitney U-test).

The larval mortality at 25 °C was significantly higher than at 20 °C (25.6% and 2.7%, respectively) ($P<0.05$; G-test).

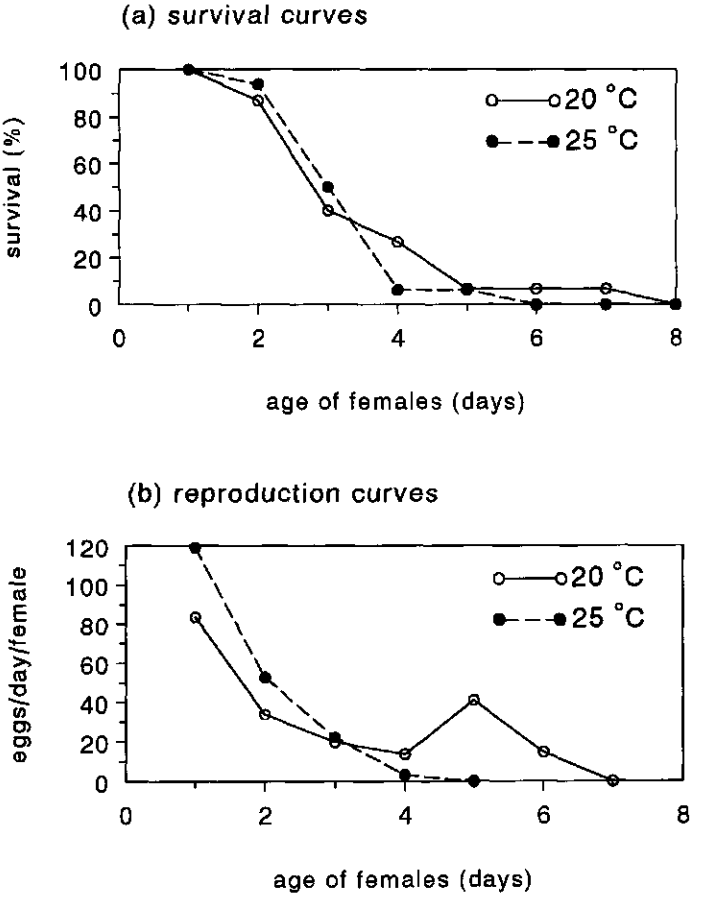

Figure 1
Survival (a) and reproduction (b) curves of adult *Lysiphlebus testaceipes* females as a function of age. The life-span and the life-time fecundity did not differ significantly between the temperatures (Mann-Whitney U-test).

Table 2
Daily fecundity of *Lysiphlebus testaceipes* at 20 °C and 25 °C (mean (s.e.)).

age of wasp	n[1]	number of aphids offered	number of aphids not parasitized	number of aphids parasitized once	number of superparasitized aphids		total number of eggs produced[2]
					2 larvae	3 larvae	
				20 °C			
1	15	200	106.9 (11.12)	76.7 (11.94)	0.9 (0.35)	0.0	83.6
2	13	200	151.1 (10.54)	31.2 (10.67)	0.2 (0.10)	0.0	33.9
3	6	150	117.3 (9.35)	17.3 (4.57)	0.0	0.0	19.7
4	4	150	125.0 (10.97)	12.3 (7.22)	0.0	0.0	13.7
5	1	100	57.0	40.0	0.0	0.0	41.2
6	1	100	74.0	13.0	0.0	0.0	14.7
7	1	100	99.0	0.0	0.0	0.0	0.0
				25 °C			
1	16	200	73.4 (7.98)	104.6 (8.31)	1.9 (0.38)	0.1 (0.09)	171.1
2	15	200	134.8 (8.35)	50.3 (9.19)	0.3 (0.15)	0.0	134.4
3	7	150	119.6 (7.46)	19.6 (6.04)	0.0	0.0	58.9
4	1	150	138.0	3.0	0.0	0.0	30.5
5	1	100	94.0	0.0	0.0	0.0	3.5

1 n = number of parasitoids still alive
2 after correction for missing aphids

Table 3
Development and immature mortality of *Lysiphlebus testaceipes* with *Aphis gossypii* as host at 20 and 25 °C.

	20 °C	25 °C
aphids without larvae at time of dissection (%)	9.9 (n = 81)[a]	19.7 (n = 76)[a]
larval mortality (%)*	2.7 (n = 59)[a]	25.6 (n = 74)[b]
mortality during the mummy stage (%)	5.3 (n = 57)[a]	5.5 (n = 55)[a]
total immature mortality (%)	9.5 (n = 59)[a]	29.6 (n = 74)[b]
development period (days (± s.e.; n))		
males	12.2 (± 0.21; n = 21)[a]	8.9 (± 0.09; n = 27)[b]
females	12.9 (± 0.15; n = 32)[a]	9.5 (± 0.21; n = 24)[b]

* after correction for aphids without larvae at time of dissection
Different letters indicate a significant difference between the temperatures ($P < 0.05$; Mann-Whitney U-test; G-test)

In the mummified aphids a mortality of about 5% occurred (Table 3). At 25 °C the total immature mortality was significantly higher than at 20 °C (Table 3) ($P<0.05$; G-test).

The biological data of *L. testaceipes* are summarized in Table 4. For calculation of the intrinsic rate of increase a sex ratio of 60% females has been used, according to Hight *et al* (1972) and Kring & Kring (1988).

Discussion

Marullo (1987) also found the life span of females to be very short; 4.3 days at 18 °C and 3.2 days at 25 °C.

The distribution of the larvae in aphids parasitized during one day does not significantly deviate from a random distribution ($P>0.50$; G-test), suggesting that *L. testaceipes* did not discriminate between parasitized and unparasitized aphids (van Lenteren *et al*, 1978). This seems in contradiction with results on host discrimination in other species within the Aphidiinae (Hågvar & Hofsvang, 1991). The random distribution of larvae in aphids parasitized in one day is probably a result of the surplus of aphids offered. The higher rate of superparasitism during the first day might be caused by the high urge to deposit eggs at this stage or because of an inability of young unexperienced females to discriminate between parasitized and unparasitized hosts (van Lenteren *et al*, 1978).

The development times of the females at 20 and 25 °C (12.9 days and 9.5 days, respectively) were comparable to those with *Schizaphis graminum* as host given by Hight *et al* (1972) (13.2 days at 21 °C and 10.8 days at 27 °C), Kring & Kring (1988) (10.9 days at an average temperature of 26 °C) and Salto *et al* (1983) (12.4 days at an average temperature of 23 °C).

Table 4
Intrinsic rate of increase of *Lysiphlebus testaceipes* and *Aphis gossypii*.

Lysiphlebus testaceipes (this study)								*Aphis gossypii* (Wyatt & Brown, 1977)	
20 °C				25 °C				18 °C	24 °C
x	l_x	m_x	r_m	x	l_x	m_x	r_m	r_m	r_m
13.9	0.905	50.15	0.296	10.5	0.704	71.50	0.400	0.38-0.44	0.37-0.45
14.9	0.784	20.35		11.5	0.660	31.69			
15.9	0.362	11.84		12.5	0.352	13.33			
16.9	0.241	8.20		13.5	0.044	1.91			
17.9	0.060	24.72		14.5	0.044	0.00			
18.9	0.060	8.81		15.5	0.000				
19.9	0.060	0.00							
20.9	0.000								

x = age in days (including immature stages); l_x = age specific survival (including immature mortality); m_x = age specific number of female offspring; r_m = intrinsic rate of increase

In the mummified aphids a mortality of about 5% occurred (Table 3), much lower than found by Kring & Kring (1988) (30% at an average temperature of 26 °C). Data from the study presented were in agreement with the low mortalities during the mummy stage as given by Hight *et al* (1972) (5% at 21 °C and 13% at 27 °C) and Marullo (1987) (11.3% at 22 °C).

If the immature mortality is combined with the egg production, the average number of adults per female would have been 116 at 20 °C and 126 at 25 °C. This is higher than a fecundity of 63.3 adults per female at 22 °C as found by Marullo (1987) and in agreement with Sekhar (1957), who found the number of offspring to be 108.2 per female at a temperature of 25-35 °C.

At 20 °C the intrinsic rate of increase of *L. testaceipes* is lower than the r_m-value of *A. gossypii* as given by Wyatt & Brown (1978) (Table 4). At 25 °C r_m-values of *L. testaceipes* and *A. gossypii* are similar.

Aphis gossypii is a good host for *L. testaceipes*, which is also concluded by Sekhar (1960). The r_m-values of *L. testaceipes* do not differ much from the r_m-values of cotton aphid on cucumber. Schlinger & Hall (1960) report that *L. testaceipes* gives an excellent degree of control of *A. gossypii* on citrus. On citrus the r_m of cotton aphid is 0.33 at 20 °C and 0.30 at 25 °C (Komazaki, 1982) which is lower than a r_m of about 0.40 on cucumber (Wyatt & Brown, 1977).

Following the guidelines for pre-introductory evaluation as presented by van Lenteren & Woets (1988), *L. testaceipes* might be a good biological control agent because:

- *L. testaceipes* does develop in *A. gossypii*
- *L. testaceipes* does not interfere with other biological control methods
- *L. testaceipes* is relatively easy to rear.

The fourth criterion proposed by van Lenteren & Woets (1988) is that the intrinsic rate of increase of the natural enemy should equal or be larger than the intrinsic rate of increase of the pest population. For *L. testaceipes* the intrinsic rate of increase is not clearly larger than the intrinsic rate of increase of *A. gossypii*, at 20 °C it is even smaller. It can be questioned whether *L. testaceipes* will be able to overtake an established aphid population when released in a seasonal inoculative way. Still, *L. testaceipes* could be an effective biological control agent if regular introductions are used. In this case a high searching capacity is important, an aspect which will be studied in future experiments.

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4.3 Life history of *Aphelinus varipes* Förster (Hymenoptera: Aphelinidae), a parasitoid of the cotton aphid *Aphis gossypii* Glover (Homoptera: Aphididae), at three constant temperatures[1]

Abstract

Life history data for *Aphelinus varipes* Förster (Hymenoptera: Aphelinidae), a candidate agent for biological control of cotton aphid, were collected at three constant temperatures in the presence of a surplus amount of second instar nymphs of *Aphis gossypii* Glover (Homoptera: Aphididae). The longevity of adult females decreased from 10.6 days at 20 °C to 2.5 days at 30 °C. At 20 °C less aphids were parasitized daily than at 25 or 30 °C, but because of the longer lifespan the life-time fecundity was highest at 20 °C. Approximately five to ten aphids were killed for host feeding daily. At 30 °C daily host feeding was largest. Development from egg to adult female took from 20.7 days at 20 °C to 10.0 days at 30 °C.

The resulting r_m-values were 0.182, 0.293 and 0.327 day^{-1} at temperatures of 20, 25 and 30 °C, respectively. Because of the habit of host feeding, the host kill rate of *A. varipes* will be higher.

Aphelinus varipes could be a valuable addition to a cotton aphid control programme. Compared with *A. colemani* its life span is longer at low temperatures and *A. varipes* is less susceptible to the high temperatures during the summer.

Introduction

In glasshouse cucumber crops the cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), is controlled with natural enemies on a large scale. As long as no aphids are present preventive introductions of *A. colemani* are used at a rate of 0.1 parasitoids/m^2/week. After aphids have been observed in a glasshouse more parasitoids are released in combination with the gall midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) (van Schelt, 1993). Still, aphid control is not always reliable, probably for three reasons.

First, the longevity of *A. colemani* is very short (van Steenis, 1993). After a preventive introduction the parasitoid density will decrease quickly. If aphids enter a glasshouse at a moment with few parasitoids, the aphid colonies can grow to such a level that rapid biological control can not be obtained anymore. A cotton aphid population can multiply up to 49 times per week (van Steenis & El-Khawass, 1995).

A second problem during biological aphid control is the wave-like interaction between the pest and its natural enemies. After successful suppression of the pest, aphid levels are very low and not many parasitoids and predators will survive, giving a chance to new aphids entering the glasshouse. During the absence of the natural enemies the aphids are able to multiply to such levels that the next generation of natural enemies is too late to establish efficient control (Ramakers & Rabasse, 1995). This delay in the reaction of the parasitoid population to increasing aphid density can result in oscillations of the aphid and parasitoid population (Krebs, 1972; Varley *et al*, 1973). The amplitude of the oscillations increases with increasing growth rates of the host and parasitoid population (Nicholson, 1933). A wave-like population development of the aphids and their natural enemies can often be seen in glasshouses

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(Ramakers & Rabasse, 1995).

Finally, in the summer problems can arise because the parasitoids are more negatively influenced by the high temperatures than *A. gossypii*. R_m-values at 20 °C do not differ much between *A. colemani* and *A. gossypii* but at 25 °C the population growth of *A. gossypii* is larger than the population growth of *A. colemani* (van Steenis, 1993; van Steenis & El-Khawass, 1995). At very high temperatures the mortality during the mummy stage increases markedly (Guenaoui, 1993).

These problems could be avoided by using parasitoids which are better adapted to high temperatures and with a larger longevity, resulting in a different and possibly better interaction between the aphid and the natural enemy population. Aphelinid parasitoids are less susceptible to high temperatures than Aphidiinae (Force & Messenger, 1964a; Bernal & González, 1993) and have a longer life span (Force & Messenger, 1965). One of the candidates is the parasitoid *Aphelinus varipes* Förster (Hymenoptera: Aphelinidae). *Aphelinus varipes* occurs also in Europe (de Graham, 1976) and has been introduced into the United States for control of grain aphids (Wharton, 1983). In this study it was thought desirable to use a strain with a tropical origin. Different lines of one species can have different life-history parameters (Haardt & Höller, 1992) and lines with a tropical origin would be better adapted to the average glasshouse temperatures. The *A. varipes*-line used in this study was collected from *A. gossypii* in cotton fields in Cameroon.

The usefulness of this *A. varipes*-line for biological control of cotton aphid was evaluated in previous experiments (van Steenis, 1995). The parasitoid parasitized *A. gossypii* successfully and showed a preference for the younger stages. During one day up to 50 aphids could be parasitized and additionally five to ten aphids were killed for host feeding. Glasshouse evaluation showed that in combination with *A. colemani* better and more stable control was obtained than when *A. colemani* was introduced alone (van Steenis, 1995). *Aphelinus varipes* in itself could not control cotton aphid, probably because population growth rates were insufficient.

In this paper life history parameters of *A. varipes* will be described at three constant temperatures. Life history data have been collected for many *Aphelinus* species, but differences in host preference and host suitability among species and lines (e.g., Raney *et al*, 1971; Kuo-Sell & Kreisfeld, 1987; Lajeunesse & Johnson, 1992; Hughes *et al*, 1994) and differences in life history traits among lines of the same species (Haardt & Höller, 1992) make it necessary to collect life history data for this particular parasitoid-host combination as well.

Materials and methods

Insect cultures

Aphis gossypii were collected from cucumber glasshouses in the Netherlands in 1990. At the Glasshouse Crops Research Station the aphids were cultured on cucumber (cvs. 'Sporu' and 'Aramon') under natural light and a minimum temperature of 18 °C.

Aphelinus varipes mummies were collected from *A. gossypii* in cotton fields in Maroua, Cameroon. From october 1992 onwards the parasitoids were reared at the Glasshouse Crops Research Station in small glasshouse compartments under natural light and at a minimum temperature of 18 °C. *Aphis gossypii* was used as the host and cucumber (cvs. 'Sporu' and 'Aramon') as the host plant.

Collection of life history data

Reproduction of adults was determined by offering unparasitized second instar aphids to female parasitoids. The mated parasitoids had an age of maximal 24 hours and had no previous access to aphids. The experiments were performed at 20, 25 and 30 (± 0.5) °C, a relative humidity of 65% and a photoperiod of 16L:8D. At a density of more than 60 aphids the number of aphids parasitized daily remains constant (van Steenis, 1995). Therefore, a surplus amount of 80 aphids was offered to individual females. After 24 hours the parasitoid was introduced into a new petri dish with 80 unparasitized cotton aphids and the number of dead and living aphids was counted. In control experiments, where no parasitoid was introduced ($n=20$) in the petri dish, on average 3.8% of the aphids died during one day. This number was subtracted from the number of dead aphids in the presence of the parasitoid to determine the number of host feedings. After three to four days at 25 °C, 65% RH and 16L:8D, the number of parasitized aphids was determined by dissection of the surviving aphids. At each temperature 21 females were studied.

The immature mortality and the sex ratio of the offspring, were determined by offering second instar cotton aphids to individual females. The females had an age of 24 to 48 hours and had mated. The parasitization process was observed and parasitized aphids were removed. Only parasitizations which took between 40 and 120 seconds were used. After they had been parasitized the aphids were kept in controlled climate cabinets (with a temperature of 20, 25 or 30 (± 0.5) °C, 65% RH and 16L:8D). After three to four days half of the aphids were dissected to determine the parasitization rate. The remaining aphids were kept until emergence of the parasitoids. Records of aphid and parasitoid development were taken daily.

To check for the presence of parthenogenesis ten unmated females were separately kept with 80 second instar cotton aphids for 24 hours at 25 °C, 65%RH and 16L:8D. The mummies were collected from the leaf disks and kept at 25 °C, 65% RH and 16L:8D until emergence.

Data analysis

Some parasitoids escaped before death (1, 3 and 1 at 20, 25 and 30 °C, respectively) and were not used in the analysis. The significance of differences was tested by analysis of variance (ANOVA). If significant differences were detected, multiple comparisons were made using an LSD-procedure ($\alpha=0.05$). Data on development times, adult reproduction and adult longevity were transformed to stabilize variances (Murdie, 1972). For comparison of parasitization and mortality rates X^2-tests were used. Calculation of r_m-values was done according to Birch (1948). Differences in r_m-values were tested for significance by estimating variances through the Jackknife technique (Meyer *et al*, 1986), followed by ANOVA. If significant differences were detected, multiple comparisons were made using an LSD-procedure ($\alpha=0.05$).

Results

The survival of adult females decreased with increasing temperatures (Figure 1). The average longevity differed significantly among the temperatures ($P<0.001$; ANOVA) (Table 1) and ranged from 10.6 days at 20 °C to 2.5 days at 30 °C. The life-time fecundity ranged from 290.5 eggs at 20 °C to 89.5 eggs at 30 °C (Table 1) and was significantly different among the temperatures ($P<0.001$; ANOVA). During the first days fewer aphids were parasitized daily at 20 °C than at 25 and 30 °C ($P<0.05$; LSD after ANOVA) (Figure 1). At 20 °C the daily parasitization remained constant for about ten days, whereas at 25 and 30 °C the daily

parasitization decreased more quickly (Figure 1). The daily number of aphids killed for host feeding at 20 and 25 °C remained constant between approximately five and ten aphids (Figure 1). At 30 °C the number of aphids killed daily was higher ($P<0.05$; LSD after ANOVA) than at the other temperatures (Table 1). Because of the larger longevity at 20 °C females killed more aphids at this temperature than at 25 or 30 °C ($P<0.05$; LSD after ANOVA) (Table 1).

Eighty to 85% of the parasitizations were successful (Table 1). No significant differences in larval or mummy mortality were found among the different temperatures (χ^2-test). The larval mortality was four to nine percent and the mortality during the mummy stage was approximately 15% (Table 1).

The development time of the immature stages shortened significantly with increasing temperatures ($P<0.001$; ANOVA) (Table 1). For females development from egg to mummy took

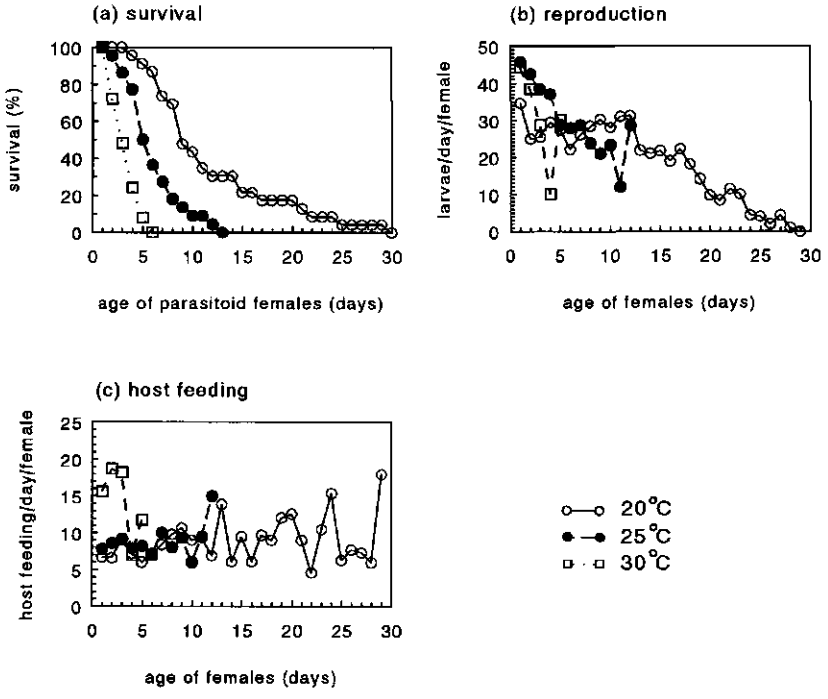

Figure 1
Life history data of adult female *Aphelinus varipes* at three different constant temperatures. (a) survival; (b) daily reproduction; (c) daily number of aphids killed for host feeding.

8.2 days at 20 °C and shortened to approximately 4 days at 30 °C (Table 1). The mummy stage of the females took 12.5 days at 20 °C and 5.6 days at 30 °C (Table 1). Total development of females took 20.7, 12.3 and 10.0 days at 20, 25 and 30 °C, respectively (Table 1). Development of males was slightly faster than the development of females (Table 1), but only at 30 °C a significant difference was present ($P<0.05$; LSD after ANOVA).

The sex ratio of the offspring was 55 to 56% and did not differ among temperatures (χ^2-test). From aphids parasitized by unmated females only male progeny emerged.

The resulting r_m-values were 0.182, 0.293 and 0.327 day^{-1} at temperatures of 20, 25 and 30 °C, respectively (Table 1). The population growth rates were significantly different among the three temperatures ($P<0.001$; ANOVA). Host feeding is not incorporated in the r_m-values and the host kill rate will, therefore, be higher than the population growth rates.

Table 1
Life history data of *Aphelinus varipes* parasitizing second instar nymphs of *Aphis gossypii* at three temperatures. Different letters indicate a significant difference between temperatures ($P<0.05$; LSD after ANOVA; χ^2-test).

		TEMPERATURE		
		20 °C	25 °C	30 °C
LIFE HISTORY OF ADULT FEMALES (AVG. (± S.E.; N))				
longevity (days)		10.6 (± 1.21; 20)[a]	5.8 (± 0.65; 18)[b]	2.5 (± 0.29; 20)[c]
life-time fecundity (eggs)		290.5 (± 41.91; 20)[a]	207.5 (± 21.41; 18)[b]	89.5 (± 12.69; 20)[c]
daily fecundity (eggs)		25.4 (± 1.37; 20)[a]	36.1 (± 1.59; 18)[b]	36.0 (± 2.39; 20)[b]
host feeding (aphids)		93.1 (± 14.32; 20)[a]	49.2 (± 5.87; 18)[b]	45.8 (± 5.65; 20)[b]
daily host feeding (aphids)		8.3 (± 0.51; 20)[a]	8.5 (± 0.62; 18)[a]	17.0 (± 1.80; 20)[b]
IMMATURE DEVELOPMENT				
parasitiz. success (% (n))		80.5 (77)[a]	86.3 (80)[a]	80.8 (78)[a]
larval mort. (% (n))		9.0 (109)[a]	4.1 (84)[a]	9.1 (99)[a]
mummy mort. (% (n))		12.8 (78)[a]	13.0 (69)[a]	15.5 (71)[a]
total imm. mort. (% (n))		37.6 (109)[a]	28.6 (84)[a]	29.4 (99)[a]
devel. time (days (± s.e.; n))				
egg-mummy	♂	8.0 (± 0.09; 30)[a]	4.8 (± 0.09; 27)[b]	4.0 (± 0.10; 27)[c]
	♀	8.2 (± 0.08; 38)[a]	5.2 (± 0.08; 33)[b]	4.3 (± 0.09; 33)[c]
mummy-adult	♂	12.7 (± 0.12; 30)[a]	7.3 (± 0.16; 27)[b]	5.8 (± 0.10; 27)[c]
	♀	12.5 (± 0.10; 38)[a]	7.4 (± 0.15; 33)[b]	5.6 (± 0.11; 33)[c]
total	♂	20.6 (± 0.13; 30)[a]	12.0 (± 0.14; 27)[b]	9.8 (± 0.12; 27)[c]
	♀	20.7 (± 0.12; 38)[a]	12.3 (± 0.12; 33)[b]	10.0 (± 0.10; 33)[c]
sex ratio (% ♀ (n))		55.9 (68)[a]	55.0 (60)[a]	55.0 (60)[a]
INTRINSIC RATE OF INCREASE				
r_m (1/day)		0.182 (± 0.02; 20)[a]	0.293 (± 0.02; 18)[b]	0.327 (± 0.05; 20)[c]

Discussion

The reproduction curves of *A. varipes* were characteristic for *Aphelinus*-species (Force & Messenger, 1964b; Cate *et al*, 1973; Mackauer, 1982; Kuo, 1986). Compared with Aphidiinae the daily oviposition decreased with age slowly. The life-time fecundity decreased with increasing temperatures but daily oviposition increased. The daily reproduction found for *A. varipes* in this study was much higher than for other *Aphelinus*-species. In these species a maximum daily reproduction of approximately 15 to 30 parasitized aphids was found (Force & Messenger, 1964b; Cate *et al*, 1973; Mackauer, 1982; Kuo, 1986). Since the life-time fecundity of *A. varipes* is comparable to data found in other studies we can assume that suitable hosts were used in most cases and that the different parasitization rates are not caused by differences in host aphid species and size of the hosts (Raney *et al*, 1971; Starý, 1988). A second explanation for the high number of aphids parasitized daily by *A. varipes* is that in other studies far less aphids were offered daily to the aphelinid females. This results in lower daily reproduction, but not necessarily in a different life-time fecundity (Mackauer, 1982).

For other *Aphelinus*-species a longevity of 14 to 55 days was found at temperatures between 20 and 25 °C (Schlinger & Hall, 1959; Force & Messenger, 1964a; Raney *et al*, 1971; Cate *et al*, 1973; Kuo, 1986; Lajeunesse & Johnson, 1992). The longevity of *A. varipes* females in this study was considerably shorter, which might also be explained by the higher number of aphids offered and parasitized daily. *Aphidius*-species live shorter in the presence of aphids (Wiąckowski, 1962; Hofsvang & Hågvar, 1975; Pandey *et al*, 1984a, 1984b), possibly because of the increased activity in the presence of hosts (Wiąckowski, 1962). This trade-off between oviposition activity and lifespan does also seem to occur in *A. varipes*. The longevity

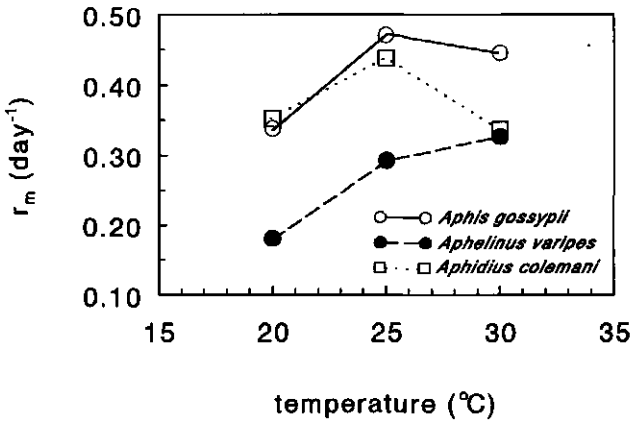

Figure 2
Population growth rates of *Aphis gossypii*, *Aphelinus varipes* and *Aphidius colemani* at three constant temperatures (data for *A. gossypii* and *A. colemani* from van Steenis (1993), van Steenis & El-Khawass (1995) and van Steenis *et al* (unpublished data)).

of *A. varipes* is larger than for *A. colemani* (van Steenis, 1993) and therefor *A. varipes* can be present in higher densities during periods of a low aphid population than *A. colemani*.

The immature mortality was very low, both as larva as during the mummy period. Also for other *Aphelinus*-species mummy mortality was low (<20%) when suitable hosts were used and under normal climatic conditions (Manglitz & Schalk, 1970; Cate *et al*, 1973; Cate *et al*, 1977; Kuo, 1986). Only at 32 °C the immature mortality of *A. semiflavus* (= *A. asychis*) became very large (Force & Messenger, 1964a).

The development time at 20 °C of *A. varipes* is comparable to the development time of *A. asychis* (Kuo, 1986). Compared to *A. mali* and *A.* sp. nr. *varipes* the development of *A. varipes*-larvae was one to three days faster at all temperatures tested (Bonnemaison, 1965; Asante & Danthanarayana, 1992; Lajeunesse & Johnson, 1992). As in most studies males emerged slightly before the females (Raney *et al*, 1971; Asante & Danthanarayana, 1992), although (with the exception of the pre-mummy stage at 30 °C) no significant differences could be detected.

The daily number of aphids killed for host feeding by *A. varipes* was much larger than for other *Aphelinus*-species, where a host-kill rate of 1 to 2 aphids per day is more usual (Cate *et al*, 1973; Hamilton, 1973; Cate *et al*, 1977; Kuo, 1986; Kuo-Sell & Kreisfeld, 1987; Bai & Mackauer, 1990). Nevertheless, the total number of aphids killed for host feeding during a parasitoid's life is similar to the 30 to 140 host feedings which were found for *A. asychis* (Cate *et al*, 1973; Kuo, 1986). Due to the larger longevity at 20 °C the total amount of aphids killed for host feeding is highest, despite the lower daily rate of host feeding.

As for other *Aphelinus*-species (Raney *et al*, 1971; Hamilton, 1973; Starý, 1988) the sex ratio of *A. varipes* was slightly female biased. The sex ratio was independent of the temperature. For *A. asychis* the percentage of males increased with increasing temperatures (Raney *et al*, 1971). Parthenogenetic reproduction as was found for some *A. asychis* (Schlinger & Hall, 1959; Force & Messenger, 1965; Botto, 1980) and *A. abdominalis* strains (Haardt & Höller, 1992) did not occur. The sex ratio found in the laboratory is not necessarily indicative for the sex ratio in glasshouses, because it can depend on the size of the host and the density of the parasitoid population (Cate *et al*, 1977; Lajeunesse & Johnson, 1992).

The intrinsic rate of increase of *A. varipes* populations is comparable to the intrinsic rate of increase of *A. semiflavus* (=*A. asychis*) (Force & Messenger, 1964b). Compared to *A. colemani* (which is used for biological control of *A. gossypii* on a large scale (van Schelt, 1993)) population growth of *A. varipes* is lower at 20 and 25 °C (Figure 2). The host kill rate (parasitization and host feeding) of *A. varipes* will be larger than the population growth rate because several aphids are killed for host feeding daily. At a temperature of 30 °C the population growth rate of *A. colemani* will decrease because of a lower daily reproduction, a longer development time and a higher immature mortality (Guenaoui, 1991; van Steenis *et al*, unpublished data). The population growth rate of *A. varipes* is at these temperatures still very high and even higher than at 25 °C.

The large population growth rate at high temperatures, the large longevity at low temperatures and the direct effect caused by host feeding make that *A. varipes* can be a valuable addition to *A. colemani* during biological control of *A. gossypii*. Direct interference of *A. varipes* with *A. colemani* is likely to be low because *Aphelinus*- and *Aphidius*-species recognize aphids parasitized by the other species (Bai & Mackauer, 1991). Additionally *A. varipes* parasitized young aphids much more easily than older instars (van Steenis, 1995),

whereas *A. colemani* does not show a clear preference for aphids of a certain size (Völkl *et al*, 1990). Because of these different host size preferences, parasitization rates in a glasshouse where both species occur are likely to be higher than parasitization rates by *A. colemani* alone (van Steenis, 1995).

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Chapter 5

Searching behaviour of *Aphidius colemani*

5 Searching behaviour of *Aphidius colemani* Viereck (Hymenoptera: Braconidae)

5.1 In-flight host location by *Aphidius colemani* Viereck (Hymenoptera: Braconidae) searching for *Aphis gossypii* Glover (Homoptera: Aphididae)[1]

Abstract

In-flight host location by *Aphidius colemani* Viereck (Hymenoptera: Braconidae) was studied in a cage, containing two cucumber plants, without a directed air stream. The results indicated a hierarchy of cues used for host location. At first a fixed proportion of the parasitoids responded to the plants, irrespective of the presence of aphids. When only one of the two plants was infested with aphids an effect of host derived stimuli was also present, and most parasitoids landed on the plant with aphids.

Oviposition experiences prior to the experiment increased the response to plants but did not change the response to aphids. Probably the behavioural change is caused by an increased searching activity. No evidence of associative learning was found. Experiences with *Aphis gossypii* Glover and *Rhopalosiphum padi* (Linnaeus) (Homoptera: Aphididae) had the same effect on the searching behaviour. Also rearing the parasitoids for one generation on *R. padi* did not influence the reaction of the parasitoids to cucumber plants or *A. gossypii*. An important implication of these results is that the use of banker plants with *R. padi* as host aphid is unlikely to influence the response of *A. colemani* to *A. gossypii* in a cucumber crop.

Introduction

Aphidius colemani Viereck (Hymenoptera: Braconidae) is used for biological control of *Aphis gossypii* Glover (Homoptera: Aphididae) in glasshouses (van Schelt, 1993; van Steenis, 1995). Out of four aphidiine parasitoids it proved to be the most promising for biological control of cotton aphid (van Steenis, 1995). Still, aphid control is not always successful. Understanding the searching behaviour of the parasitoids might give more insight into the mechanisms by which successful control is obtained.

Parasitoids used for biological control in glasshouses have to search for patchily distributed hosts, and an efficient foraging behaviour is important for their performance as biological control agent (van Lenteren & Woets, 1988). Hosts can be located through cues from the microhabitat and the host plant and through indirect and direct cues from the host (Godfray, 1994).

Olfactometer and wind tunnel experiments have shown that aphid parasitoids can be attracted by volatiles emanated by host plants (Read *et al*, 1970; Schuster & Starks, 1974; Singh & Sinha, 1982; Powell & Zhang Zhi-Li, 1983; Grasswitz & Paine, 1993) or by hosts (Schuster & Starks, 1974; Powell & Zhang Zhi-Li, 1983; Bouchard & Cloutier, 1985). However, considerable differences with respect to the use of cues for host location are present among parasitoid species. Some species only respond to host aphids and not to host plants (Bouchard & Cloutier, 1985), others only respond to host plants and not to host aphids (Read *et al*, 1970), whereas a third group responds to both (Schuster & Starks, 1974; Powell & Zhang Zhi-Li, 1983). These differences can probably be related to differences in the degree of specificity of

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the parasitoid or the aphid host. Parasitoids attacking aphids with a narrow host range can use plant derived stimuli as indicators for the presence of hosts, whereas parasitoids attacking aphids with a broad host range are likely to respond to aphid derived cues (Bouchard & Cloutier, 1985; Vet & Dicke, 1992).

A more reliable aphid control can be obtained by introducing the parasitoids through an open rearing, which consists of cereals with *Rhopalosiphum padi* (Linnaeus) (Homoptera: Aphididae) (Bennison, 1992). Parasitoids emerging from these banker plants are likely to come into contact with *R. padi* before they start searching for *A. gossypii* in the crop. Numerous studies have shown that parasitoid responsiveness to host-associated cues can be modified as a result of experience (Lewis *et al*, 1990). Also for aphid parasitoids experiences can change the searching behaviour through associative learning (Sheehan & Shelton, 1989; Grasswitz & Paine, 1993). Therefore, the influence of previous rearing and experiences on the searching behaviour of *A. colemani* was also studied.

Positive results concerning the reaction to volatile cues in olfactometer studies do not imply longer-range attraction under field conditions (Kennedy, 1965). A major drawback of olfactometer experiments is that parasitoids cannot perform their normal searching behaviour, because the limited size of the experimental arena prevents flight. Secondly, it is questionable whether directed air streams, as used in both olfactometer and wind tunnel experiments, are present in glasshouses. To avoid these drawbacks, in-flight host location of *A. colemani* foraging for *A. gossypii* on cucumber plants was studied in a cage without a directed air stream.

Materials and methods

Insect cultures

Aphis gossypii were collected from cucumber glasshouses in the Netherlands in 1990. At the Glasshouse Crops Research Station the aphids were cultured on cucumber (cvs. 'Sporu' and 'Aramon') under natural light and a minimum temperature of 18 °C.

Aphidius colemani is an endoparasitoid parasitizing many Aphididae species. It originates from the boundary area between the Mediterranean and Central Asia (Starý, 1975). *Aphidius colemani* parasitoids were collected in 1990 from *A. gossypii* in Dutch cucumber glasshouses, where biological control was successful. Thereafter the parasitoids were reared at the Glasshouse Crops Research Station in small glasshouse compartments under natural light and at a minimum temperature of 18 °C. *Aphis gossypii* was used as the host and cucumber (cvs. 'Sporu' and 'Aramon') as the host plant.

Experimental setup

In-flight host location by *A. colemani* was studied in a cage with a width of 70 cm, a height of 60 cm and a depth of 44 cm. In the cage two potted cucumber plants (cv. 'Aramon') (with one full-grown leaf) were placed 35 cm apart. During the observation the temperature was 22 °C (± 2 °C).

The parasitoid mummies were taken from the culture and held individually in tubes until emergence. Parasitoids were only used once. Each female was introduced in a small tube (∅ 7 mm, length 5 cm) which was placed in between the plants. The distance from the tube opening to the cucumber plant was approximately 31 cm.

Two parameters were used in the analysis: (1) time from opening of the tube until flight, and (2) location where the parasitoid landed (plant one, plant two or somewhere in the cage). The

observation was terminated as soon as: (1) the parasitoid landed on a plant or somewhere else in the cage after flight, (2) the parasitoid did not fly but walked out of the tube or (3) the parasitoid did not leave the tube for ten minutes.

Two experiments were carried out: (1) influence of experience of the parasitoids and the level of aphid infestation on in-flight host location and (2) influence of experiences with the alternative host *R. padi* (during one generation or as post-emergence experience) on in-flight host location.

Experiment 1 - Influence of experience and the level of aphid infestation

Three levels of aphid infestation were used: (1) none of the plants contained aphids, (2) one plant contained aphids and (3) both plants contained aphids. Aphid colonies were made on one leaf by placing ten adult aphids on the leaf two days before the experiment. In this way the aphid colonies contained approximately 70 aphids (min.: 46, max.: 122) at the time the plant was used in the experiment. The behaviour of naive and experienced parasitoids was compared. Experienced females had oviposited in five cotton aphids on a cucumber leaf disk and were tested within ten minutes after the experience.

After five observations plant treatment and parasitoid experience was changed. Within a plant treatment the position of the plants was changed regularly, to exclude bias because of their position in the cage.

When both plants received the same treatment 50 observations were made for naive and experienced parasitoids each. When only one plant contained aphids 100 observations were made for naive and experienced parasitoids each.

Experiment 2 - Influence of experiences with an alternative host

In this experiment the effect of different rearing methods and different kinds of experiences were compared. Only one of the two plants in the cage contained aphids. Again the position of the plants was changed regularly.

Two types of parasitoids were used: (1) parasitoids from the *A. gossypii* culture and (2) parasitoids which had been reared on *R. padi* for one generation. *Rhopalosiphum padi* is readily accepted for oviposition by *A. colemani* (Tardieux & Rabasse, 1986). Within each type of parasitoid two types of oviposition experiences were used: (1) five ovipositions on *A. gossypii* on a cucumber leaf disk and (2) five ovipositions on *R. padi* on cereal leaves.

For each combination of culture and oviposition experience 100 observations were made.

Data analysis

Latency times were analyzed by analysis of variance (ANOVA) after a logarithmical transformation of the data to stabilize variances (Murdie, 1972). If a significant difference was found pairwise comparisons were made using an LSD procedure ($\alpha = 0.05$). Rates were analyzed with a X^2-test. All tests were performed at a significance level of 0.05.

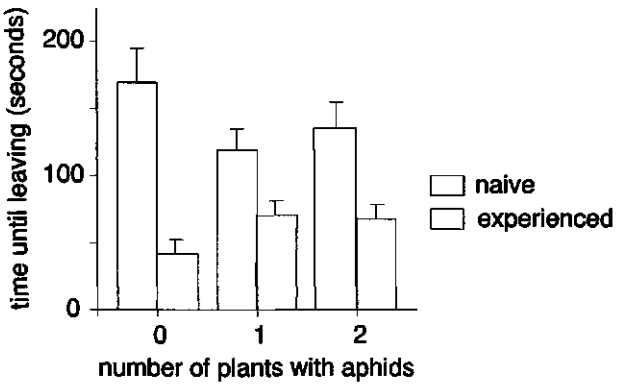

Figure 1
Time until naive and experienced *Aphidius colemani* females leave the tube at different levels of aphid infestation. Experienced females left the tube significantly faster ($P < 0.001$; ANOVA). The number of plants with aphids did not influence the time until leaving ($P = 0.813$; ANOVA).

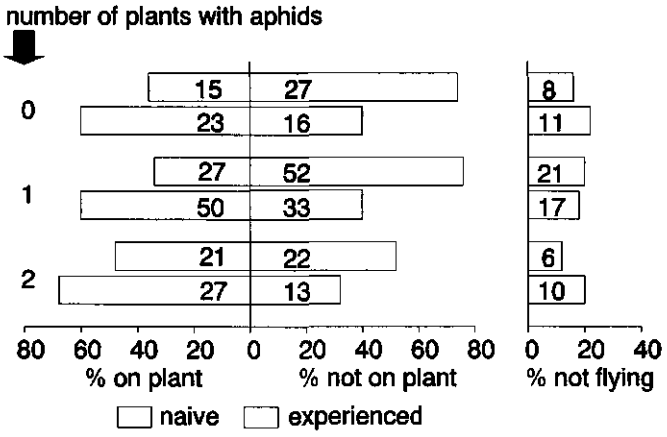

Figure 2
Response of *Aphidius colemani* females to cucumber plants at different levels of aphid infestation. The number of observations is given inside the bars. Experienced females flew significantly more frequently to the plants than naive females ($P < 0.05$; X^2-test). The number of plants with aphids did not influence the response (X^2-test).

Results

Most of the parasitoids (82%) left the release tube flying from the top of the tube. About 14% walked out of the tube directly onto the floor and 4% did not leave within ten minutes. There was no influence of parasitoid experience or plant treatment on these rates (X^2-test). Experienced female parasitoids left the tube more quickly than the naive ones ($P<0.001$; ANOVA) (Figure 1). The average latency time of naive parasitoids was 132.9 (s.e. = 8.9) seconds while it was 64.9 (s.e. = 6.5) seconds for the experienced parasitoids. The number of plants with aphids did not influence the latency time of *A. colemani* ($P=0.813$; ANOVA).

Experienced parasitoids flew significantly more frequently to a plant than naive parasitoids ($P<0.05$; X^2-test) (Figure 2). On average 37.7% of the naive parasitoids flew to a plant, whereas 61.6% of the experienced parasitoids landed on a plant. The number of plants with aphids did not influence the percentage of parasitoids that flew to a plant (X^2-test) (Figure 2).

In the choice situation, most of the parasitoids that flew to a plant landed on the plants with aphids ($P<0.05$; X^2-test), irrespective of the experience (X^2-test) (Figure 3). On average 68.0% of the parasitoids, that landed on a plant, had flown to the aphid infested plant.

Also in the second experiment most of the parasitoids left the release tube flying (77%). About 20% walked away and 3% did not leave the tube within ten minutes. These rates did not differ for the two experiences and the cultures (X^2-test). The latency time of *A. colemani* was not influenced by the type of experience ($P=0.583$; ANOVA) or culture ($P=0.981$; ANOVA) (Figure 4). The average latency time ranged from 55.3 (s.e. = 5.9) to 65.1 (s.e. = 8.0) seconds.

As in the first experiment most of the parasitoids flew to the plants, irrespective of culture and type of experience (X^2-test) (Figure 5).

More parasitoids landed on the infested plants (70.9%) than on the aphid-free plants ($P<0.05$, X^2-test) (Figure 6), irrespective of culture or experience (X^2-test).

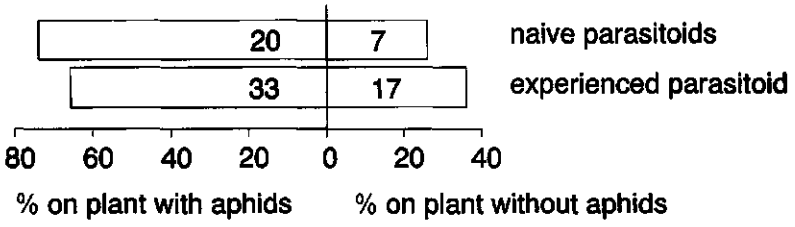

Figure 3
Response of *Aphidius colemani* females to *Aphis gossypii* colonies in a choice situation. The number of observations is given inside the bars. The parasitoids flew significantly more frequently to the plant with aphids ($P<0.05$; X^2-test). Experience did not change the response to aphids (X^2-test).

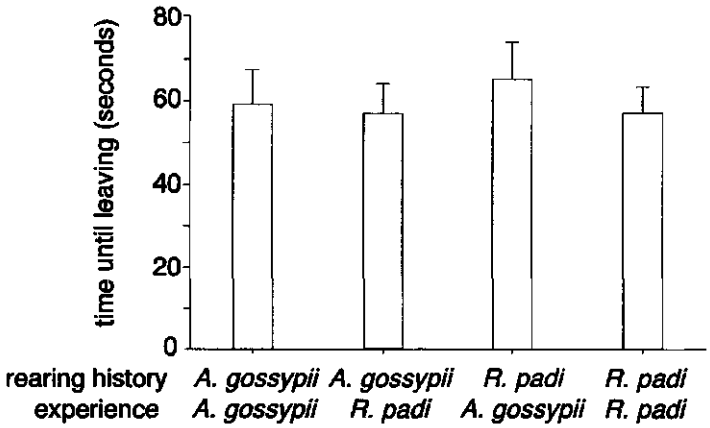

Figure 4
Time until *Aphidius colemani* females with different experiences and rearing histories leave the tube. No influence of experience (P = 0.583; ANOVA) or rearing history (P = 0.981; ANOVA) was present.

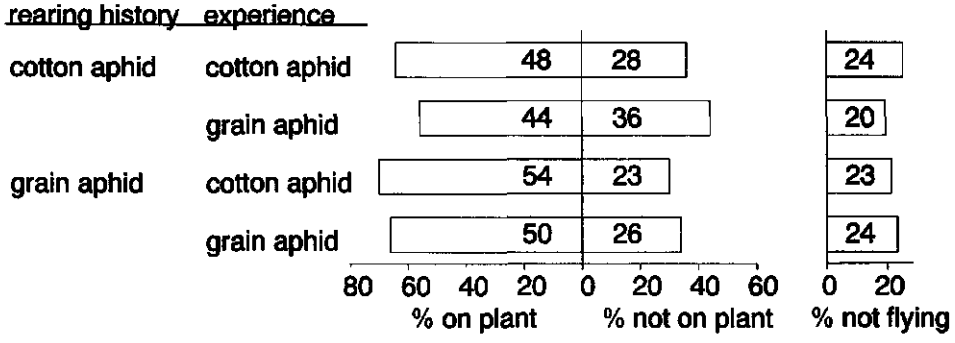

Figure 5
Response of *Aphidius colemani* females with different experiences and rearing histories to cucumber plants. Only one of the plants contained aphids. The number of observations is given inside the bars. No influence of experience or rearing history was present (X^2-test).

Discussion

When no aphids were present on the plants the number of parasitoids flying to the plants did not differ from when both plants contained aphids. Also the time until leaving the tube was independent of the presence of aphids. However, when only one of the two plants contained aphids, most parasitoids flew to the plant with aphids. So, even though the presence of aphids did not influence the response to host plants, the parasitoids did use host-associated cues for host location. Vet & Dicke (1992) argued that the role of stimuli from different trophic levels depends on the degree of specificity of the parasitoid and the host. Thus, the specific parasitoid *Diaeretiella rapae*, which parasitizes *Brevicoryne brassicae* on cruciferous hosts, shows a strong response to host plants and less to host related cues (Read *et al*, 1970), while polyphagous parasitoids parasitizing polyphagous aphids respond more to host associated cues than to host plants alone (Bouchard & Cloutier, 1985; Grasswitz & Paine, 1993; Guerrieri *et al*, 1993). Our results indicate a hierarchy of cues used for host location. At first a fixed proportion of the parasitoids respond to plants, irrespective of the presence of aphids. This response to host plants is much stronger than the response to host-derived stimuli. Only in a choice situation an effect of host-derived stimuli was detected.

Parasitoids, which had oviposited in cotton aphids prior to the experiment, flew to a plant more quickly and more often than naive parasitoids, irrespective of the presence of aphid colonies. When the parasitoid could choose between a clean and an aphid infested leaf previous oviposition experience did not increase the response to aphid colonies. It is not surprising that oviposition experience with different suitable host aphid species had the same effect since aphid

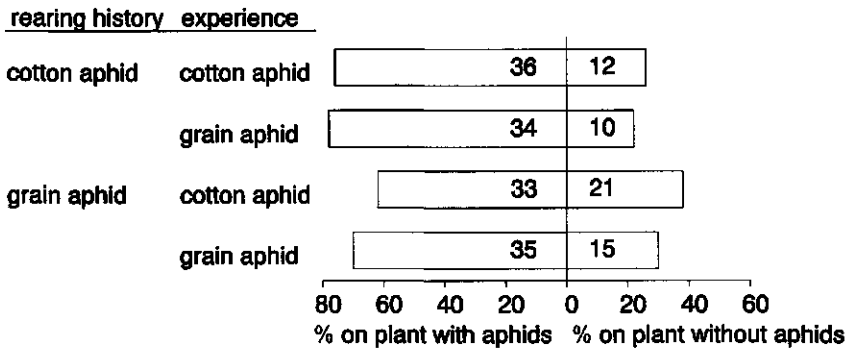

Figure 6
Response of *Aphidius colemani* females with different experiences and rearing histories to *Aphis gossypii* colonies in a choice situation. The number of observations is given inside the bars. No influence of experience or rearing history was present (X^2-test).

parasitoids are likely to be attracted by nonspecific volatiles emanating from aphids and/or their honeydew (Bouchard & Cloutier, 1985). These aphid related volatiles are very reliable indicators of the presence of aphids and are therefore expected not to change much through experience (Lewis *et al*, 1990; Vet *et al*, 1990).

Experience with the plant-host complex increased the response of *L. testaceipes* to aphid infested and uninfested wheat plants and associative learning has been shown (Grasswitz & Paine, 1993). In our experiments the response of *A. colemani* to cucumber plants did not change when the parasitoids had oviposited on *R. padi* on cereal leaves. If associative learning was involved the parasitoids experienced on cereal leaves would have linked reliable aphid related cues to plant related cues (Vet *et al*, 1990; Vet & Dicke, 1992), and the response to cucumber plants should differ from the response of parasitoids experienced on cucumber leaves. It is therefore likely that the behavioural change, which occurred after oviposition in aphids, is mainly caused by a general increase in responsiveness (sensitization) (Godfray, 1994), resulting in an increased activity and "motivation" to continue searching on plants.

These results show that *A. colemani* can use cues from aphid colonies or the host plants to locate their hosts during flight. It is not known whether *A. colemani* uses kairomones produced by the host and its products or by host induced plant synomones (Vet & Dicke, 1992) or maybe by visual stimuli. Oviposition in aphids does not seem to alter responses to aphid colonies but encourages the parasitoid to start searching. When parasitoids are reared and experienced on wheat plants with *R. padi* the reaction to cucumber plants and *A. gossypii* does not differ from parasitoids experienced with *A. gossypii*. It can be concluded that introduction of parasitoids through an open rearing on *R. padi* in the glasshouse does not change their behaviour. Compared to releases of unexperienced adult parasitoids it will even be better to use open rearings in IPM programmes. Parasitoids from an open rearing will always be experienced and will have a higher tendency to start searching for *A. gossypii* in the cucumber crop.

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5.2 Behaviour of *Aphidius colemani* Viereck (Hymenoptera: Braconidae) searching for *Aphis gossypii* Glover (Homoptera: Aphididae): functional response and reaction to previously searched aphid colonies[1]

Abstract

Understanding the searching strategy of *Aphidius colemani* Viereck (Hymenoptera: Braconidae) might give more insight into the mechanisms by which control of *Aphis gossypii* Glover (Homoptera: Aphididae) is obtained in glasshouses and provide information on how to improve biological control of aphids. The functional response of *A. colemani* in petri dishes is described, as well as the effects of reentering a previously visited leaf disk with aphids.

The number of aphids attacked during the first visit followed a sigmoid functional response. The increase of the parasitization rates was clearest at densities of up to 10 aphids per leaf disk.

The duration of the first visit to a leaf disk increased with increasing aphid density. After re-entering a recently visited leaf disk the parasitoid stayed for a much shorter time than the first visit, and the effect of host density on the duration of the visit was not present anymore. No evidence of patch marking was found, so the reduction of visiting times was probably caused by encounters with parasitized hosts.

Introduction

Aphis gossypii Glover (Homoptera: Aphididae) is an important pest in glasshouse cucumber crops, because of its high reproductive capacity on cucumber (van Steenis & El-Khawass, 1995) and its resistance to selective insecticides (Furk & Hines, 1993). *Aphis gossypii* can only be controlled with broad-spectrum insecticides which inhibit the use of biological control methods for other pests. Therefore, successful biological control of *A. gossypii* is a prerequisite for implementation of IPM programmes. Several aphid parasitoid species (Hymenoptera: Braconidae: Aphidiinae) have been tested for their usefulness as biological control agent. Based on population growth rates, searching capacity and host preferences, *A. colemani* proved to be the most promising (van Steenis, 1995). *Aphidius colemani* is a solitary endoparasitoid, which parasitizes many aphid species belonging to the Aphididae (Starý, 1975). It originates from the boundary area between the Mediterranean and Central Asia (Starý, 1975).

Functional responses are usually divided into three types (Holling, 1959): (1) type I, with a linear rise of the number of hosts attacked with increasing host density until a maximum is reached, (2) type II, with a decreasing parasitization rate towards a maximum as host density increases and (3) type III, which shows a sigmoid response towards a maximum parasitization rate as host density increases. If host exploitation is included in Holling's type II functional

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response the functional response can be described by the 'random parasite equation' (Rogers, 1972):

$$N_a = N * \left(1 - e^{\left(-\frac{a' * T}{1 + a' * T_h * N}\right)}\right) \quad [1]$$

in which N_a is the number of hosts parasitized, N the number of hosts available, T the period during which aphids and parasitoid are exposed to each other (seconds), a' the intrinsic rate of attack and T_h the handling time. T_h and a' are estimated by linear regression of 1/ln(proportion of hosts surviving) against host density.

The type III sigmoid response can be described by fitting a logistic function. We chose the following equation:

$$N_a = a + \frac{c}{1 + e^{-b*(N-m)}} \quad [2]$$

in which N_a is the number of hosts parasitized, N the number of hosts available. a, b, c and m are parameters of the function, where a+c is the maximum number of aphids that can be parasitized at a given searching time and m is the point of inflection.

A type III functional response, with increasing parasitization rates as host density increases, can be a regulating factor in the population dynamics of the pest and the natural enemy (Holling, 1959). Therefore, for many aphid parasitoid species functional responses have already been determined (Hågvar & Hofsvang, 1991). In general a type II response was found when the duration of exposure of the parasitoid to aphids is large compared to the number of aphids available. Under these circumstances the parasitization rates at lower densities will be overestimated because of repeated visits to the leaf with hosts (van Lenteren & Bakker, 1976, 1978; Hassell *et al*, 1977), and the sigmoid functional response will be obscured. The functional response in a field situation is therefore probably described best by the number of attacks during the first visit. Occasionally a type III response was found in petri dishes with short exposure times (Pandey *et al*, 1982, 1984), or with longer exposure times on a larger area (Bhatt & Singh, 1991; Hughes *et al*, 1992). However, even in a more realistic experimental set-up, in which large plants had to be searched for aphids, only one out of seven aphidiine parasitoids showed a type III functional response (Hughes *et al*, 1992). In this paper on the searching behaviour of *A. colemani* the functional response in petri dishes will be described.

Many studies have shown that aphid parasitoids can discriminate between parasitized and unparasitized aphids (see Hågvar & Hofsvang (1991) for a review). In glasshouses many aphid colonies will contain parasitized aphids because the colonies were visited by parasitoids before. Visit times to these aphid colonies may be significantly reduced through patch marking or a reaction to encounters with parasitized hosts (Godfray, 1994). For these reasons, also the effect of re-entering a previously visited leaf disk with aphids on the searching behaviour was studied.

Materials and Methods

Aphid and parasitoid cultures

Aphis gossypii were collected from cucumber glasshouses in the Netherlands in 1990. At the Glasshouse Crops Research Station the aphids were cultured on cucumber (cvs. 'Sporu' and 'Aramon') under natural light and a minimum temperature of 18 °C.

The parasitoids used in these experiments were collected in 1989 by Koppert BV from *A. gossypii* in Dutch cucumber glasshouses, where biological control was successful. From 1990 onwards the parasitoids were reared at the Glasshouse Crops Research Station in small glasshouse compartments under natural light and at a minimum temperature of 18 °C. *Aphis gossypii* was used as the host and cucumber (cvs. 'Sporu' and 'Aramon') as the host plant.

Experimental setup

Second instar cotton aphids were collected from cucumber plants and put on a piece of cucumber leaf (ϕ 3.5 cm) in different numbers (0, 1, 2, 4, 6, 8, 10, 25, 50 and 100). The leaf disk was put at the edge of a large petri dish (ϕ 14 cm). One mated female parasitoid was introduced at the other side of the large petri dish. The parasitoids were between 4 and 24 hours old and did not have any oviposition experience prior to the experiment. The behaviour of the parasitoid was observed until 30 minutes after the parasitoid had arrived on the leaf disk. At each host density ten observations were made. The following parameters were recorded: (1) leaf arrival time, (2) duration of each leaf visit, (3) number of antennal encounters with hosts per leaf visit and (4) number of attacked hosts per leaf visit. During the observation the temperature was 20 °C (± 2 °C).

Data analysis

To stabilize variances, numbers were transformed to their square root value, times were transformed to their logarithmic values and ratios were transformed to $\sqrt{}$arcsin-values (Murdie, 1972). Transformed data were analyzed with analysis of variance at a significance level of 0.05. If significant differences were found, multiple comparisons were made using an LSD procedure ($\alpha = 0.05$). If possible, correlations were analyzed by linear regression analysis, otherwise nonlinear regression analysis was used (Genstat 5 release 2.2) (Payne *et al*, 1987)..

Results

Leaf arrival times decreased with increasing aphid densities on the leaf disk ($P = 0.006$; Anova) (Figure 1), although no significant linear, exponential or logarithmic regression equation could be fitted through the data. At the higher densities (>10 aphids) leaf arrival times were very short, but at lower aphid densities a large variation was observed.

The duration of the first leaf visit increased with increasing aphid density and could be described by a logarithmic equation ($F_{1,7} = 30.24$; $r = 0.886$; $P < 0.001$) (Figure 2). The first visit to a leaf disk without aphids was not included in the equation, because these visits were very short (22.6 sec; s.e. = 5.73; n = 10), and had a great effect on the regression line. At low aphid densities the aphids were not always discovered during the first visit. In this case visit times were very short (63.9 sec; s.e. = 8.36; n = 130), but still significantly longer than when no aphids were present ($P < 0.001$; Anova).

Since the parasitoid was not able to leave the large petri dish, several visits to the leaf disk were made during the experimental period, though the exposure period was short. At low aphid

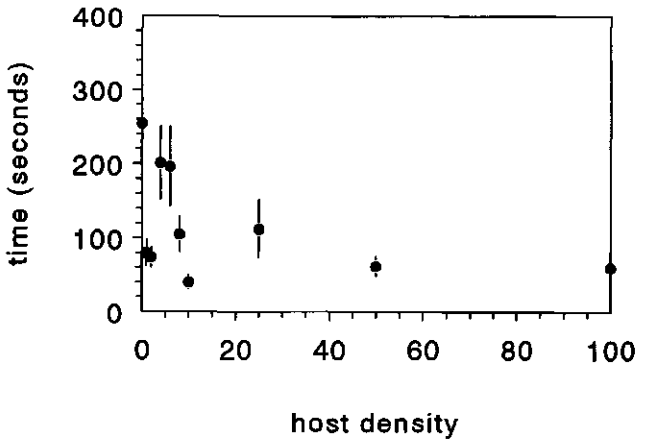

Figure 1
The influence of aphid density on the leaf arrival time (seconds) of *Aphidius colemani*. The standard errors are given by the vertical bars.

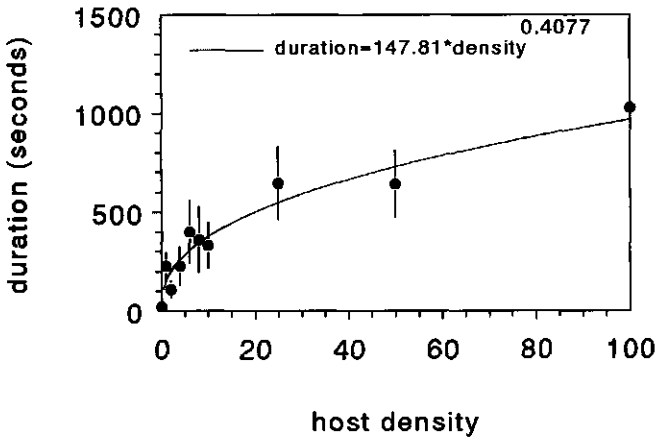

Figure 2
The duration of the first leaf visit (seconds), as a function of aphid density. The standard errors are given by the vertical bars. The solid line is the logarithmic equation that was fitted through the data ($F_{1,7}=30.24$; $r=0.886$; $P<0.001$).

densities the leaf disk was visited more times than at high aphid densities. The number of attacks during the first visit is given in Figure 3. It is assumed here that each attack resulted in deposition of an egg, and that none of the aphids was attacked more than once. The Random Parasite Equation could not be fitted through the data successfully ($F_{2,6}=0.04$; $P=0.85$). Fitting the logistic function gave good results ($F_{3,5}=416.12$; $r=0.997$; $P<0.001$), with $a=-37.7$, $b=0.0342$, $c=93.2$ and $m=11.9$ (Figure 3). At high aphid densities the maximum number of hosts that could be attacked during the first visit was 55.5. Since approximately 80% of the attacks will be successful (van Tol & van Steenis, 1994), the maximum number of parasitized aphids was 45.5. At low aphid densities there was an increase in the percentage of parasitized aphids (Figure 3b), which also shows that the functional response is of type III. According to the functional response equation the point of inflection was at 11.9 aphids.

The second successful visit (the second visit in which aphids were encountered) was much shorter than the first successful visit ($P<0.001$; Anova) and the influence of host density on the duration of the visit could no longer be observed ($P=0.14$; Anova) (Figure 4). When no aphids were present the duration of second successful visit did not decrease ($P=0.80$; Anova).

The number of encounters per minute was not significantly different between successive leaf visits ($P=0.14$; Anova), but clearly increased with increasing aphid density ($P<0.001$; Anova) (Figure 5). Though the rate of encounter did not differ between the first and the second successful visit, the number of attacked aphids will be lower in the second successful visit, because the attack rate (attacks/encounter) during the second visit was lower than during the first visit ($P<0.001$; Anova) (Figure 6) and because of the shorter duration of the second visit (Figure 4). The attack rate did not differ among different aphid densities ($P=0.16$; Anova) (Figure 6).

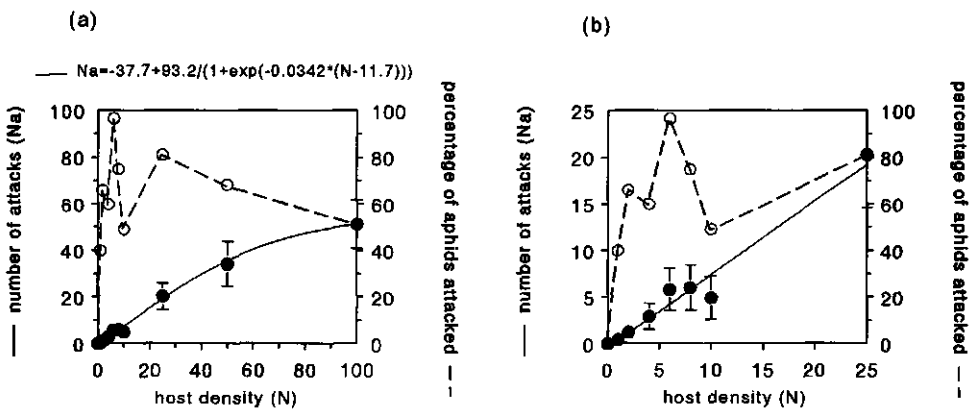

Figure 3
Functional response of the attacks during the first leaf visit and the sigmoid functional response that was fitted through the data ($F_{3,5}=416.12$; $r=0.997$; $P<0.001$). (a) total functional response, (b) functional response at low aphid densities.

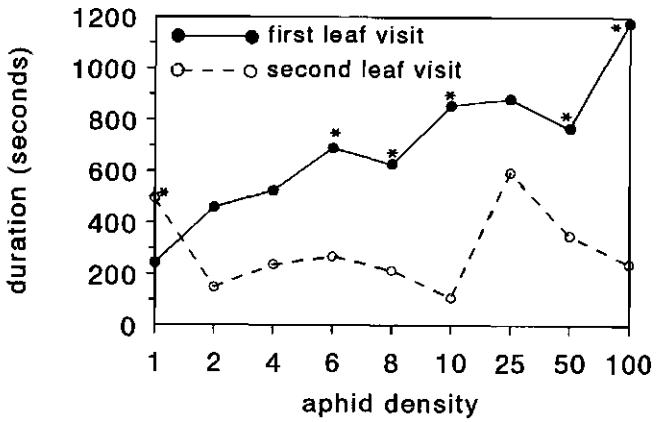

Figure 4
The duration of the first and the second leaf visit (in seconds) in which aphids were encountered at different aphid densities. Significant differences between the first and second visit at a particular density are given by an asterisk ($P<0.05$; LSD after Anova). Overall the second leaf visit was significantly shorter ($P<0.001$; Anova).

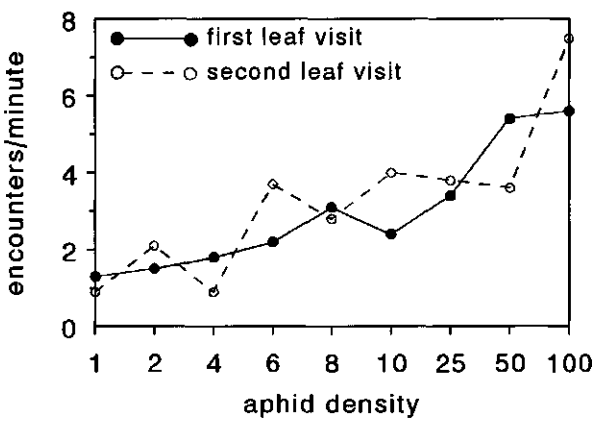

Figure 5
The number of aphids encountered per minute during the first and the second leaf visit in which aphids were encountered at different aphid densities. No significant differences between the first and the second leaf visit could be detected ($P=0.14$; Anova).

Discussion

At densities above ten aphids, leaf arrival times were always short. Below this density leaf arrival times were longer but there was a large variation. In a similar setup Pandey *et al* (1982) (using *Trioxys indicus*) and Pandey *et al* (1984) (using *Diaeretiella rapae*) got comparable results. Only at higher densities of aphids (more than 20) leaf arrival times were significantly lower. From this setup it is not clear whether the shorter leaf arrival time is due to a directed search after the aphids have been detected (Powell & Zhang Zhi-Li,1983; Bouchard & Cloutier, 1985) or by a general increase in activity because of the nearby presence of aphids.

The duration of the first visit to the leaf disk increased with increasing host density. A similar increase was found for many other aphid parasitoids (e.g., 't Hart *et al*, 1978; Pandey *et al*, 1982; Pandey *et al*, 1984), and can be due to contacts with hosts (van Roermund *et al*, 1994; van Steenis *et al*, unpublished), arrestment by honeydew (Bouchard & Cloutier, 1984; Gardner & Dixon, 1985; Budenberg, 1990), or detection of aphid kairomones (Powell & Zhang Zhi-Li, 1983; Bouchard & Cloutier, 1985; Singh & Srivastava, 1989). Arrestment by honeydew or detection of aphid kairomones would also explain why visits to a leaf disk without aphids were shorter than visits to a leaf disk with aphids, but without an encounter with an aphid.

When a parasitoid returned to a patch with parasitized aphids, the duration of the visit was short and did not differ between the densities anymore. Also for other parasitoids like *Nemeritis canescens* and *Leptopilina heterotoma* return visits were much shorter and did not differ in length between different host densities (van Lenteren & Bakker, 1978; Waage, 1979). Patch marking can influence the duration of return visits and has been recorded for several parasitoid

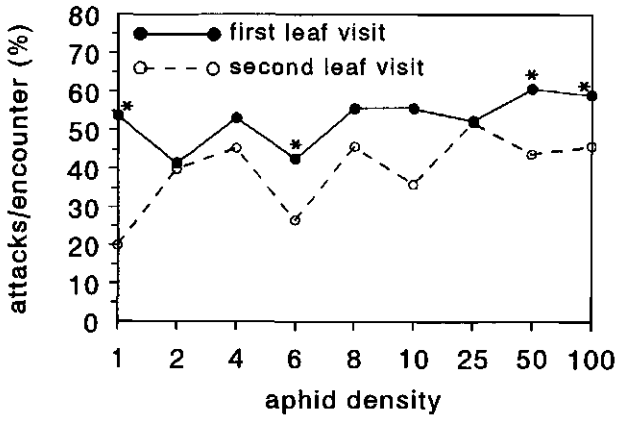

Figure 6
The attack rate of the parasitoids (percentage of encounters resulting in an attack) during the first and the second leaf visit (in seconds) in which aphids were encountered at different aphid densities. Significant differences between the first and the second leaf visit at a particular aphid density are given by an asterisk ($P<0.05$; LSD after Anova). During the second leaf visit the attack rate was significantly lower than during the first visit ($P<0.001$; Anova).

species (Greany & Oatman, 1972; Galis & van Alphen, 1981; van Lenteren, 1981; Sheehan *et al*, 1993). For *A. colemani* no evidence of patch marking was found since the duration of successive visits to a clean leaf disk did not decrease. During the second visit a larger proportion of the aphids encountered was rejected, but the number of encounters per minute was not influenced. Because at the second visit part of the aphids will be parasitized when the parasitoids enter the leaf disk, the increase of the rate of rejection is likely to be caused by an increased number of encounters with parasitized aphids. This indicates that *A. colemani* is able to discriminate between parasitized and unparasitized aphids, as was also found for some other aphid parasitoids ('t Hart *et al*, 1978; Chow & Mackauer, 1984; Chow & Mackauer, 1986; Hofsvang, 1988). The increase of encounters with parasitized hosts probably has shortened the visit times on previously visited host patches as was also found for *L. heterotoma* (van Lenteren, 1991). Also a stronger defence reaction by recently parasitized aphids can prevent successful attack and reduce visit times (Gardner *et al*, 1984).

The number of attacks during the first visit showed that parasitization rates at low aphid densities increased with aphid density. The increase of the parasitization rates was most clear at densities of up to ten aphids per leaf disk. This logistic type of functional response can theoretically be a regulating factor in the population dynamics (Holling, 1959). However, the point of inflection is at very low aphid densities (11.9 aphids/leaf disk), as was also found for other aphid-parasitoid combinations (Pandey *et al*, 1982; Pandey *et al*, 1984; Hughes *et al*, 1992). At higher aphid densities a strong numerical response is present through aggregation at places with high aphid densities (Hågvar & Hofsvang, 1987). As a consequence aphid colonies will be visited repeatedly and parasitization rates at these places can become much higher than during one visit. The combination of a sigmoid functional response at low aphid densities and a strong numerical response at higher aphid densities might account for the successes obtained with biological control of aphids with *A. colemani*.

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5.3 Time allocation of the parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae) foraging for *Aphis gossypii* Glover (Homoptera: Aphididae) on cucumber leaves[1]

Abstract

The time allocation of individual *Aphidius colemani* Viereck (Hymenoptera: Braconidae) female parasitoids foraging for *Aphis gossypii* Glover (Homoptera: Aphididae) nymphs on cucumber leaves has been investigated. Apart from experiences on the current leaf (such as density of hosts on the current leaf, density of hosts on a neighbouring leaf and encounters with hosts on the current leaf), the effect of previous leaf visits on the time allocation was studied. Behavioural records were analyzed by means of the proportional hazards model, to determine the tendency of leaving the current leaf.

The leaving tendency only decreased on leaves with a high host density (100 aphids), thus increasing the giving up time since the latest encounter. Rejection of aphids had no influence on the leaving tendency. To assess the effect of the number of hosts encountered on the leaving tendency, we considered three different classes: 0-30 encounters, 31-100 encounters and more than 100 encounters with hosts. The effect of the number of hosts encountered differed at different aphid densities. When less than ten aphids were present the leaving tendency was much larger after 30 encounters than beforehand. At a density of 100 aphids the leaving tendency was lower than at the other aphid densities and increased only after 100 encounters. The density of hosts on a neighbouring leaf, ranging from 0 to 100 hosts, had a negligible effect on the leaving tendency.

Repeated visits to leaves with ten unparasitized aphids resulted in an increase in the leaving tendency after ten visits. It is argued that the parasitoids have some innate expectancy of host availability and that they concentrate on high density patches.

Introduction

Parasitoids used in programmes for biological control of aphids often have to search for hosts in an environment where host patches are scarce and highly clustered. The rate at which host are parasitized is an important factor for the number of offspring realized per parasitoid (i.e. fitness) and its success as a biological control agent. Patch time allocation determines the parasitization rates in an environment with patchily distributed hosts to a large extent.

Charnov (1976) showed that an efficient forager stays in a given patch until the capture rate falls below the average capture rate in the environment. Theory predicts that if other suitable hosts are nearby and the parasitoid can sense their presence, the residence time on the colony where the parasitoid is searching should be shorter than when no other aphid colonies are available (Stephens and Krebs, 1986). Some aphid parasitoid species respond to volatiles emanated by aphid colonies (Powell and Zhang Zhi-Li, 1983; Bouchard and Cloutier, 1985), and they might use this information. Additionally, some knowledge of the availability and distribution of hosts in the environment facilitates patch time allocation for the parasitoids (Stephens and Krebs, 1986). If experiences in patches previously visited help parasitoids to determine overall host availability, repeated visits to low density patches will have a different impact on patch

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time allocation than repeated visits to high density patches.

From other studies it is known that aphidiine parasitoids can distinguish between unparasitized and parasitized hosts avoiding parasitism of the latter (Hågvar and Hofsvang, 1991). Encounters with parasitized hosts can change a parasitoids' foraging behaviour (van Steenis, 1995). Among others, patch leaving rules were studied for *Asobara tabida* parasitizing *Drosophila melanogaster* larvae (van Alphen and Galis, 1983), *Leptopilina heterotoma* and *L. clavipes* parasitizing *Drosophila* larvae (Haccou *et al*, 1991; van Lenteren, 1991; Hemerik *et al*, 1993) and for *Encarsia formosa* parasitizing whitefly larvae (van Roermund *et al*, 1994). Oviposition in an unparasitized host did increase the giving up time in all these studies. For *A. tabida*, *E. formosa*, and *L. heterotoma* encounters with parasitized hosts had no effect on the giving up time (van Alphen and Galis, 1983; Haccou *et al*, 1991; van Roermund *et al*, 1994). However, in patches with a large number of parasitized hosts, the residence times of *L. heterotoma* were much shorter than on patches with unparasitized hosts (van Lenteren, 1991). When *L. clavipes* encountered a parasitized host as the first host in its life time the leaving tendency increased. If it encountered a healthy host first no effect on the leaving tendency was found (Hemerik *et al*, 1993).

We studied patch leaving decisions in *Aphidius colemani* Viereck (Hymenoptera: Braconidae). *A. colemani* is used for biological control of the cotton aphid, *Aphis gossypii* Glover, and the green peach aphid, *Myzus persicae* Sulzer (Homoptera: Aphididae), in glasshouse vegetables in the Netherlands, and in the UK (van Schelt *et al*, 1990; Bennison & Corless, 1993). The effects of (a) host density, (b) encounters with parasitized and unparasitized hosts, (c) the presence of differently sized aphid colonies close to the colony on which the parasitoid was introduced and (d) repeated visits to leaves with 10 or 100 aphids, on patch time allocation were investigated.

Data were analyzed with the proportional hazards model (Cox, 1972; Kalbfleisch and Prentice, 1980) (see materials and methods for a detailed explanation). Once a parasitoid enters an aphid colony a basic leaving tendency is set, which can be changed by intra- and interpatch experiences. The model makes no assumptions about the statistical distribution of leaving tendencies in time and censored data are handled accurately. A censored observation of the giving up time since the latest encounter occurs when the parasitoid encounters a host: it is not known when the parasitoid would have left the leaf if no host had been encountered (Hemerik *et al*, 1993).

Material and methods

Insect cultures

Aphis gossypii were collected from cucumber glasshouses in the Netherlands in 1990. At the Glasshouse Crops Research Station the aphids were cultured on cucumber (cvs. 'Sporu' and 'Aramon') under natural light and a minimum temperature of 18 °C.

Aphidius colemani is an endoparasitoid parasitizing many Aphididae species. It originates from the transition area between the Mediterranean and Central Asia (Starý, 1975). *Aphidius colemani* parasitoids were collected in 1989 from *A. gossypii* in Dutch cucumber glasshouses, where biological control was successful. From 1990 onwards the parasitoids were reared at the Glasshouse Crops Research Station in small glasshouse compartments under natural light and at a minimum temperature of 18 °C. *Aphis gossypii* was used as the host and cucumber (cvs. 'Sporu' and 'Aramon') as the host plant.

Experimental methods

Observations were carried out in a laboratory at a temperature of 20 ± 1 °C and 65 ± 5% RH on leaves of a potted cucumber plant (cv. 'Sporu'). At the start of each observation one mated *A. colemani* female was introduced to the lower side of the second leaf from ground level. On this leaf cotton aphids were present in different densities. The aphids were put on the lower side of the leaf two hours before the parasitoid was introduced. The parasitoids had no previous oviposition experience. Their age was four to 24 hours.

Continuous observation started immediately after the introduction of the parasitoid. During the visit, antennal encounters without attack (rejection) and antennal encounters followed by an attack (acceptance) were recorded. When the parasitoid walked on the stem of the plant or flew away to another part of the plant or the cage wall, the observation ended.

Two types of experiments were conducted. In experiment 1 a parasitoid was observed during one leaf visit and in experiment 2 a parasitoid was allowed to forage for eight hours on a varying number of leaves. All of the leaves visited during this period contained the same initial number of unparasitized hosts.

Experiment 1

Experiment 1 was conducted to study the effect of the following factors on the patch time allocation: (a) host density on the introduction leaf, (b) the number of encounters with hosts on the current leaf (attacks and rejections) and (c) the density of hosts on a nearby alternative leaf.

The leaf of introduction (leaf two from ground level) contained 0, 1, 10 or 100 second instar *A. gossypii*. On another leaf of the plant (leaf three, which is opposite to leaf two) one of the following aphid densities were used: 0, 10 and 100 second instar *A. gossypii*. For each combination ten observations were made.

Experiment 2

Experiment 2 was conducted to assess the effect of the following factors on the patch time allocation: (a) the number of leaves visited before the current one and (b) the number of encounters with hosts on the current leaf (attacks and rejections). Either 10 (2a) or 100 (2b) second instar *A. gossypii* were used. Every time the parasitoid left the leaf, it was introduced to another cucumber leaf with the same initial density of unparasitized aphids. This procedure was continued for eight hours. For each host density five observations of eight hours were obtained.

Description of the model

The proportional hazards model

The model is formulated in terms of the hazard rate, i.e. the probability per unit time that a certain event occurs since the latest renewal point, given that it has not occurred yet. The hazard rate can be considered as a tendency to perform a certain behaviour. In the present study leaving the leaf is the event, a so-called failure, under study. Renewal points occur at times of encounters with hosts, because these interrupt the foraging process of the parasitoid. It is assumed that parasitoids have a basic tendency to leave the leaf (base line hazard), which is reset after the renewal points. The observed hazard rate is assumed to be the product of the base line hazard and a factor that gives the joint effect of a set of p covariates $z_1,\ldots,z_p$. The covariates are, for instance, binary variables which code for the density of hosts in a patch. They are called fixed since they do not change between two renewal points. The general form

of the model with fixed covariates is:

$$h(t;z) = h_0(t)\ \exp\{\sum_{i=1}^{p} \beta_i\ z_i\} \qquad [1]$$

where $h(t;z)$ denotes the observed hazard rate, $h_0(t)$ the base line hazard, t the time since the latest renewal point and $\beta_1,\ldots,\beta_p$ the relative contributions of the fixed covariates $z_1,\ldots,z_p$. The form of the base line hazard in time is left unspecified; $h_0(t)$ as well as $\beta_1,\ldots,\beta_p$ are estimated simultaneously from the data by means of likelihood maximization (Haccou and Hemerik, 1985; Kalbfleisch and Prentice, 1980 for further details). The survivor function corresponding with the hazard rate given in eqn. [1] is

$$F(t;z) = \exp\left[-\int_0^t h(u;z)\mathrm{d}u\right] \qquad [2]$$

The name 'proportional hazards model' stems from the assumption that for different values of z_i the hazard rates $h(t;z)$ are proportional (see Haccou and Hemerik, 1985). For a graphical test of this assumption we need to introduce $F_{0k}(t)$ as

$$F_{0k}(t) = \exp\left[-\int_0^t h_0(u)\exp\{\sum_{i=0,\,i\neq k}^{p} \beta_i z_i\}\mathrm{d}u\right] \qquad [3]$$

If the proportionality assumption is justified for a certain binary covariate, z_k, the graphical test consists of plotting the value of $\log(-\log F_{0k}(t))$ against time for each value (0 or 1) of the k-th covariate separately (Kalbfleisch and Prentice, 1980). If the plotted curves run more or less parallel the proportionality assumption is justified.

Moreover, to visualize the effect of one factor the hazard rate is estimated for each different value of this factor separately. First, all covariates coding for this factor are eliminated from eqn. [1] and second the total sample is divided into subgroups according to the values of this factor. For each different subgroup the base line hazard rate is estimated. The resulting base line hazards are plotted together in one figure (see Kalbfleisch and Prentice 1980; Haccou and Hemerik, 1985). For example, in experiment 1 the factor density on the current leaf is coded by three binary covariates (z_1, z_2, z_3). Thus for density 0 holds: $(z_1, z_2, z_3) = (0,0,0)$, density 1: $(z_1, z_2, z_3) = (1,0,0)$, density 10: $(z_1, z_2, z_3) = (0,1,0)$ and density 100: $(z_1, z_2, z_3) = (0,0,1)$. For this case the estimated base line hazard rates are given in Figure 2.

The effect of covariates is given by a multiplication factor $\exp(\beta)$ for each stratum. If the $\exp(\beta)$ is below 1 the leaving tendency is reduced, above 1 the leaving tendency is increased. If the assumption on proportionality of hazard rates is valid and the correlation between covariates is low, the effects of covariates can be multiplied to find the combined effect.

The procedure to test the significance of the estimated effects $\beta_1,\ldots,\beta_p$ is explained in Hemerik *et al* (1993). The test statistic T is distributed as a χ^2 with p degrees of freedom (Kalbfleisch and Prentice, 1980).

Experiment 1

The data used in the regression model were the observed time periods from being placed on

the leaf until the first encounter, between successive encounters and from the last encounter until leaving the leaf. It should be noted that handling times were not included in the time periods which were analyzed. When no encounters occurred, the residence time was used. When studying the leaving tendency of a parasitoid, the encounter with a host causes a censored observation.

The tendency to leave the leaf in experiment 1 is given by equation (1) with seven fixed covariates: (a) the density of hosts on the current leaf is coded by three binary covariates (see above), (b) the number of encounters with hosts on the current leaf (attacks and rejections) is coded by two binary covariates representing three different classes and (c) the density of hosts on the alternative leaf is also coded by two binary covariates representing 0, 10 or 100 aphids. The base line hazard is estimated from the observations on leaves without aphids.

Experiment 2

In experiment 2b the effect of the following fixed covariates on the leaving tendency were estimated: (a) the number of encounters with hosts on the current leaf is coded by two binary covariates (see experiment 1) and (b) the number of leaves visited before the current one is coded by one covariate representing two classes. In experiment 2a the number of encounters on one leaf always was less than 100. Thus, only two classes were distinguished and coded by one binary covariate. For each density the base line hazard is estimated from the observations on the first leaf.

Results

The initial leaving tendency (base line hazard) and median giving up times since the latest encounter in experiment 1, 2a and 2b are given in Table 1. The combined effect of all covariates together was significant in experiment 1 and in experiment 2a.

Experiment 1

The base line hazard was approximately a straight line. Thus, the leaving tendency remained approximately constant over time ($1.096\ 10^{-3}\ s^{-1}$, Table 1). The corresponding median giving up time was 10.5 minutes. In a preliminary analysis attacks and rejections were analysed as separate factors, but the parasitoids reacted in a similar way to rejections and ovipositions. Therefore, the number of experienced encounters (attacks + rejections) was analysed. Graphical inspection of the hazard rates for different values of the number of encounters showed that encounters with hosts influenced the leaving tendency in a rather capricious way. For clarity three classes were distinguished: 0-30 encounters, 31-100 encounters and 100 or more encounters. The effect of encounters on the leaving tendency is given in Figure 1. Log minus log plots (see descripton of the model) showed that the assumption of proportionality was justified.

At a density of 100 aphids the leaving tendency was significantly lower than at low aphid densities (0, 1 or 10 aphids per leaf), thus increasing the giving up time since the latest encounter (Table 2). Among leaves with 0, 1 or 10 aphids no difference in leaving tendency was found (Figure 2).

Table 1
Estimated initial leaving tendency (base line hazard), median giving up times (GUT) since the latest encounter and the value of the test statistic T (degrees of freedom) for the combined effect of all covariates on the leaving tendency in experiment 1 and 2.

	Base line hazard (sec^{-1})	Median giving up time (minutes)	T (df)
Experiment 1	$1.096*10^{-3}$	10.5	20.56 (7) *
Experiment 2a (density 10)	$0.842*10^{-3}$	13.7	12.98 (2) *
Experiment 2b (density 100)	$0.157*10^{-3}$	74.1	5.05 (3)

*: $P < 0.05$

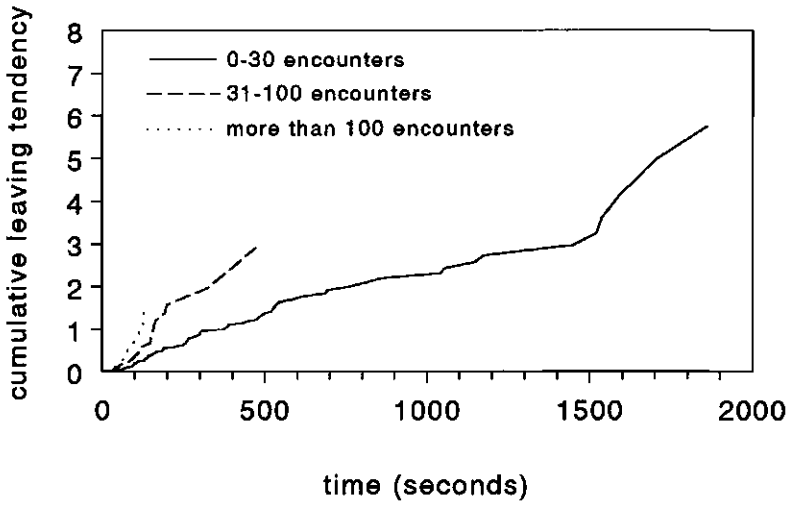

Figure 1
Cumulative leaving tendency (hazard rate in sec^{-1}) of *Aphidius colemani* in experiment 1 for 0-30 (base line hazard), 31-100 and more than 100 encounters with aphids.

The combined effect of aphid density at the current leaf and the number of hosts encountered can be found by multiplying the individual effects. From Table 2 it is clear that at a density of 1 or 10 aphids the leaving tendency after 30 encounters was very high and much higher than when no aphids were present (approximately 4.7 = 0.97 * 4.88 times the base line hazard). At the same number of encounters on a leaf with 100 aphids the leaving tendency was lower than the base line hazard (0.63 = 0.13 * 4.88). Only if more than 100 aphids were encountered the leaving tendency was higher than the base line hazard (1.24 = 0.13 * 9.53).

The presence and size of a second aphid colony had no influence on the leaving tendency of the foraging parasitoids (Table 2).

Table 2
Estimated effects (exp (β)) of covariates on the leaving tendency in experiment 1 and the value of the test statistic T. If exp (β) < 1 then the leaving tendency is reduced, if exp (β) > 1 the leaving tendency is increased. For further explanation see the materials and methods section.

	effect	T (df)
Aphid density on current leaf		
base line hazard: 0 aphids on current leaf		
1. 1 aphid on current leaf	0.98	0.007 (7)
2. 10 aphids on current leaf	0.96	1.674 (7)
3. 100 aphids on current leaf	0.13	16.916 (7) *
Number of aphids encountered		
base line hazard: ≤ 30 aphids encountered		
4. 31 ≤ no. aphids encountered ≤ 100	4.88	11.259 (7) *
5. no. aphids encountered > 100	9.53	15.396 (7) *
Aphid density on alternative leaf		
base line hazard: 0 aphids at alternative leaf		
6. 10 aphids on alternative leaf	1.07	0.093 (7)
7. 100 aphids on alternative leaf	1.21	0.665 (7)

*: $P < 0.05$

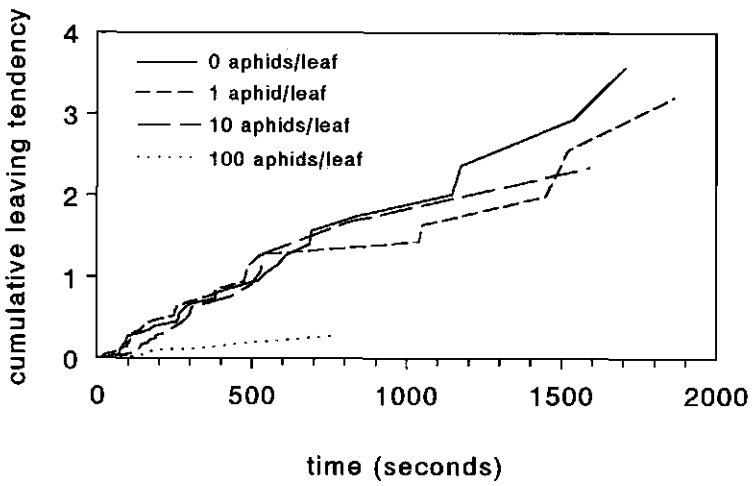

Figure 2
Cumulative leaving tendency (hazard rate in sec^{-1}) of *Aphidius colemani* in experiment 1 at a density of 0 (base line hazard), 1, 10 and 100 aphids per leaf.

Table 3
Estimated effects (exp β) of covariates on the leaving tendency in experiment 2 (at a density of 10 unparasitized aphids per leaf only) and the value of the test statistic T. If exp (β) < 1 then the leaving tendency is reduced, if exp (β) > 1 the leaving tendency is increased. For further explanation see the materials and methods section.

	effect	T (df)
Number of aphids encountered		
base line hazard: ≤ 30 aphids encountered		
1. no. aphids encountered > 30	6.93	13.693 (2) *
Previous leaf visits		
base line hazard: first 10 visits		
2. after 10 visits	2.50	18.376 (2)*

*: P < 0.05

Experiment 2a

At a density of 10 aphids per leaf the leaving tendency increased with the number of leaves visited previously (Table 3). In these five replicates the base line hazard is comparable to the hazard rate at densities 0, 1 or 10 aphids in experiment 1 (Table 1). Thus, the parasitoids in experiment 1 and 2a had the same initial leaving tendency. Graphical inspection of the hazard rates for different values of the number of leaves visited revealed that after about 10 leaf visits residence times became shorter. Therefore, the number of leaves visited was divided into two classes: (1) 10 or less leaves visited previously and (2) more than 10 leaves visited previously. In figure 3 this effect is visualized. After visiting 10 leaves with an initial density of 10 unparasitized aphids the leaving tendency was multiplied by 2.50. The effect of encounters with aphids on the leaving tendency was similar to the effect in experiment 1 (Table 2 and 3).

Experiment 2b

At 100 aphids per leaf no influence of previous leaf visits on the leaving tendency was found. The lack of significant effects at a density of 100 aphids is probably due to a low failure to censor ratio: only 19 failures were registered together with 1524 censored bouts. The base line hazard ($0.157\ 10^{-3}\ s^{-1}$, Table 1) approximately equalled the base line hazard in experiment 1 at density 100: multiply the effect of density 100 (Table 2) with the observed base line hazard in experiment 1 ($0.142\ 10^{-3}\ s^{-1}$).

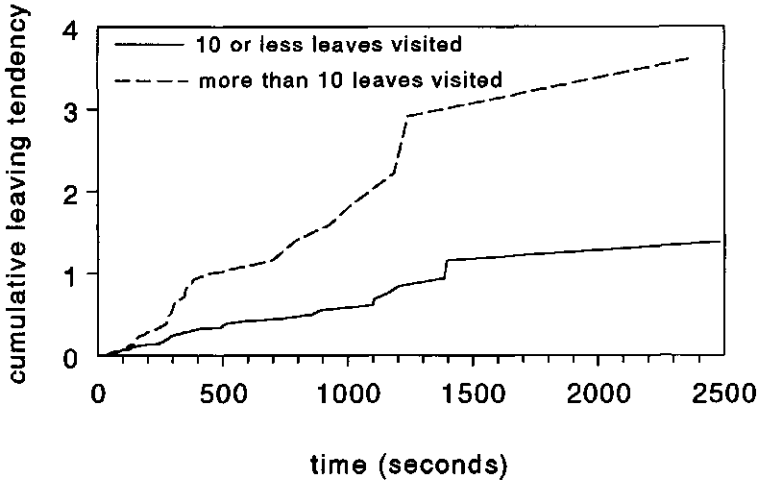

Figure 3
Cumulative leaving tendency (hazard rate in sec^{-1}) of *Aphidius colemani* in experiment 2a for 10 or less (base line hazard) or more than 10 leaves visited previously.

Discussion

The leaving tendency was strongly influenced by the number of aphids on the leaf and the number of aphids that had been encountered. At high aphid densities the leaving tendency was smallest. We found no effect of aphid densities up to 10 aphids per leaf on the leaving tendency. Apparently, the parasitoid 'classified' these densities as low and might have 'expected' that larger aphid colonies should be near. Aphid colonies grow quickly and the aphids react to the detoriation of the food plant by walking and flying off (Rabasse & Wyatt, 1985). As a consequence large aphid colonies will be surrounded by many smaller colonies (Rabasse, 1980; Rabasse & Wyatt, 1985), and the presence of a few aphids on a leaf will be a strong indication that a larger aphid colony is close by. Also for other parasitoids searching for patchily distributed hosts a strong effect of host density on patch time allocation was found (van Lenteren & Bakker, 1978; Waage, 1979; van Alphen & Galis, 1983). For parasitoids searching for more uniformly distributed hosts, a fixed number rule would be more efficient (Iwasa *et al*, 1981), as was found for *Venturia canescens* (Driessen *et al*, 1994).

The effect of encounters differed among the aphid densities on the leaf. At low densities, 31 to 100 encounters increased the leaving tendency, whereas at a density of 100 aphids the leaving tendency was still reduced at less than 100 encounters. The combined effect of a density of 100 aphids and 31 to 100 encounters was 0.63. No effect of rejection of aphids was found. Patch time allocation of *A. tabida* and *E. formosa* was also not influenced by rejection of parasitized hosts (van Alphen & Galis, 1983; van Roermund *et al*, 1994). However, in one of our studies with *A. colemani* return visits to an aphid colony were considerably shorter and less aphids were attacked during this return visit (van Steenis & El-Khawass, 1995a). Though this experiment did not show whether this difference was caused by direct recognition of parasitized aphids (Chow & Mackauer, 1986; Hofsvang, 1988) or a stronger defence reaction of parasitized aphids (Gardner *et al*, 1984), parasitoid behaviour did change when parasitized aphids were encountered and rejected. Also for *L. heterotoma* frequent contacts with parasitized hosts led to a decrease of the foraging time (van Lenteren, 1991). It looks as though the effect of encounters with parasitized hosts upon entering a patch differs from the effect of encounters with parasitized hosts later on.

The present study shows that encounters with unsuitable aphids do not influence the leaving tendency while still searching in a colony with unparasitized aphids. Possibly the parasitoids use some kind of estimate of colony size upon entering an aphid colony. This could be done by kairomone levels (Powell & Zhang Zhi-Li, 1983; Bouchard & Cloutier, 1985), the degree of honeydew accumulation (Budenberg, 1990), or the initial rate of encounter, as all these factors are positively correlated with aphid density.

The presence of an aphid colony close to the colony where the parasitoid is searching had no influence on the departure behaviour of the parasitoid. If the parasitoid is able to detect the presence of a colony nearby this would mean that travel risks are smaller than when such an aphid colony is not detected (and thus is at a longer distance). Optimal foraging theory predicts that at low travel costs the parasitoid should leave the current colony earlier when another colony is close by. Apparently, the parasitoid *A. colemani* is not able to detect a nearby colony from within another aphid colony. This is in accordance with the previous statement that upon encounters with aphids, the nearby presence of other colonies is likely. There seems to be no additional advantage to be able to detect these colonies. Experiments on the in-flight host location by *A. colemani* showed that the parasitoids are able to detect aphid infested leaves in

flight (van Steenis & El-Khawass, 1995b).

Another way to estimate overall host availability would be through experiences during previous visits to different leaves. When overall host availability is low and travel costs are not negligible, patch times should be longer than at high host availability (Charnov, 1976). If the parasitoid uses experiences in several previously visited patches this would imply that after visiting a number of low density patches the residence time should increase relative to the residence time when visiting high density patches. However, we found the opposite. After ten or more visits to a leaf with 10 aphids giving up times since the latest encounter were shorter than beforehand. This parasitoid species seems to have an innate expectancy of a clumped aphid distribution in the field. Again, this is adaptive since the presence of a few aphids is an indication for the presence of more and larger aphid colonies close by.

In summary it is suggested that *A. colemani* might have an innate expectancy of a clumped aphid distribution. This expectancy does not seem to change with experiences. The leaving tendency is determined by an estimate of the size of the aphid colony and is only slightly influenced by encounters with aphids.

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Chapter 6

Application of *Aphidius colemani*

6 Application of *Aphidius colemani* Viereck (Hymenoptera: Braconidae) to control *Aphis gossypii* Glover (Homoptera: Aphididae) in glasshouses

6.1 Different parasitoid introduction schemes determine the success of biological control of *Aphis gossypii* Glover (Homoptera: Aphididae) with the parasitoid *Aphidius colemani* Viereck (Hymenoptera: Braconidae)[1]

Abstract

Three introduction schemes of the parasitoid *Aphidius colemani*, in which timing and size of the introductions differed, were compared for control of *Aphis gossypii*. The first introduction of each scheme was made one day after aphids had been introduced.

An introduction scheme of 100 female *A. colemani* every two weeks suppressed the growth of the aphid population almost immediately. With introduction rates of 50 female parasitoids per week or 25 female parasitoids twice a week, it took two weeks before the aphid population started to decline. With these introduction rates the first offspring of the introduced parasitoids was responsible for successful control.

The results show that natural enemies have to be present in large numbers to obtain sufficient and immediate control. With lower introduction rates not all aphids will be parasitized. As a consequence the aphid population keeps on growing and sufficient control is only obtained when the parasitoid population has build up sufficiently.

In spring control was sufficient with all introduction schemes, but in summer control totally failed. With each of the three introduction methods not all aphid colonies were discovered immediately. In summer these undiscovered colonies will grow much faster than in spring because of the higher temperatures. When the first offspring of the introduced parasitoids emerged these colonies had grown to such a size that parasitism was insufficient to stop aphid population growth.

The total eradication of the aphid population in spring and oscillations in the number of aphids in summer suggest that the interaction between natural enemies and aphids is not stable. Reliable control could be enhanced by ensuring a continuous presence of a sufficient amount of natural enemies.

Introduction

Aphis gossypii Glover (the cotton aphid) (Homoptera: Aphididae) is an important pest in glasshouse grown cucumber (van Schelt, 1993). The rapid population growth (van Steenis & El-Khawass, 1995b) and its resistance to selective aphicides (Furk & Hines, 1993) make it very difficult to obtain good and long lasting control.

Chemical control of *A. gossypii* disturbs the biological control of other pests. Several parasitoid species have been evaluated to determine their potential as agent for biological control of *A. gossypii*. Based on population growth rates, host preferences and searching efficiency *Aphidius colemani* Viereck (Hymenoptera: Braconidae) proved to be the best parasitoid available (van Steenis, 1995). However, control is not always reliable. Especially in

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summer it is difficult to obtain sufficient control. Growers use weekly preventive introductions of *A. colemani* as long as no aphids are observed in the glasshouse (van Schelt, 1993). One of the main disadvantages with these preventive introductions is the short life span of the parasitoid (van Steenis, 1993). As a consequence the size of the parasitoid population decreases quickly after an introduction. If aphids enter the glasshouse at a moment that very few parasitoids are present, the aphid colonies can grow to such sizes that effective control cannot be obtained anymore. Even if parasitoids are introduced shortly after the aphids came in, control will not always succeed. Aphids parasitized as adults will produce nymphs for several days after parasitization (van Steenis & El-Khawass, 1995c). This means that sufficient parasitoids have to be present for several days to parasitize the offspring of parasitized aphids too.

Density dependent parasitism (through a density dependent functional or numerical response and aggregation) has been listed as one of the mechanisms through which a stable and low parasitoid and host population can be maintained (Beddington *et al*, 1978). A good searching efficiency and a strong aggregative response have, therefore, been mentioned as important features of successful natural enemies (Huffaker *et al*, 1976). Evidence of density dependent processes and its effect on the equilibrium population size are, however, scarce (Murdoch *et al*, 1985; Murdoch, 1994).

Although the functional response of *A. colemani* is density dependent, parasitization rates increased only up to a density of 10 aphids per leaf disk (van Steenis & El-Khawass, 1995a). With a daily reproduction of 5.3 to 5.9 nymphs per aphid (van Steenis & El-Khawass, 1995c), a colony started by one adult, will be larger than 10 aphids within a few days. Growth rates of aphid populations are maximally 49 times per week at a temperature of 25 °C (van Steenis & El-Khawass, 1995c). Because of the high growth rates aphid populations can pass the region where control is successful very quickly (van Emden, 1988). Therefore, it is important that parasitoids discover aphid colonies fast.

The numerical response, which can be divided into the reproductive and spatial numerical response, is probably also very important. The growth rate of *A. colemani* (0.352 and 0.438 day^{-1} at 20 and 25 °C, respectively (van Steenis, 1993)) does not differ much from the growth rate of *A. gossypii* (0.339 and 0.471 day^{-1} at 20 and 25 °C, respectively (van Steenis & El-Khawass, 1995c)), but at low aphid densities the parasitoids will not reach their maximum reproductive capacity. Because of the large growth rates, *A. colemani* seems to be a natural enemy that should be able to keep up with the development of the aphid population.

Aggregation of natural enemies at places with an initially high host density can lead to a locally stable model (Hassell & May, 1973). Aggregation of aphid parasitoids at places of high aphid density has been shown for *Ephedrus cerasicola* (Hågvar & Hofsvang, 1987).

An example of a globally stable interaction is the biological control of the Walnut aphid with *Trioxys pallidus* (van den Bosch *et al*, 1979). After introduction of the parasitoid the equilibrium aphid population has lowered considerably and is stable on a large scale, but local outbreaks still occur. Also in glasshouses wave-like patterns in aphid abundance occur, even though aphid control may be successful (Ramakers & Rabasse, 1995).

Stability and the density dependent processes mentioned above, are considered essential in classical biological control where the natural enemy is introduced once or a few times and long-term pest suppression is the goal (van Lenteren, 1993). With seasonal inoculative biological control in glasshouses natural enemies are introduced several times during one growing season

(van Lenteren, 1993) and it is possible to influence the parasitoid-host interaction more than in classical biological control programmes.

In this study three introduction methods were compared, which all might have different impacts on the parasitoid and aphid population dynamics. One extreme consisted of frequent releases of a low number of parasitoids to ensure a continuous presence of parasitoids during the initial phase of biological control. The other extreme consisted of very few introductions with a large number of parasitoids. An equal total number of parasitoids were released in each treatment, but the timing and size of individual introductions differed among the treatments. The experiment was performed once in spring and once in summer. We studied development of the aphid and parasitoid population to learn more about the interactions that play a role during biological control of aphids in glasshouses.

Materials and methods

Insect cultures

Aphis gossypii were collected from cucumber glasshouses in the Netherlands in 1990. At the Glasshouse Crops Research Station the aphids were cultured on cucumber (cvs. 'Sporu' and 'Aramon') under natural light and a minimum temperature of 18 °C.

The parasitoids used in these experiments were reared at the Glasshouse Crops Research Station in small glasshouse compartments under natural light and at a minimum temperature of 18 °C since 1990. *Aphis gossypii* was used as the host and cucumber (cvs. 'Sporu' and 'Aramon') as the host plant.

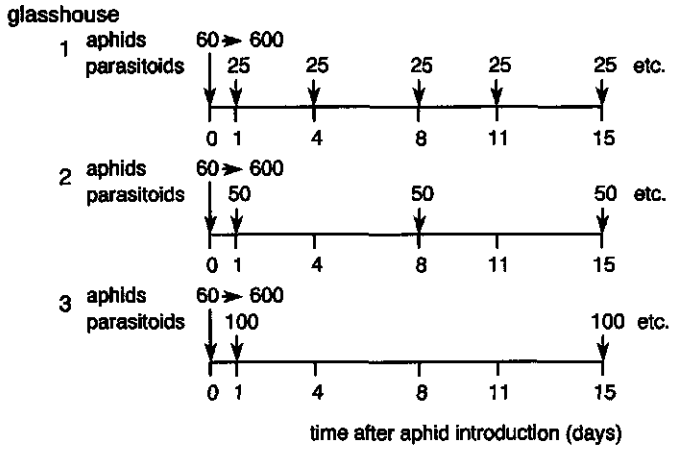

Figure 1
Timing and size of the aphid and parasitoid introductions. Before introduction of the parasitoids the aphid population in each glasshouse had grown to approximately 600 individuals.

Experimental setup

Three glasshouses of 101 m² with 107 cucumber plants (cv. 'Flamingo') were used. In each glasshouse one leaf (leaf 14 or 15 from below, at a height of approximately 1.5 m) of 14 different plants was infested with five adult aphids. The infestation sites were distributed regularly through the glasshouse. One day later the size of the aphids colonies was on average 42 (min.: 22; max.: 54) aphids per leaf and parasitoids were released at different rates. Three introduction schemes were used: (1) 25 female parasitoids twice a week, (2) 50 female parasitoids once a week and (3) 100 female parasitoids fortnightly (Figure 1). Parasitoids were introduced at one point in the middle of the glasshouse.

Twice a week in each aphid colony the number of adult aphids (winged or wingless), nymphs, parasitoid mummies and emerged mummies (divided in *A. colemani* and hyperparasitoids) were recorded. Aphid numbers were compared by analysis of variance after a transformation of the data to stabilize variances (Murdie, 1972). Parasitization rates were compared with binomial regression analysis in Genstat 5 (Payne *et al*, 1987). Additionally, four yellow plates were present in each glasshouse. They were changed weekly and checked for the number of winged aphids, parasitoids and hyperparasitoids.

The spring experiment started on February 25, 1993 and ended on April 27, 1993. The summer experiment started on June 24, 1993 and ended on October 3, 1993. The average temperature was 20.8 °C (min.: 17.3 °C; max.: 26.6 °C) during the spring experiment and 22.3 °C (min.: 17.6 °C; max.: 33.1 °C) during the summer experiment.

Thrips, whitefly and spider mite were successfully controlled with commercial applications of *Amblyseius cucumeris*, *Encarsia formosa* and *Phytoseiulus persimilis*, respectively.

Results

Spring experiment

Only when 100 female parasitoids were introduced the growth of the aphid population was suppressed within a few days after release of the parasitoids (Figure 2). With an introduction of 100 female parasitoids the size of individual aphid colonies did not grow beyond 200 aphids per leaf. The average colony size remained below 100 aphids per leaf (Figure 2). With the other introduction methods a few aphid colonies kept growing until 300 to 600 individuals. In all colonies the rise to a maximum number of aphids was followed by a rapid decline. When 25 or 50 female parasitoids were introduced it took longer before the aphid population started to decline.

Plotting the number of mummies in an aphid colony against the colony size one week earlier showed no sign of spatial density dependence. Parasitization rates were very variable (between 0 and 100%) and independent of colony size. Temporal density dependence is difficult to trace because of the short time span of the experiments.

During the first week the average colony size was largest in the glasshouse where 25 parasitoids were introduced twice a week ($P<0.05$; LSD after ANOVA). From day 11 to day 25 the average colony size was significantly smaller in the glasshouse where 100 parasitoids were released once every two weeks ($P<0.05$; LSD after ANOVA). After four weeks no significant differences in the average size of an aphid colony could be detected (ANOVA).

The first mummies appeared one week after the first introduction of parasitoids so we assumed that colonies with mummies were discovered one week before the appearance of the mummies. At an introduction of 25 female parasitoids twice a week colonies are found less

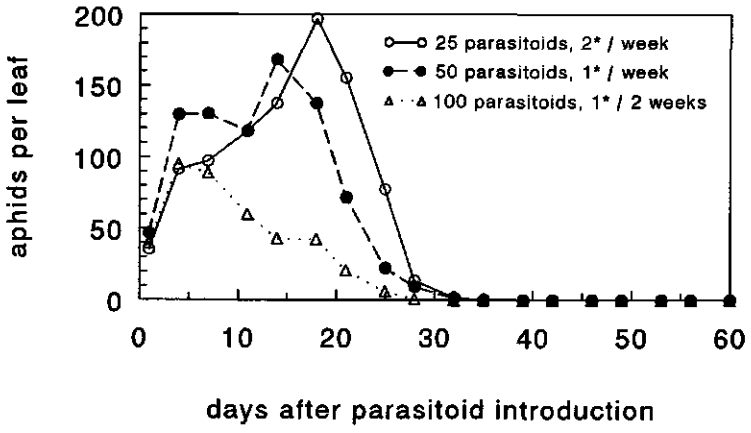

Figure 2
Development of the aphid population on the leaves of introduction during the spring experiment. Three different introduction schemes of *Aphidius colemani* were applied. During the first week the average colony size was significantly higher in the glasshouse where 25 parasitoids were released twice a week ($P<0.05$; LSD after ANOVA). From day 11 to day 25 the number of aphids were significantly lower in the glasshouse where 100 parasitoids were introduced fortnightly ($P<0.05$; ANOVA).

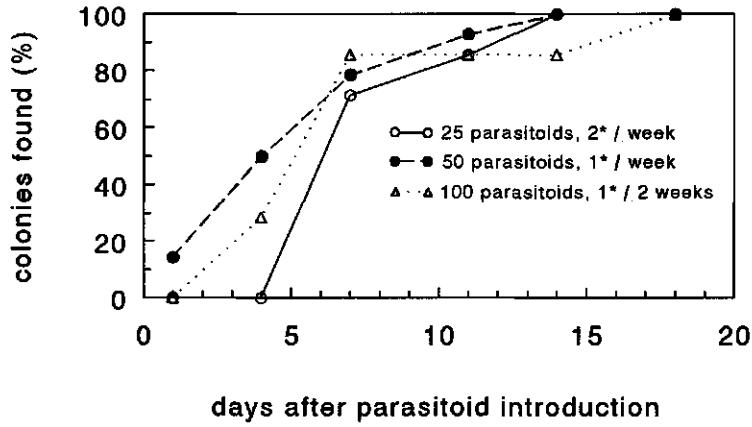

Figure 3
Percentage of colonies found with three introduction schemes of *Aphidius colemani*. It is assumed that a colony was discovered one week before the first mummies appeared.

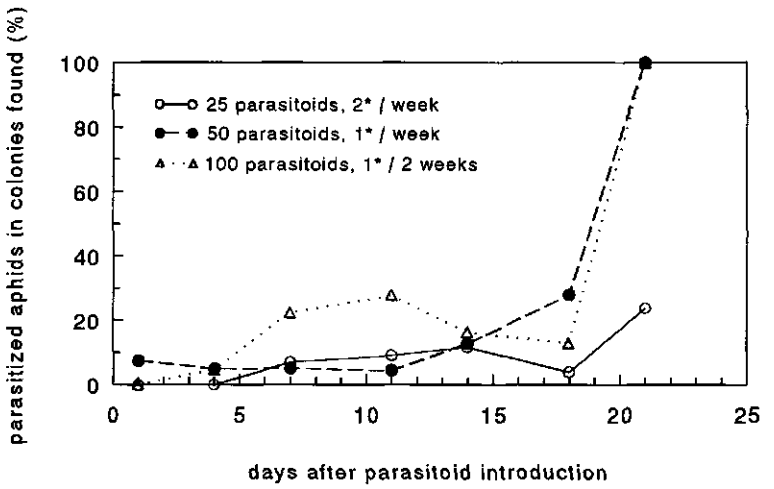

Figure 4
Parasitization rates in colonies found by *Aphidius colemani*. It is assumed that mummified aphids result from parasitization one week earlier. During the first two weeks parasitization rates were significantly higher when 100 parasitoids had been introduced ($P<0.05$; binomial regression analysis).

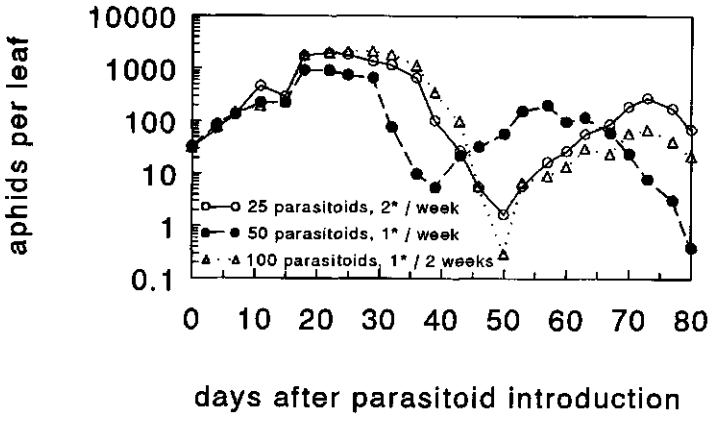

Figure 5
Development of the aphid population on the leaves of introduction during the summer experiment. Three different introduction schemes of *Aphidius colemani* were applied.

quickly than with the other introduction methods (Figure 3). Introduction of 50 female parasitoids per week seems to gives the fastest discovery of aphid colonies.

Parasitization rates in colonies found by parasitoids were determined by relating the number of mummies to the number of aphids one week earlier. When 100 female parasitoids were released the parasitization rate in colonies found during the first two weeks was higher than with the other introduction schemes ($P<0.05$; BRA) (Figure 4). Only the mummies that appeared before day 14 can be attributed to the released parasitoids because there after the first glasshouse generation will have emerged.The parasitization rates in colonies found increased rapidly after the first glasshouse parasitoid generation emerged (Figure 4).

Hyperparasitoids were present at a low level during the entire experiment. On average in each glasshouse one hyperparasitoid was caught on the yellow plates per week.

Summer experiment

In summer control of *A. gossypii* totally failed. After two weeks the number of aphids started to rise dramatically (Figure 5) and only declined after very high aphid levels were reached. A decline phase of several weeks followed until the aphid population started to increase again.

One week after the first parasitoid introduction only 40% of the colonies were discovered, a low percentage compared with approximately 80% during the spring experiment ($P<0.05$; BRA) (Figure 6). Although control failed, the number of mummies and the parasitization rates in colonies found were higher than in the spring experiment (Figure 7). In contrast with the spring experiment the first glasshouse generation of the parasitoids could not control the further

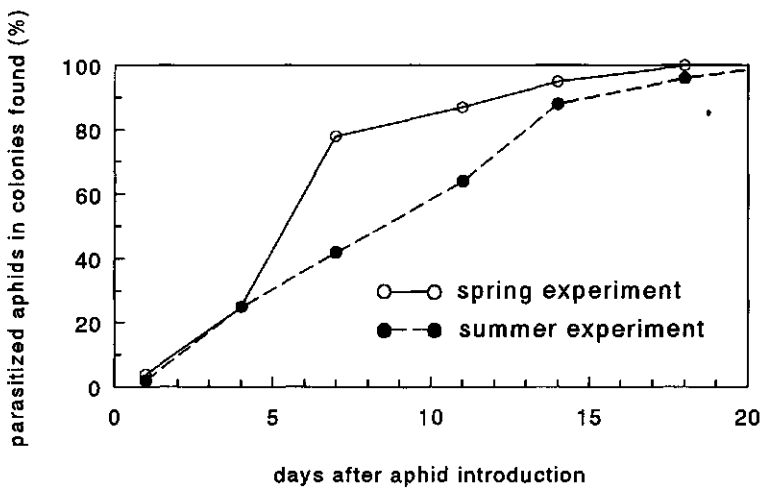

Figure 6
Percentage of colonies found in spring and in summer. Data for the three introduction schemes are taken together. It is assumed that a colony was discovered one week before the first mummies appeared. During the first week of the spring experiment significantly more colonies were found during the first week of the summer experiment ($P<0.05$; binomial regression analysis).

development of the aphid population (Figure 7). Again no evidence of spatial density dependent parasitism was found.

Six weeks after the start of the experiment large numbers of hyperparasitoids (mainly *Dendrocerus aphidum* (Rondani) (Hymenoptera: Megaspilidae) were caught on the yellow plates. During the first six weeks few hyperparasitoids were caught and on a level that was comparable to the spring experiment. After this period the number of hyperparasitoids increased and the hyperparasitoid:parasitoid ratio became much larger than in the spring experiment.

Discussion

Both in the spring as in the summer experiment the maximum daily reproduction of the parasitoids was never reached. At the moment of the first parasitoid introduction the average aphid colony size was 42 aphids per leaf, which results in a total of approximately 600 aphids in each glasshouse. One female parasitoid will parasitize approximately 70% of the aphids in a colony of 50 aphids (van Steenis & El-Khawass, 1995a). In the glasshouse more than one visit can be made to individual aphid colonies and parasitization rates should be higher, even though parasitoids react to colonies with many parasitized aphids with shorter visit times (van Steenis & El-Khawass, 1995a). The cumulative number of emerged mummies was lower than was expected from the size of the aphid population. This was also observed during biological control of *Myzus persicae* Sulzer with *Ephedrus cerasicola* Starý (Hofsvang & Hågvar, 1979). Since no other mortality factors like pathogens or predators were observed, the difference between the expected and observed number of mummies is probably due to the actions of parasitoids. Aphids are disturbed when a parasitoid searches on the leaf, and consequently they let themselves drop from the leaf or disperse (Tamaki *et al*, 1970; Hight *et al*, 1972; Ruth *et al*,

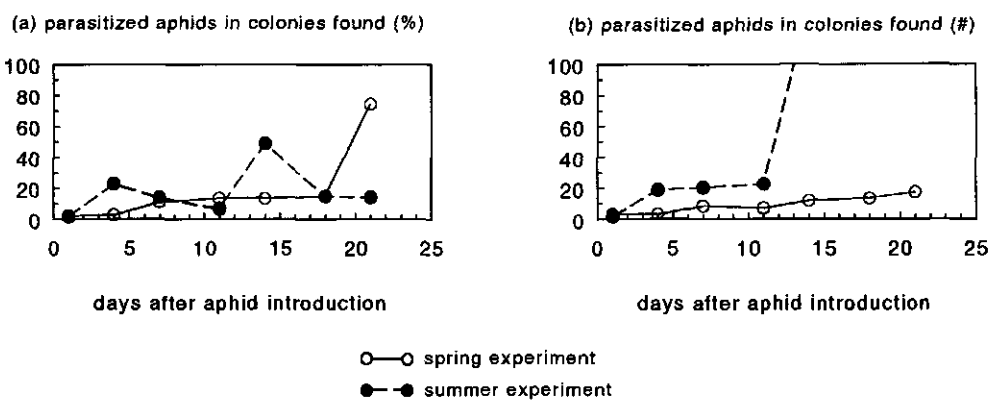

Figure 7
Parasitization rates in colonies found in spring and in summer. Data for the three introduction schemes are taken together. It is assumed that mummified aphids result from parasitization one week earlier. (a) parasitization rates, (b) absolute number of parasitized aphids.

1975). Also parasitized aphids behave differently compared to unparasitized aphids (Brodeur & McNeil, 1992). Therefore, the parasitization rates in the aphid colonies will be underestimated.

Only when 100 female parasitoids were released (a parasitoid:aphid ratio of 1 to 6) the development of the aphid population was suppressed immediately. With the other introduction schemes it took 15 to 20 days before the aphid population size started to decrease. In spring the difference among the introduction methods is caused by a lower rate of discovery of aphid colonies with introductions of 25 female parasitoids twice a week and higher parasitization rates in colonies found with an introduction of 100 female parasitoids fortnightly. Because of the large population growth rate of *A. gossypii* (van Steenis & El-Khawass, 1995c) colonies that are not found immediately can grow to such a size that the introduced parasitoids cannot control these colonies anymore. Only when after two weeks many parasitoids emerge from the parasitized aphids in the glasshouse (the development time of *A. colemani* is approximately 12 days at 20 °C (van Steenis, 1993)) the growth of the aphid population in these colonies can be suppressed too.

The failure of control during the summer experiment might at least be partly caused by the higher temperatures. During the first two weeks the average temperature in spring was 19.8 °C, in the summer experiment the temperature during the first two weeks was on average 24.5 °C. In summer fewer colonies were found during the first week, which might be attributed to the shorter life span of the parasitoids at 25 °C compared to 20 °C. At 20 °C the parasitoids live 1.4 days longer (van Steenis, 1993) and have therefore more time to find the aphid colonies. Additionally, at 25 °C the population growth rate of *A. gossypii* is much larger than at 20 °C (0.339 and 0.471 day^{-1} at 20 and 25 °C (van Steenis & El-Khawass, 1995c)), whereas the population growth rate of *A. colemani* does not increase as rapidly (0.352 and 0.438 day^{-1} at 20 and 25 °C, respectively (van Steenis, 1993)). As a consequence in colonies that are not discovered immediately, the aphid population will grow much faster in summer than in spring. These colonies can become a source from which aphid spread into the glasshouse and parasitoids cannot obtain immediate control.

In both experiments hyperparasitoids were observed. During the spring experiments the number of hyperparasitoids caught on the yellow plates stayed low, but in the summer experiment many hyperparasitoids were observed. Because of the low daily fecundity and the long generation time hyperparasitoids will not have an immediate impact on the parasitoid population (Hågvar & Hofsvang, 1991; Mackauer & Völkl, 1993; Brodeur & McNeil, 1994). Nevertheless, the greater longevity of the hyperparasitoids can result in accumulation of hyperparasitoids which can have a large impact on the parasitoid population at the end of a cropping period (Brodeur & McNeil, 1994). During the initial phase of the aphid population increase few hyperparasitoids were observed in both experiments. It is most likely that the occurrence of hyperparasitoids was a response to the large number of parasitoids which occurred after the peak of the aphid population in the summer experiment. Once these numbers of hyperparasitoids occur it will be difficult to establish sufficient aphid control again.

Considering the fact that aphid parasitoids respond to volatiles emanated by aphid colonies and have a strong aggregational response (Hågvar & Hofsvang, 1987; van Steenis & El-Khawass, 1995b), it seems surprising that the parasitoids were not able to find all aphid colonies at the first introductions and that spatial density dependence could not be detected. Also, the concept of a low and stable equilibrium population did not seem to apply to biological control of aphids in glasshouses. In the spring experiment the parasitoids were able to eliminate

the aphids. In the summer experiment two peaks were found in the number of aphids present in the glasshouses. These observations suggest that it is difficult to obtain a stable interaction between the aphids and the parasitoids. Efficiently searching natural enemies are able to reduce the pest population to low levels but are, according to Murdoch *et al* (1985), also a cause of instability and inefficiently searching natural enemies are potentially able to keep the pest population stable, but probably on a much higher level. As a consequence there is a trade-off between stability and maintenance of a low pest density (Murdoch *et al*, 1985). Metapopulation dynamics in the field can be stable but apparently a glasshouse is too small to result in a stable aphid-parasitoid system.

The oscillations in aphid density that do occur do not have to be a problem as long as the economic injury level is not crossed, but because of the high economic value of glasshouse crops damage threshold are usually very low.

It needs to be stressed that the timing of the parasitoid introductions has been extremely well synchronized with the occurrence of aphids. With preventive introductions in commercial glasshouses it is not known when the aphids will enter the glasshouse. Our results suggest that even if the preventive introductions would have been in the right time these introductions are not as reliable as often is suggested. Preventive introductions as long as no aphids are observed in the glasshouse can be useful, but because of the large growth rate of aphid populations many parasitoids have to be introduced frequently. Only when many parasitoids are present a large amount of the aphids will be parasitized soon enough to prevent an increase in aphid numbers. Once aphid levels are too high it is impossible to obtain good control without considerable damage to the plants. In summer more parasitoids should be introduced than in spring because of the larger growth rate of aphid populations at the high summer temperatures.

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6.2 Control of the cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), through introduction of parasitoids (*Aphidius colemani* Viereck (Hymenoptera: Braconidae)) on banker plants[1]

Abstract

The use of an open rearing unit in the glasshouse to introduce *Aphidius colemani* Viereck (Hymenoptera: Braconidae) has been investigated. This system, consisting of *Rhopalosiphum padi* Rondani (Homoptera: Aphididae) on wheat, provided good control of *Aphis gossypii* Glover (Homoptera: Aphididae) on cucumber. Compared to biweekly introductions of parasitoids, the cotton aphid population stayed much lower in the glasshouses with an open rearing unit.

After several weeks the number of cotton aphids increased in the glasshouses with an open rearing unit, because hyperparasitoids accumulated on the parasitized *R. padi* on the banker plants. In the other glasshouse hyperparasitoids occurred too, but here the biweekly introductions of parasitoids were sufficient to control the cotton aphid population.

Introduction

The cotton aphid (*Aphis gossypii* Glover (Homoptera: Aphididae)) is an important problem in glasshouse crops, especially in cucumber and melon, and its occurrence in other crops is increasing (van Schelt, 1993). Populations of this aphid can multiply 49 times per week (van Steenis & El-Khawass, 1995c). Without control measures a total collapse of the crop can follow within five weeks after introduction of a few aphids (Scopes & Biggerstaff, 1976).

Aphidius colemani Viereck (Hymenoptera: Braconidae) was the most promising biological control agent out of several parasitoids tested (van Steenis, 1995) and is used for biological control of cotton aphid on a large scale (van Schelt, 1993). Growers use weekly preventive introductions of *A. colemani* as long as no aphids are observed in the glasshouse (van Schelt, 1993). When aphids are present, the biological control programme is extended by releases of the gall midge *Aphidoletes aphidimyza* (Rondani) (Diptera: Cecidomyiidae) or by the selective aphicide pirimicarb (van Schelt, 1993). Despite the use of efficient natural enemies, aphid control is not always reliable (van Steenis & El-Khawass, 1995a). Furthermore, cotton aphid is resistant against pirimicarb, the only selective aphicide available (Furk & Hines, 1993). For maintaining the possibility of biological control of other pests, a more effective biological control programme for cotton aphid had to be developed as well.

In field populations, the natural enemies can control aphid populations but the development of the natural enemy population lags behind the development of the aphid population (Huffaker & Kennet, 1956). This delay can result in oscillations of the aphid and parasitoid population (Nicholson, 1933; Krebs, 1972). Also in glasshouses a wave-like population development of the aphids and their natural enemies can be seen (Ramakers & Rabasse, 1995). For sufficient control it is essential that large numbers of parasitoids are introduced to obtain immediate control (van Steenis & El-Khawass, 1995a) and natural enemies should be present in sufficiently large numbers during the entire cropping period.

Even when successful control is obtained, the development of the aphid and parasitoid population is wave-like and periods of good aphid control can be alternated by periods with high

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aphid densities (Ramakers & Rabasse, 1995). Aphidiinae are specific aphid parasitoids and are, therefore, expected to have an efficient searching behaviour (Vet & Dicke, 1992). Indeed, it was found that *A. colemani* can detect an aphid colony during flight (van Steenis & El-Khawass, 1995b). In these systems, with natural enemies that are highly adapted to finding and attacking prey, extinction is very likely to occur on a small scale whereas on a larger scale the chances of extinction will be almost zero because local extinctions cancel out (Murdoch *et al*, 1985). As a consequence the spatial scale at which the interaction between the parasitoid and the host is studied will be important for the population dynamics. In small glasshouses the interaction between the whitefly *Trialeurodes vaporariorum* and its parasitoid *Encarsia formosa* was often unstable, whereas in a commercial glasshouse a globally stable situation was present (Noldus & van Lenteren, 1990). In small glasshouses (100 m²), parasitoids can eliminate an aphid population (van Steenis & El-Khawass, 1995a). Although total eradication of an aphid population in a commercial glasshouse might be rare, the occurrence of wave-like interactions between natural enemies and aphids (Ramakers & Rabasse, 1995) indicates that even the size of a commercial glasshouse is relatively small and for this aphid-parasitoid system, a globally stable situation does not always occur.

One way to establish many parasitoids and to try to stabilize the host-parasitoid interaction is to introduce the pest and the natural enemy simultaneously (Huffaker & Kennet, 1956; Hofsvang & Hågvar, 1979). Growers are, however, very reluctant to use this method (Ramakers & Rabasse, 1995). Another way to introduce many parasitoids and to obtain a more stable interaction is by creating places with an alternative host. The presence of refuges for the natural enemies can result in a stable and low equilibrium pest population outside the refuge (Murdoch *et al*, 1995). The use of banker plants with the bird-cherry oat aphid *Rhopalosiphum padi* (Rondani) (Homoptera: Aphididae) has given good results, both when gall midges and parasitoids were used to control cotton aphid (Hansen, 1983; Kuo-Sell, 1989b; Bennison, 1992; Starý, 1993).

In this study the usefulness of these open rearings will be evaluated and compared with normal repeated releases of parasitoids.

Materials and methods

Insect cultures

Aphis gossypii were collected from cucumber glasshouses in the Netherlands in 1990. At the Glasshouse Crops Research Station the aphids were cultured on cucumber (cvs. 'Sporu' and 'Aramon') under natural light and a minimum temperature of 18 °C.

The parasitoids used in these experiments were reared at the Glasshouse Crops Research Station in small glasshouse compartments under natural light and at a minimum temperature of 18 °C since 1990. *Aphis gossypii* was used as the host and cucumber (cvs. 'Sporu' and 'Aramon') as the host plant.

Experimental set-up

The experiments were done in six glasshouses of 17 m² each. Each compartment was ventilated by means of a separate ventilator. The inflow and outflow holes were covered with a gauze to prevent aphids and parasitoids entering the glasshouse from outside. In each glasshouse 26 cucumber plants (cv. 'Aramon') were grown in the same way as in commercial glasshouses (on rockwool).

The experiments were done from 15 July 1991 until 17 October 1991. During the experiment the temperature inside the glasshouses was on average 22.5 °C. At night a temperature of 20 °C was maintained. During daytime the temperatures ranged from 20 to 32 °C. Thrips, whitefly and spider mite were successfully controlled with commercial applications of *Amblyseius cucumeris*, *Encarsia formosa* and *Phytoseiulus persimilis*, respectively.

Two introduction schemes were used, each of them in three glasshouses: (1) repeated introduction of parasitoids and (2) an open rearing on *R. padi*. The repeated introduction consisted of the release of 13 female and 13 male parasitoids twice a week. The first release was made on 22 July, one week before the introduction of cotton aphids. The plants and aphids for the open rearing method were introduced on 15 July, two weeks before the introduction of cotton aphid. The open rearing consisted of the bird cherry-oat aphid *R. padi* on winter wheat (cv. 'Malinka'). The wheat was grown on rockwool blocks covered with sand and was placed on the same rockwool as the cucumbers were grown on. During the first two weeks five female and five male aphid parasitoids were released on the grain aphids twice a week. Afterwards no introductions of parasitoids took place.

In each glasshouse five leaves were infested with five cotton aphids each on 30 July. Twice a week the number of nymphs, alatae, apterae, mummies and emerged parasitoids on these leaves were recorded. Mummies from which a parasitoid had emerged, were removed with a brush. After the data were transformed to stabilize variances (Murdie, 1972) the size of the aphid populations were statistically compared for each day by analysis of variance (ANOVA). Parasitization rates were compared with binomial regression analysis (BRA) in Genstat 5 (Payne *et al*, 1987).

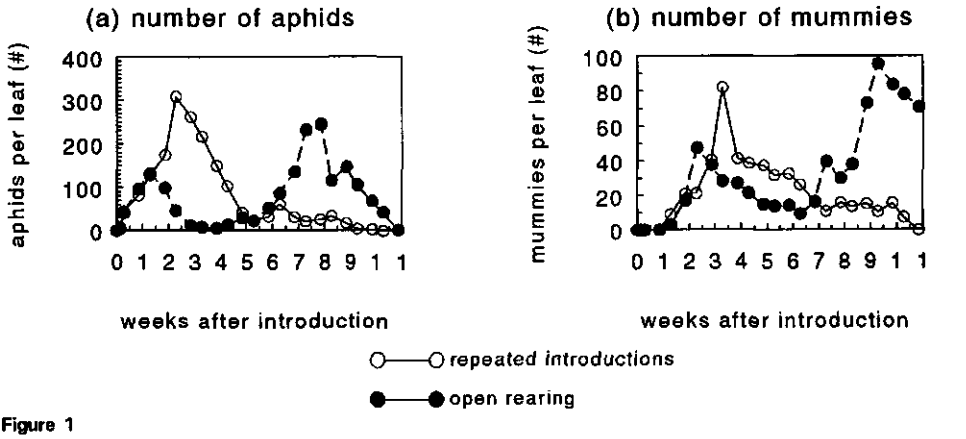

Figure 1
Number of healthy (a) and mummified (b) cotton aphids per leaf (avg. (s.e.; n)) in glasshouses where repeated introductions of *Aphidius colemani* are used and in glasshouses with banker plants. From the second to the fourth week the number of aphids in the glasshouses with the open rearing was significantly lower ($P<0.05$; ANOVA). From weeks seven to ten the number of aphids was significantly lower in glasshouses with repeated parasitoid introductions ($P<0.05$; ANOVA).

Results

In one glasshouse where regular introductions of parasitoids were used the cucumber plants had to be removed because of too high aphid densities five weeks after the introduction of aphids. Data from this glasshouse were not used in the analysis.

At first, the open rearing method gave a much better control of cotton aphid than regular releases of parasitoids (Figure 1). From the second to the fourth week the number of aphids in the glasshouses with the open rearing were significantly lower ($P<0.05$; ANOVA). At this stage very high numbers of parasitoids could be observed flying around the banker plants. After about six weeks, however, an increase of the numbers of aphids could be observed in the glasshouses with an open rearing method (Figure 1), resulting in a significantly higher population density in the glasshouses with an open rearing than in the glasshouses with repeated introductions from week seven to ten ($P<0.05$; ANOVA).

The first mummies appeared after one week. Therefore, it was assumed that colonies with mummies were discovered one week before the appearance of the mummies. The parasitization rates in colonies found by parasitoids were determined by relating the number of mummies to the number of aphids one week earlier. The number of colonies found during the first week after introduction of the aphids did not differ significantly (BRA). After one week all colonies in the glasshouses were found (Figure 2).

Only the parasitization rates during the first two weeks can be attributed to the released parasitoids. After 12 days the first offspring of the introduced parasitoids will emerge in the glasshouses. The first day after the introduction of aphids the parasitization rates in the aphid colonies were significantly higher in the glasshouses where an open rearing was present ($P<0.05$; BRA) (Figure 3). During the second week the parasitization rates were significantly

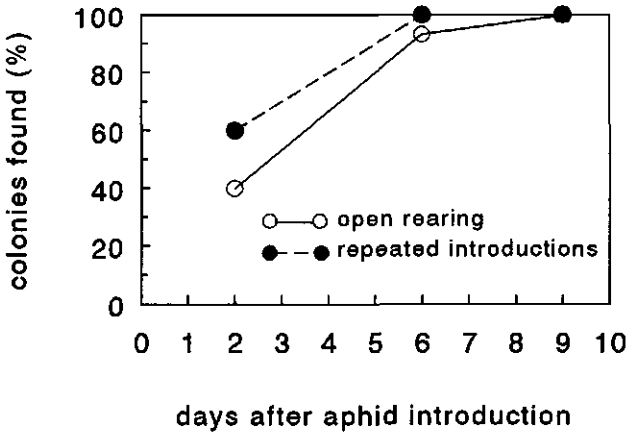

Figure 2
Percentage of colonies found during the first week after introduction of the cotton aphids. No significant differences were present between the introduction methods (binomial regression analysis).

higher in the glasshouses with repeated parasitoid introductions ($P<0.05$; BRA).

Discussion

The use of an open rearing method to introduce *A. aphidimyza* in glasshouses has been investigated by Kuo-Sell (1987, 1989a, 1989b) and Hansen (1983). It was shown that the presence of natural enemies before the aphids entered the glasshouse gave very good results. Also a combination of *A. colemani* and *A. aphidimyza* gave reliable control when the natural enemies were released through an open rearing method (Bennison, 1992). A normal repeated introduction (0.5 *A. colemani*/m²/2 weeks and 1 *A. aphidimyza*/m²/week) did not give good aphid control (Bennison, 1992).

The present study shows that the introduction of parasitoids through an open rearing on *R. padi* gave rapid control of cotton aphids in cucumber. The first day after the introduction of aphids the parasitization rate in the aphid colonies were higher than with repeated introductions. Later no differences between the two introduction methods could be detected and after one week the parasitization rates were higher in the glasshouses with repeated introductions. Because of the high parasitization rate during the first days after aphid introduction, the aphid population in the glasshouses with an open rearing unit stayed considerably lower. Apparently, a high initial parasitization rate is very important to obtain good control.

Also with the standard repeated introductions sufficient control was obtained, although it took longer before the aphid population started to decline. The introduction rates were, however, much higher than those usually applied in commercial glasshouses (0.5

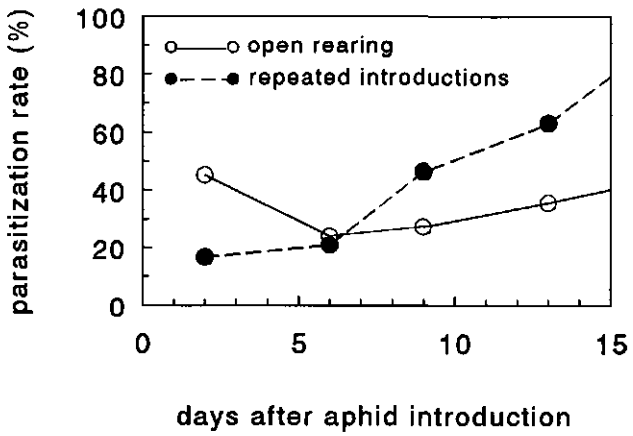

Figure 3
Parasitization rates in colonies found by at least one parasitoid with two different introduction methods. The first day after the introduction of aphids parasitization rates were significantly higher in the glasshouses where an open rearing was present ($P<0.05$; binomial regression analysis). During the second week the parasitization rates were significantly higher in the glasshouses with repeated parasitoid introduction ($P<0.05$; binomial regression analysis).

parasitoids/m²/week), but also with these introduction rates good control can be obtained as long as parasitoids are introduced at the right time and as long as the glasshouse temperatures are not too high (van Steenis & El-Khawass, 1995a).

Several weeks after the first aphid introduction the number of aphid increased significantly in the glasshouses with an open rearing. In these glasshouses many hyperparasitoids were observed (mainly *Dendrocerus aphidum*), which probably emerged from the parasitized aphids in the open rearing. Because of the low daily fecundity and the long generation time hyperparasitoids will not have an immediate impact on the parasitoid population (Hågvar & Hofsvang, 1991; Mackauer & Völkl, 1993; Brodeur & McNeil, 1994). However, the continuous presence of parasitized aphids on the banker plants, makes accumulation of hyperparasitoids possible and can result in a large mortality among the aphidiine parasitoids. In the other glasshouses hyperparasitism also took place, but on a much lower level than in the glasshouses with an open rearing unit. Apparently, the repeated introductions of parasitoids were sufficient to keep the aphid population under control.

The use of an open rearing can result in a more stable and low aphid population in glasshouses. The first peak in the aphid population density was very low compared with the normal introductions. Had no hyperparasitoids been present (hyperparasitoids are mainly a problem in autumn croppings (Ramakers, 1989)) it is very likely that the aphid population would have remained on a low level. Also population models show that the presence of a refuge where suitable host or prey is present continuously, can result in stable pest-natural enemy interaction (Murdoch *et al*, 1985) and field experiments seem to point in the same direction (Murdoch *et al*, 1995).

The experienced problems with hyperparasitoids might be avoided in commercial glasshouses by registration of the number of hyperparasitoids. Once they start to occur on a certain level other natural enemies, like *A. aphidimyza* can be introduced on the banker plants.

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6.3 Use of *Aphidius colemani* Viereck (Hymenoptera: Braconidae) for control of other aphid species frequently occurring in glasshouses[1]

Abstract

The suitability of *Aphis gossypii* Glover, *Macrosiphum euphorbiae* (Thomas) and *Myzus persicae* Sulzer (Homoptera: Aphididae) as host for the aphid parasitoids *Aphidius colemani* Viereck (one strain cultured on *A. gossypii* and one strain cultured on *M. persicae*), *A. matricariae* Haliday and *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae) was tested in the laboratory. Thirty aphids of one species were offered to individual parasitoid females for two hours. Suitability was measured as the number of mummies found. Numbers were corrected for mortality of aphids assuming that parasitized and unparasitized aphids had the same chance of dying.

None of the parasitoids produced mummies on *M. euphorbiae*. *Aphidius colemani* produced on average 21 to 24 mummies on *A. gossypii* and 14 to 17 mummies on *M. persicae*. No significant differences between the two strains were found. *Aphidius matricariae* produced on average 13 mummies on *M. persicae*, but less than two on *A. gossypii*. *Lysiphlebus testaceipes* produced on average eight mummies on *A. gossypii* and less than two on *M. persicae*. It is concluded that *A. colemani* seems to be the most suitable species for use in aphid control. *Lysiphlebus testaceipes* might be used for control of *A. gossypii*, but is unsuitable for control of *M. persicae*.

Introduction

Several aphid species can be important pests in glasshouse crops. In the Netherlands most problems occur with the cotton aphid, *Aphis gossypii* Glover (Homoptera: Aphididae), in cucumber crops (van Schelt *et al*, 1990). Cotton aphid is highly resistant to selective insecticides (Cross *et al*, 1983), and the use of broad spectrum pesticides inhibits the use of other biological control methods. Because biological control of cotton aphid is not reliable, research is done on the usefulness of several aphid parasitoids for control of cotton aphid.

It would be an incentive for general aphid control if the parasitoids used for biological control of cotton aphid, also could be used for biological control of other important aphid species, like the sweet potato aphid (*Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphididae)), and the green peach aphid (*Myzus persicae* Sulzer (Homoptera: Aphididae)).

Macrosiphum euphorbiae is the most important aphid pest on tomato and egg plant. Although this aphid species still can be controlled by selective aphicides it is useful to test whether aphid parasitoids can be used for control too, to anticipate on possible development of resistance. *Myzus persicae* is the most important aphid pest on sweet pepper. Biological control is used successfully on a large area. The natural enemies used are *Aphidius colemani* Viereck and *A. matricariae* Haliday (Hymenoptera: Braconidae) and the gall midge *Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae) (van Schelt *et al*, 1990).

The suitability of the aphid species mentioned above as host for the parasitoids *A. colemani* (two strains), *A. matricariae* and *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae)

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[1] Published in slightly different form as: VAN STEENIS, M.J. (1993). Suitability of *Aphis gossypii* Glov., *Macrosiphum euphorbiae* (Thom.), and *Myzus persicae* Sulz. (Hom.: Aphididae) as host for several aphid parasitoid species (Hym.: Braconidae). *W.P.R.S./I.O.B.C. Bulletin* **26(2)**: 157-160.

has been tested under laboratory conditions.

Materials and methods

The parasitoids tested are reared in small glasshouse compartments on different hosts and host plants as shown in Table 1. All cultures are maintained on the same host plant and host aphid species as the parasitoids were collected from. Cultures have been maintained at the Glasshouse Crops Research Station under natural light and a minimum temperature of 20 °C from December 1990 onwards.

Individual females were released into a petri dish with a sweet pepper leaf with 30 second instar individuals of the aphid species to be tested. After the parasitoid had parasitized the first aphid, it was left in the petri dish for two hours. Afterwards the aphids were transferred to a petri dish with agar and a leaf disk of the preferred host plant (cucumber for *A. gossypii*, egg plant for *M. euphorbiae* and sweet pepper for *M. persicae*). The aphids were followed in their development until the formation of mummies. Leave disks were replaced with fresh ones every three to four days. The number of mummies produced was corrected for mortality of aphids assuming that parasitized and unparasitized aphids had the same chance of dying. Each aphid-parasitoid combination consisted of ten replicates.

Data were analyzed with binomial regression analysis (BRA) in Genstat 5 at a significance level of 0.05 (Payne *et al*, 1987).

Results

The average number of mummies produced in each aphid-parasitoid combination is given in Figure 1. *Myzus persicae* is a good host for *A. colemani* and *A. matricariae*, although parasitization by *A. matricariae* was significantly lower than parasitization by *A. colemani* cultured on *A. gossypii* ($P<0.05$; BRA). There was no significant difference between the two strains of *A. colemani*.

None of the parasitoids produced mummies when *M. euphorbiae* was offered as host, though all of the parasitoids were observed to start parasitizing *M. euphorbiae*.

Lysiphlebus testaceipes was very unsuccessful in parasitizing *M. persicae*. The number of mummies produced was significantly lower than for both *Aphidius* species ($P<0.05$; BRA).

The number of mummies found on *A. gossypii* was clearly different among the parasitoid species. *Aphidius matricariae* did not parasitize *A. gossypii* successfully. The number of mummies found for *A. colemani* was significantly higher than for the other species ($P<0.05$; BRA). Within *A. colemani* there was no significant difference between the two strains (BRA). *Lysiphlebus testaceipes* did parasitize *A. gossypii* successfully, but the number of mummies

Table 1
Rearing conditions of the aphid parasitoids

Parasitoid species	Host aphid	Host plant
Aphidius colemani-A	*Aphis gossypii*	Cucumber
Aphidius colemani-M	*Myzus persicae*	Sweet pepper
Aphidius matricariae	*Myzus persicae*	Sweet pepper
Lysiphlebus testaceipes	*Aphis gossypii*	Cucumber

found was much lower than for *A. colemani* ($P<0.05$; BRA).

Discussion

The suitability in these tests is a combination of host acceptance cf. Vinson (1976) (willingness of the female parasitoid to deposit an egg) and host suitability in strict sense (survival of the egg to adulthood (in the present study: survival until formation of the mummy)). Probably the results are a combination of both processes. It took for example a long time from the introduction of the parasitoids until the first attack when *M. euphorbiae* was offered. If a suitable host was offered however (e.g., *M. persicae* for *A. colemani* and *A. matricariae*), the first parasitization occurred generally within a few seconds.

Aphis gossypii and *M. persicae* were shown to be good hosts for *A. colemani* in a previous study by Tardieux & Rabasse (1986). They also did not observe formation of mummies on *M. euphorbiae* even though the parasitoid showed parasitization behaviour. Tardieux & Rabasse (1986) did not find any first instar larvae in attacked *M. euphorbiae*. It is however still not

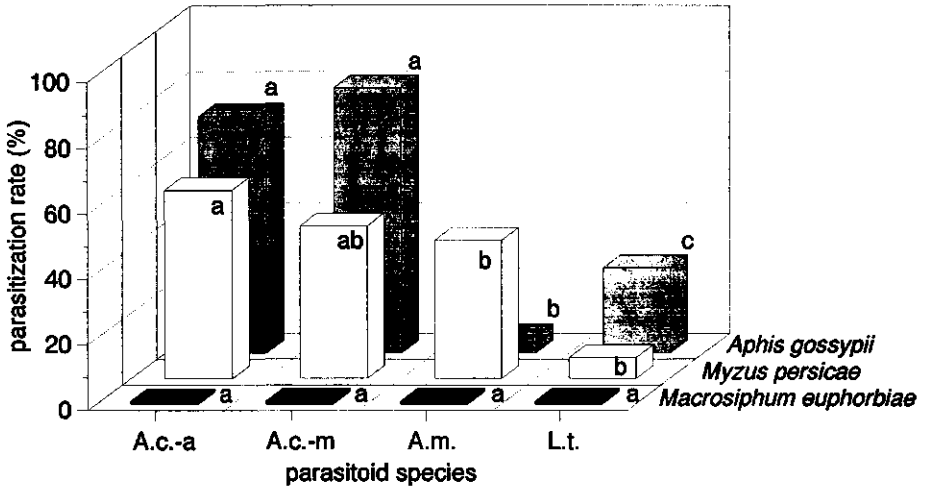

Figure 1
Number of mummies produced on *Aphis gossypii*, *Macrosiphum euphorbiae* and *Myzus persicae* by several parasitoid species (n = 10). Data were corrected for mortality of aphids assuming that parasitized and unparasitized aphids had the same chance of dying. Different letters indicate a significant difference between parasitoid species within an aphid species ($P<0.05$; binomial regression analysis).
A.c.-A = *Aphidius colemani* cultured on *Aphis gossypii*
A.c.-M = *Aphidius colemani* cultured on *Myzus persicae*
A.m. = *Aphidius matricariae*
L.t. = *Lysiphlebus testaceipes*

known whether the absence of larvae is due to rejection by the parasitoid during the process of oviposition or due to mortality in the egg stage. Present findings are contradicted by Starý & Schmutterer (1975), who did find *A. colemani* emerging from *M. euphorbiae* in the field.

Powell & Wright (1988) have shown that there can be differences in suitability of an aphid species as host for different strains of the same parasitoid species. In the present study no differences were found between two strains of *A. colemani*, even though the parasitoids have been reared on the same aphid species for at least 1.5 years.

Aphidius matricariae has been recorded from *A. gossypii* several times (Starý, 1966, 1976, 1979). The low number of mummies produced by *A. matricariae* on *A. gossypii*, as found in this study, is confirmed by records from Schlinger & Mackauer (1963). They rarely found *A. matricariae* on *A. gossypii* in the field. They also quoted that *A. matricariae* has been recorded from *M. euphorbiae* although they questioned whether this observation was correct. In the present study no mummies were found on *M. euphorbiae*.

The suitability of *A. gossypii*, the low suitability of *M. persicae* and the non-suitability of *M. euphorbiae* as host for *L. testaceipes* has also been shown by Carver (1984) and Schlinger & Hall (1960).

It can be concluded that none of the parasitoids is suitable for use in biological control of *M. euphorbiae*. *Aphidius matricariae* is clearly unsuitable for use in biological control of cotton aphid. Only very few mummified *A. gossypii* could be found in the tests. *Lysiphlebus testaceipes* could be useful for biological control of cotton aphid. A major drawback of this species is that is does not parasitize *M. persicae* very well. This implies that if *L. testaceipes* is used for control of *A. gossypii*, still another parasitoid might be needed for biological control of *M. persicae*. The most promising species for use in biological control of both *A. gossypii* as *M. persicae*, is *A. colemani*.

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Chapter 7

General discussion

7 General discussion

7.1 Evaluation of natural enemies

The large number of natural enemies of aphids makes it impossible to evaluate all of them on their usefulness for biological control of *A. gossypii*. Nevertheless, it is necessary to be able to assess whether a natural enemy is promising, before it is used in commercial glasshouses. Introduction of an unsuitable natural enemy would result in bad control and reduced confidence in biological control. In the introduction of this thesis criteria for evaluation of natural enemies as given by van Lenteren & Woets (1988) were presented. A number of these criteria were applicable to aphid-parasitoid systems: (1) climatic adaptation, (2) a good culture method, (3) a high reproductive potential and host-kill rate and (4) a good searching efficiency. Also density dependent parasitism or predation has been mentioned as an important feature of a successful natural enemy (Huffaker *et al*, 1976). Theoretically, density dependent parasitism through aggregation of natural enemies (either at places of high host density or independent of host density) can result in a stable pest-natural enemy interaction (Hassel & May, 1973; Murdoch, 1994).

On the basis of a literature study it was concluded that parasitoids had the best prospect for use in biological control programmes. After the studies presented in this thesis the use and application of these criteria can be evaluated.

Application of evaluation criteria

Glasshouse experiments showed that the ***climatic adaptation*** of aphidiine parasitoids is not perfect. In summer successful control is more difficult to obtain than in spring, probably because of high temperatures (van Steenis & El-Khawass, 1995b). Aphidiine parasitoids live shorter and have a larger immature mortality at high temperatures, resulting in a reduced intrinsic rate of increase (Force & Messenger, 1964a, 1964b; Guenaoui, 1991; van Steenis, 1993, 1994). The life history parameters of *Aphis gossypii* Glover (Homoptera: Aphididae), however, do not differ much between 25 and 30 °C (Kocourek *et al*, 1994; van Steenis & El-Khawass, 1995d). With increasing temperatures, the difference between the population growth rate of *A. gossypii* and that of *Aphidius colemani* Viereck (Hymenoptera: Braconidae) increases and as a consequence it will be more difficult to obtain sufficient control in summer than in spring.

Laboratory studies showed that population growth rates of *Aphelinus varipes* Förster (Hymenoptera: Aphelinidae) are larger at 30 than at 25 °C, whereas the population growth rates of *A. colemani* clearly decrease (van Steenis, 1995d). *Aphelinus varipes* might, therefore, be a valuable addition to biological control of aphids during periods with high temperatures.

Although mass rearing is often implemented at the end of the evaluation of a natural enemy, ***a good culture method*** is a very important characteristic. For example, in glasshouses many predator species do occur spontaneously (Ramakers, 1989) and can have a large impact on the aphid population, but the absence of a good and efficient mass rearing technique is the main cause that not many predator species can be used for biological control in glasshouses, especially because no continuous populations are formed (Tulisalo & Tuovinen, 1975; Hämäläinen, 1977; Chambers, 1986). The gall midge (*Aphidoletes aphidimyza* Rondani (Diptera: Cecidomyiidae)), which can be reared more easily), is the only predator that is used for aphid

control on a large scale (Ramakers & Rabasse, 1995). Another exception is the coccinellid *Hippodamia convergens* Guérin (Coleoptera: Coccinellidae), which is released to eliminate existing aphid infestations quickly (Ramakers & Rabasse, 1995). The latter species is, however, not reared but collected in dormancy sites and subsequently released in glasshouses in very large numbers (Ramakers & Rabasse, 1995).

Huffaker *et al* (1976) and van Lenteren & Woets (1988) suggest that the ***reproductive potential or host-kill rate*** of the natural enemy should be larger than the population growth rate of the pest. This supposition does not hold for cotton aphid and its natural enemy, *A. colemani*. The population growth rate of *A. colemani* is lower than the population growth rate of *A. gossypii* at the entire range of glasshouse temperatures (van Steenis, 1993; van Steenis & El-Khawass, 1995d). Nevertheless, sufficient control can be obtained with this parasitoid as long as parasitoids are introduced at the right time (van Steenis & El-Khawass, 1995b). Several factors might explain why biological control can still be successful. First, searching parasitoids cause an additional mortality among the aphids because of disturbance. Aphids react to a searching parasitoid by walking away or dropping to the floor and not all of these aphids will be able to return to a plant (Tamaki *et al*, 1970; Hight *et al*, 1972; Ruth *et al*, 1975). This phenomenon is probably also the main cause of the fact that during biological control less mummies are found than is expected on the basis of the number of aphids that has been present (van Steenis & El-Khawass, 1995b). Because of the higher mortality the population growth rate of *A. gossypii* will be smaller than is found under laboratory conditions. The exact effect of this phenomenon on biological control in glasshouses is difficult to estimate. Secondly, in the presence of parasitoids the aphid population will not be able to reach its potential growth rate because aphids parasitized by *A. colemani* before the fourth instar do not reproduce (van Steenis & El-Khawass, 1995d). Because the population growth rate of the natural enemies is lower than the population growth rate of the pest, it cannot be expected that the natural enemies will be able to suppress an existing aphid population. Only when the natural enemies are able to cause a high mortality among the aphids during the initial phase of the development of the aphid population, sufficient control will be obtained (van Steenis & El-Khawass, 1995b).

The experiments have shown that population growth rates are not indicative for the effectiveness of natural enemies. The intrinsic rates of increase of the parasitoids *A. colemani* and *Lysiphlebus testaceipes* Cresson (Hymenoptera: Braconidae) are not very different (van Steenis, 1993, 1994). In glasshouses, however, very different parasitization rates are obtained and *L. testaceipes* is clearly inferior to *A. colemani* (van Steenis, 1995c). Even though the reproductive potential of the natural enemy is not always a measure of suitability of the control agent, a high population growth rate remains an important attribute of a natural enemy, because the enemies have to be able to react to increasing aphid populations with a quick increase of parasitoid numbers (numerical response). The larger the difference between the population growth rate of the pest and the natural enemy, the more aphids will have to be killed to reduce the growth of an aphid population sufficiently. Only when a sufficient amount of aphids is parasitized by the introduced parasitoids, the next parasitoid generation is able to control the growing aphid population (van Steenis & El-Khawass, 1995b).

Compared with *A. colemani*, the aphelinid parasitoid *Aphelinus varipes* Förster (Hymenoptera) has a lower population growth rate at temperatures below 25 °C (van Steenis, 1995d). The habit of host feeding of this parasitoid will increase the host kill rate, but in itself this parasitoid

is not able to control cotton aphid in cucumber (van Steenis, 1995b). In contrast with *A. colemani*, *A. varipes* has a large population growth rate at high temperatures. A combination of both *A. colemani* and *A. varipes* gives very good control (van Steenis, 1995b).

An aphid infestation will start with low aphid densities. Under these circumstances ***a good searching efficiency*** is an important attribute of an effective natural enemy (Huffaker *et al*, 1977). A good searching efficiency is also important because aphid colonies grow fast (van Steenis & El-Khawass, 1995d). To prevent the aphid colonies from becoming too large they have to be found quickly after the first aphids have established. Glasshouse experiments have shown that high parasitization rates immediately after aphids are introduced in the glasshouse are very important for obtaining successful control (van Steenis & El-Khawass, 1995b). In glasshouses the searching capacity of *A. colemani* is much better than that of the three other aphidiine parasitoids which were evaluated (van Steenis, 1995c). For *A. colemani* the searching behaviour was studied in the laboratory in more detail.

The searching efficiency of natural enemies cannot be defined as a characteristic that can be compared among several parasitoid species. A relative measure of searching efficiency can be obtained when several natural enemies share the same biology (like aphidiine parasitoids) (van Steenis, 1995c). Even then it is difficult to extrapolate data on the searching behaviour in the laboratory to the more complex glasshouse situation (Kennedy, 1965; Waage & Mills, 1992). The only way to compare the searching efficiency is, therefore, in glasshouses where aphid colonies have been established. Then parasitoids can be released and the amount of aphid colonies that are found by the parasitoids can be compared (as long as no other than the introduced parasitoids are present) (van Steenis, 1995c).

Density dependent parasitism is found in the laboratory. The functional response of individual parasitoids is positively density dependent at low aphid densities and inversely density dependent at high aphid densities (van Steenis & El-Khawass, 1995a). Even though density dependent parasitism results in a stable host-parasitoid interaction in theoretical models, evidence of density dependent processes in the field are scarce (Murdoch, 1994). Also in glasshouses density dependent parasitization rates cannot be detected. Parasitization rates by *A. colemani* in aphid colonies are very variable and do not depend on the initial size of the aphid colony (van Steenis & El-Khawass, 1995b). The importance of density dependence for regulation of the pest population has been questioned by Murdoch *et al* (1985). Even in well regulated systems none of the density dependent processes that are known seemed to act as a stabilizing mechanism (Murdoch, 1994).

Integration of individual criteria

Evaluation criteria are a tool to choose between useless and promising natural enemies (van Lenteren, 1993). Integration of characteristics of natural enemies (obtained in laboratory studies) to a unique value which gives an indication for the usefulness in biological control programmes is almost impossible for several reasons. Firstly, trade-offs between characteristics are likely to occur (Waage & Mills, 1992). Secondly, laboratory measures of effectivity can differ from the effectivity in the field (Kennedy, 1965; Waage & Mills, 1992; Höller & Haardt, 1993; Hughes *et al*, 1994). This was shown for *L. testaceipes*, a parasitoid with a large population growth rate on *A. gossypii*, but with low parasitization rates in the glasshouse (van

Steenis, 1994; van Steenis, 1995c). When *A. varipes* was also studied and had to be compared with *A. colemani* the problems with integration of individual characteristics became apparent. A small laboratory test was not possible, because the different reproduction strategies (Starý, 1988a, 1988b) would cause very large differences in parasitization rates in the laboratory. Also r_m-values can be obtained for both species but as explained earlier these data are not very reliable as predictors of parasitoid effectiveness. It was decided (after it had been established that *A. gossypii* was a good host for *A. varipes*) to do glasshouse experiments to compare *A. varipes* and *A. colemani*. When both *A. colemani* and *A. varipes* are introduced in glasshouses both species survive and high parasitization rates are obtained (van Steenis, 1995b).

Thirdly, the importance of the individual criteria will depend on the system that is studied and the type of control that has to be obtained. In classical biological control programmes long-term suppression of the pest population has to be obtained (Ehler, 1990) and the emphasis lies on natural enemies that fit into the ecology of the pest (Waage & Mills, 1992). In inundative and seasonal inoculative control on the other hand the main interest lies in the short-term suppression of the pest (Ehler, 1990) and other characteristics of natural enemies will be of special importance. Aphids are a pest with a large potential population growth rate and relatively few aphids can cause economic damage in glasshouse crops. The only way to keep the aphid density low is by using very effective enemies early in the season and an efficient searching behaviour is a very important characteristic of an effective natural enemy. The enemies are able to reduce the aphid population to a very low level because of an efficient searching behaviour (for a review see Hågvar & Hofsvang (1991)), a large population growth rate (Starý, 1988a; 1988b) and the absence of aphid stages which are invulnerable to parasitoid attack (Völkl *et al*, 1990; van Steenis & El-Khawass, 1995d). Because the aphid population can be reduced to a very low level, not many natural enemies will eventually survive in the glasshouse. The system is, therefore, very sensitive to aphids entering the glasshouse from outside. Natural enemies will have to be introduced throughout the season at relatively large numbers to reduce the risk of unwanted fluctuations in aphid density.

7.2 Introduction methods for *Aphidius colemani*

In field populations, the natural enemies can control aphid populations but the development of the natural enemy population lags behind the development of the aphid population (Huffaker & Kennet, 1956). This delay can result in fluctuations of the aphid and parasitoid population (Nicholson, 1933; Krebs, 1972). Also in glasshouses a wave-like population development of the aphids and their natural enemies can be seen (Ramakers & Rabasse, 1995). For sufficient control it is essential that large numbers of parasitoids are introduced to obtain immediate control (van Steenis & El-Khawass, 1995b).

Even when successful control is obtained, the development of the aphid and parasitoid population is wave-like and periods of good aphid control can be alternated by periods with high aphid densities (Ramakers & Rabasse, 1995). *Aphidius colemani* is an efficient searcher and has a high numerical increase (van Steenis, 1993; van Steenis & El-Khawass, 1995c). Efficiently searching natural enemies are able to reduce the pest population to low levels, but are, according to Murdoch *et al* (1985), also a cause of instability. Nevertheless, an efficiently searching natural enemy is necessary as explained in the previous section.

Parasitoid-host models suggest that spatial heterogeneity, the patchy distribution of the host and the differential exploitation of these patches by the parasitoid provide the key to most

causes of successful biological control (Beddington *et al*, 1978). These processes can stabilize the interaction between the host and the parasitoid (Godfray & Hassell, 1994). In these systems extinction is very likely to occur on a small scale, but on a larger scale the chances of extinction will be almost zero because local extinctions will cancel out (Murdoch *et al*, 1985). The occurrence of wave-like interactions between natural enemies and aphids and the fact that parasitoids are able to eliminate an aphid population (van Steenis, 1995a; van Steenis & El-Khawass, 1995b) indicates that the size of a glasshouse is too small for heterogeneity to be effective in stabilizing the host-parasitoid interaction. As a consequence natural enemies will have to be present in sufficiently large numbers during the entire cropping period, to parasitize immigrating aphids quickly.

The pest-natural enemy interaction during seasonal inoculative control in glasshouses can be influenced more easily than in classic biological control programmes. Glasshouse experiments with several introduction schemes showed that introduction of a large amount of parasitoids at the right time results in good control. Because in commercial glasshouses it is not known when the first aphids will appear, a continuous presence of parasitoids has to be ensured. This can be done by regular releases of many parasitoids. However, the life span of *A. colemani* is very short (van Steenis, 1993) and these releases will have to be made very frequently. Costs may prevent such a system from being implemented.

Another way to establish a high number of parasitoids and to try to stabilize the host-parasitoid interaction is to introduce the pest and the natural enemy simultaneously (Huffaker & Kennet, 1956; Hofsvang & Hågvar, 1979). Because it is known when the aphids have been introduced in the glasshouse the parasitoid introductions can be made at the right time. Growers are, however, very reluctant to introduce a pest organism on purpose (Ramakers & Rabasse, 1995). A third way to introduce many parasitoids and to obtain a more stable interaction is by creating places with an alternative host. The presence of refuges for the natural enemies can result in a stable and low equilibrium pest population outside the refuge (Murdoch *et al*, 1985; 1995). Through the use of an open rearing unit of *A. colemani* on *Rhopalosiphum padi* Linnaeus (Homoptera: Aphididae) rapid control of cotton aphids in cucumber is obtained (van Steenis, 1995a).

The occurrence of hyperparasitoids, which probably emerged from the parasitized aphids in the open rearing, can result in lower parasitoid numbers and thus in an increase of the aphid population (van Steenis, 1995a). However, hyperparasitoids are mainly a problem in autumn croppings (Ramakers, 1989) and once they start to occur on a certain level also *A. aphidimyza* or a combination of *A. aphidimyza* and *A. colemani* can be introduced in glasshouses through open rearing units (Hansen, 1983; Kuo-Sell, 1987, 1989a, 1989b; Bennison, 1992).

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CURRICULUM VITAE

Machiel van Steenis werd geboren op 7 mei 1966 te Rotterdam. In september 1984 begon hij zijn studie biologie aan wat toen nog de Landbouwhogeschool Wageningen heette. In september 1990 studeerde hij af aan de Landbouwuniversiteit Wageningen in de richting Biologie en met als specialisatie Ecosysteem en de afstudeervakken dieroecologie, plantenoecologie, natuurbeheer, theoretische produktieoecologie en statistiek. Voor de vakken natuurbeheer en dieroecologie heeft hij stage gelopen, respectievelijk in Wareham, Engeland en Hódmezövásárhely, Hongarije.
Na het afstuderen begon hij met zijn promotieonderzoek "biologische bestrijding van bladluizen, in het bijzonder katoenluis, in de groenteteelt onder glas". In opdracht van de vakgroep Entomologie werd hij gedurende vier jaar gestationeerd op het Proefstation voor Tuinbouw onder Glas te Naaldwijk. Deze baan werd gevolgd door een tijdelijke aanstelling als wetenschappelijk onderzoeker aan het project "geïntegreerde bestrijding van *Myzus nicotianae* in paprika" op het proefstation.

Appendix

Appendix - host plants of the cotton aphid, *Aphis gossypii* Glover

1. PRIMARY HOST PLANTS

anholocyclic hibernation

CRUCIFERAE
Capsella bursa-pastoris (Inaizumi, 1981)

LABIATAE
Lamium amplexicaule (Inaizumi, 1981)

SCROPHULARIACEAE
Veronica persica (Inaizumi, 1981)

holocyclic hibernation

BIGNONIACEAE
Catalpa bignonioides (Kring, 1959)

CELASTRACEAE
Celastrus orbiculatus (Inaizumi, 1981)

CRASSULACEAE
Sedum purpureum (Patch, 1925)

MALVACEAE
Hibiscus syriacus (Inaizumi, 1981)

RHAMNACEAE
Rhamnus nipponica (Inaizumi, 1981)

RUBIACEAE
Rubia cordifolia var. Mungista (Inaizumi, 1981)

RUTACEAE
Citrus trees (Komazaki *et al*, 1979)

2. SECONDARY HOST PLANTS

ACANTHACEAE
Crossandra infundibuliformis (L.) Nees (=*C. undulaefolia* Salisb.) (Calilung, 1969); *Thunbergia erecta* (Starý, 1981)

ALISMATACEAE
Sagittaria latifolia Willd. (Patch, 1925)

AMARANTHACEAE
Amaranthus viridis L. (Goff & Tissot, 1932)

ANNONACEAE
Annona muricata L. (Goff & Tissot, 1932; Calilung, 1969)

ANACARDIACEAE
Mangifera indica (Starý *et al*, 1987)

APOCYNACEAE
Catharanthus roseus (L.) Don (Calilung, 1969); *Vinca sp.* (Starý, 1981)

ARACEAE
Colocasia antiquorum (Starý, 1981); *Colocasia antiquorum* var. *esculenta* (Inaizumi, 1981); *Colocasia esculenta* (Starý, 1981; Takada, 1988; Stechmann & Völkl, 1990; Carver *et al*, 1993); *Colacasia esculentum* (L.) Schott (Calilung, 1969); *Richardia (=Zantedeschia) scabra* St. Hil. (Goff & Tissot, 1932)

ASCLEPIADACEAE
Asclepias sp. (Gillette, 1908); *Asclepias verticullata* L. (Goff & Tissot, 1932); *Calotropis procera* (Starý, 1981); *Cryptostegia grandiflora* (Knight, 1944)

BEGONIACEAE
Begonia sp. (Paddock, 1919; Batchelder, 1927); *Begonia semperflorence* Link and Otto (Patch, 1925)

BIGNONIACEAE

Catalpa bignonioides Walt. (Kring, 1959); *Catalpa speciosa* (in summer) (Gillette, 1908); *Spathodea campanulata* Beauv.

BOMBACEAE
Ceiba petandra (L.) Gaertn. (=*Eriodendrion anfractuosum* DC.) (Calilung, 1969)

BUDDLEJACEAE
Buddleja officinalis Maxim (Goff & Tissot, 1932)

BURSERACEAE
Bursera simaruba (L.) Sarg. (Goff & Tissot, 1932; Calilung, 1969)

CAESALPINIACEAE
Cassia occidentalis (Carver *et al*, 1993); *Plumeria rubra* (Starý, 1981)

CARYOPHYLLACEAE
Spergula arvensis L. (Patch, 1925); *Stellaria media* Smith (Patch, 1925)

CELASTRACEAE
Euonymus japonica (Starý *et al*, 1975; Inaizumi, 1981)

CHENOPODIACEAE
Chenopodium album L. (Patch, 1925); *Beta vulgaris* L. (Calilung, 1969)

COMMELINACEAE
Commelina sp. (Calilung, 1969; Carver *et al*, 1993); *Commelina communis* (Inaizumi, 1981)

COMPOSITAE
Ageratum conyzoides L. (Calilung, 1969; Starý *et al*, 1987); *Ambrosia trifada* (Gillette, 1908); *Bidens frondosa* L. (Patch, 1925); *Bidens pilosa* (Starý, 1981); *Chrysanthemum sp.* (Goff & Tissot, 1932); *Chrysanthemum morifolium* (Tamaki & Allen, 1969); *Cosmos molifolium* var. *sinensis* (Inaizumi, 1981); *Dedranthemum grandiflora* Tzvelev. (Vehrs *et al*, 1992); *Erigeron canadensis* (Gillette, 1908); *Erigeron ramosus* (Walt.) B.S.P. (Goff & Tissot, 1932); *Eupatorium sp.* (Starý, 1981); *Eupatorium petaloideum* Britt. (Goff & Tissot, 1932); *Eupatorium villosum* (Starý, 1981); *Gerbera jamesonii* Bolus (Goff & Tissot, 1932); *Gnaphalium obtusifolium* L. (Goff & Tissot, 1932); *Gnaphalium spathulatum* Lam. (Goff & Tissot, 1932); *Helianthus sp.* (Starý, 1981); *Lactuca sp.* (Goff & Tissot, 1932); *Lactuca sativa* L. (Calilung, 1969); *Leontodon autumnale* L. (Patch, 1925); *Senecio vulgaris* L. (Patch, 1925); *Taraxacum dens-leonis* (Gillette, 1908)

CONVOLVULACEAE
Convolvulus sp. (Gillette, 1908); *Convolvulus sepium* L. (Patch, 1925); *Ipomoea batatas* L. (Poir.) (Goff & Tissot, 1932; Calilung, 1969); *Ipomoea pandurata* L. (Goff & Tissot, 1932)

CRASSULACEAE
Sedum purpureum Tausch (Patch, 1925)

CRUCIFERAE
Brassica sp. (Patch, 1925); *Brassica chinensis* L. (Calilung, 1969); *Brassica integrifolia* O.E. Schulz (Calilung, 1969); *Brassica oleracea* var. *capitata* L. (Calilung, 1969); *Brassica oleracea* var. *italica* Plench. (Calilung, 1969); *Capsella bursa-pastoris* (Gillette, 1908; Patch, 1925; Batchelder, 1927; Inaizumi, 1981); *Lepidium virginicum* (Gillette, 1908); *Raphanus sativus* L. (Calilung, 1969)

CUCURBITACEAE
Benincasa hispada (Thumb.) Cogn. (Calilung, 1969); *Citrullus lanatus* (Gillette, 1908; Goff & Tissot, 1932; Moursi *et al*, 1985; Ekukole, 1990; Stechmann & Völkl, 1990); *Citrullus vulgaris* L. (Paddock, 1919; Calilung, 1969; Ekukole, 1990); *Cucumis dispsacus* (Starý, 1981); *Cucumis melo* L. (Paddock, 1919; Patch, 1925; Batchelder, 1927; Gillette, 1908; Goff & Tissot, 1932; Calilung, 1969; Kennedy & Kishaba, 1976; Starý, 1981); *Cucumis sativus* L. (Gillette, 1908; Paddock, 1919; Patch, 1925; Batchelder, 1927; Goff & Tissot, 1932; Calilung, 1969; Wyatt & Brown, 1977; Inaizumi, 1981; Attia & El-Hamaky, 1984; Ferrándiz Puga & Gutiérrez Pérez, 1986); *Cucurbita foetidissima* (Gillette, 1908; Goff & Tissot, 1932); *Cucurbita maxima* Duch. (Gillette, 1908; Paddock, 1919; Patch, 1925; Batchelder, 1927; Goff & Tissot, 1932; Khalifa & Sharaf El-Din, 1964; Calilung, 1969); *Cucurbita pepo* (Gillette, 1908; Paddock, 1919; Patch, 1925; Batchelder, 1927; Aldyhim & Khalil, 1993); *Hagenaria vulgaris* (Paddock, 1919); *Lagenaria siceraria* Standl. (=*L. leucantha* (Duch.)) (Calilung, 1969); *Luffa spp.* (Calilung, 1969); *Momordica* (=*Eiballium*) *sp.* (Starý, 1981); *Momordica charantia* L. (Calilung, 1969); *Sechium edule* Sw. (Calilung, 1969)

EUPHORBIACEAE
Acalypha sp. (Goff & Tissot, 1932; Starý, 1981); *Acalypha alopecuroides* (Starý, 1981); *Acalypha hispida* Burm. (Calilung, 1969); *Acalypha wilkesiana* (Starý, 1981); *Breynia rhamonoides* (Retz.) Muell.-Arg. (Calilung, 1969); *Euphorbia hirta* L. (Calilung, 1969); *Securinega flexuosa* Muell.-Arg. (Calilung, 1969)

IRIDACEAE
Gladiolus (Goff & Tissot, 1932)

LABIATAE
Nepeta hederacea Trevisan (Patch, 1925); *Salvia coccinea* (Carver *et al*, 1993); *Salvia splendens* (Patch, 1925); *Scutellaria multigrandulosa* (Kearney) (Goff & Tissot, 1932);

LAURACEAE
Persea americana Mill. (Calilung, 1969; Carver *et al*, 1993); *Persea persea* Cockerell. (Goff & Tissot, 1932)

LEGUMINOSAE
Arachis hypogea L. (Calilung, 1969; Ekukole, 1990); *Cajanus cajan* (L.) Millsp. (Calilung, 1969); *Calliandra portoricensis* (Jacq.) Benth. (Calilung, 1969); *Cassia sophora* (Starý, 1981); *Cassia tora* L. (Goff & Tissot, 1932); *Dolichos lablab* L. (Calilung, 1969); *Gliricida sepium* (Jacq.) (Calilung, 1969); *Medicago sativa* L. (Patch, 1925); *Melilotus alba* Lam. (Patch, 1925); *Phaseolus multiflorus* Willd. (Patch, 1925); *Phaseolus lunatus* L. (Calilung, 1969); *Phaseolus radiatus* L. (=*P. aureus* Roxb.) (Calilung, 1969); *Phaseolus vulgaris* L. (Calilung, 1969); *Pisum sativum* L. Chicaro (Calilung, 1969); *Psophocarpus tetragonolubus* (L.) DC. (Calilung, 1969); *Trifolium pratense* L. (Patch, 1925); *Vigna sinensis* (L.) Sev. (Calilung, 1969); *Vigna sesquipedalis* Fruw. (Calilung, 1969); *Vigna unginculata* (Paddock, 1919)

LILIACEAE
Asparagus officinalis L. (Patch, 1925); *Lilium candidum* L. (Goff & Tissot, 1932); *Lilium longiflorum* Thunb. (Goff & Tissot, 1932; Calilung, 1969); *Tulipa sp.* (Goff & Tissot, 1932)

LOGANIACEAE
Strychnos spinosa Lam. (Goff & Tissot, 1932)

MALVACEAE
Abelmoschus esculentus (L.) Moenck (Calilung, 1969; Kandoria & Jamwal, 1988); Ekukole, 1990); *Althaea sp.* (Starý, 1981); *Gossypium sp.* (Calilung, 1969); *Gossypium barbadense* (Khalifa & Sharaf El-Din, 1964); *Gossypium herbaceum* L. (Paddock, 1919; Patch, 1925; Kring, 1959; Ekukole, 1990); *Gossypium hirsutum* L. (Gillette, 1908; Dunnam & Clark, 1938; Agarwala & Saha, 1986; Akey & Butler, 1989; Ekukole, 1990); *Hibiscus sp.* (Starý *et al*, 1987; Carver *et al*, 1993); *Hibiscus cannabinus* L. (Starý, 1981; Ekukole, 1990); *Hibiscus esculentus* L. (Paddock, 1919; Goff & Tissot, 1932; Khalifa & Sharaf El-Din, 1964; Azab *et al*, 1965; Moursi *et al*, 1985); *Hibiscus rosasinensis* L. (Goff & Tissot, 1932; Calilung, 1969; Cruz & Bernardo, 1971; Starý, 1981; Starý *et al*, 1987); *Hibiscus sabdariffa* L. (Calilung, 1969; Ekukole, 1990); *Hibiscus syriacus* (Kring, 1959; Inaizumi, 1981; Takada, 1988); *Malva alcea* L. (Patch, 1925); *Malva parviflora* (Moursi *et al*, 1985); *Malva rotundifolia* (Patch, 1925; Batchelder, 1927); *Sida sp.* (Ekukole, 1990); *Sida acuta* Burm. (Goff & Tissot, 1932); *Sida cordifolia* L. (Goff & Tissot, 1932); *Urena sp.* (Ekukole, 1990); *Urena lobulata* L. (Goff & Tissot, 1932)

MYRTACEAE
Psidium guajava L. (Goff & Tissot, 1932; Calilung, 1969; Starý, 1981)

NYCTAGINACEAE
Bougainvillea (Goff & Tissot, 1932)

ONAGRACEAE
Oenothera biennis L. (Patch, 1925; Batchelder, 1927)

PIPERACEAE
Piper sp. (Starý, 1981)

PLANTAGINACEAE
Plantago lanceolata L. (Patch, 1925); *Plantago major* L. (Patch, 1925); *Plantago ovata* L. (Sagar, 1989); *Plantago virginica* L. (Goff & Tissot, 1932)

POLYGONACEAE
Antigonon leptopus Hook & Arn. (Goff & Tissot, 1932); *Coccoloba sp.* (Starý, 1981); *Fagopyrum esculentum* (Inaizumi, 1981); *Rumex sp.* (Gillette, 1908); *Rumex acetosella* (Patch, 1925; Batchelder, 1927); *Rumex crispus* L. (Patch, 1925); *Triplaris cumingiana* Fisch. (Calilung, 1969)

PORTULACACEAE
Portulaca oleraceae L. (Patch, 1925)

PRIMULACEAE
Lysimachia stricta Ait. (Patch, 1925)

RHAMNACEAE
Rhamnus catharctica (Gillette, 1908)

ROSACEAE
Fragaria sp. (Oatman & Platner, 1972; Oatman *et al*, 1983); *Fragaria chiloensis* Duchesne (Patch, 1925); *Fragaria virginica* (Batchelder, 1927); *Pyrus communis* L. (Goff & Tissot, 1932); *Pyrus japonica* Thunb. (Patch, 1925)

RUBIACEAE

Borreria articularis (L.f.) F.N. Williams (Calilung, 1969); *Borreria verticillata* (Starý, 1981); *Coffea arabica* L. (Calilung, 1969); *Ixora coccinae* Starý, 1981); *Mussaenda erythrophylla* Schumm. & Thonn. (Calilung, 1969)

RUTACEAE
Citrus spp. (Goff & Tissot, 1932; Rosen, 1967; Starý, 1967; Starý *et al*, 1975; Starý, 1981); *Citrus aurantifolia* (Christm.) (Calilung, 1969); *Citrus aurantium* L. (Patch, 1925; Calilung, 1969); *Citrus grandis* Osb. (Calilung, 1969); *Citrus nobilis* Lour. (Calilung, 1969); *Citrus sinensis* (L.) Osbeck (Schlinger & Hall, 1960); *Citrus unshiu* (Komazaki, 1982)

SAXIFRAGACEAE
Philadelphus coronarius L. (Patch, 1925)

SCROPHULARIACEAE
Veronica cinerea (Starý, 1981); *Veronica officinalis* L. (Patch, 1925; Batchelder, 1927); *Veronica persica* (Inaizumi, 1981; Nozato, 1987a, 1987b); *Veronica serpyllifolia* L. (Patch, 1925)

SOLANACEAE
Campsis annuum L. (Calilung, 1969); *Capsicum sp.* (Starý, 1981); *Capsicum annuum* (Jawal *et al*, 1988; Kandoria & Jamwal, 1988); *Capsicum frutescens* L. (Calilung, 1969); *Datura stramonium* L. (Patch, 1925; Goff & Tissot, 1932; Khalifa & Sharaf El-Din, 1964); *Lycopersicon lycopersicum* (L.) Karsten (Calilung, 1969); *Nicotiana tabacum* L. (Goff & Tissot, 1932); *Solanum sp.* (Starý, 1981); *Solanum aculeatissimum* Jacq. (Goff & Tissot, 1932); *Solanum melongena* L. (Patch, 1925; Goff & Tissot, 1932; Calilung, 1969; Cruz & Bernardo, 1971; Inaizumi, 1981; Moursi *et al*, 1985; Jawal *et al*, 1988); *Solanum torvum* (Starý, 1981); *Solanum tuberosum* L. (Goff & Tissot, 1932; Calilung, 1969; Inaizumi, 1981; Starý, 1981); *Solanum verbascifolium* L. (Goff & Tissot, 1932); *Withania somnifera* L. (Subba Rao & Sharma, 1962)

STERCULIACEAE
Theobroma cacao (Starý, 1981)

UMBELLIFERAE
Apium graveolens L. (Patch, 1925; Goff & Tissot, 1932); *Coriandrum sativum* (Hayat, 1972)

URTICACEAE
Urtica sp. (Samanta *et al*, 1985)

VERBENACEAE
Callicarpa purpurea Juss. (Patch, 1925); *Clerodendron siphonanthus* R.Br. (Goff & Tissot, 1932); *Clerodendron thomsonae* Balf. (Patch, 1925); *Clerodendrum intermedium* Cham. (Calilung, 1969); *Lantana sellowiana* Link and Otto (Goff & Tissot, 1932); *Petrea volubilis* L. (Calilung, 1969); *Premna odorata* Blanco (Calilung, 1969); *Verbena sp.* (Goff & Tissot, 1932); *Verbena bracteosa* Michx (Patch, 1925)

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OTHERS
Alsine media L. Chickweed (Goff & Tissot, 1932)
Boerhaavia diffusa Starý, 1981a)
Boerhaavia erecta Starý, 1981a)
Boerhaavia viscosa Lag. & Rodr. (Goff & Tissot, 1932)
Callophyllum antillianum Starý, 1981a)
Callophyllum inophyllum L. Ball Kamani (Goff & Tissot, 1932)
Cayratia japonica (Inaizumi, 1981)
Cestrum diurnum L. Day Jessamine (Goff & Tissot, 1932); Starý, 1981a)
Chaptalia sp. Starý, 1981a)
Chrozophora plicata Khalifa & Sharaf El-Din (1964)
Chrysobalanus oblongifolius Micx. Pigeon Plum (Goff & Tissot, 1932)
Clotalaria striata DC. (Goff & Tissot, 1932)
Cuphea micropetala Hbk. (Goff & Tissot, 1932)
Duranta repens Starý, 1981a)
Eriobotrya japonica Lindl. Loquat (Goff & Tissot, 1932)
Melantherum deltoidea Starý, 1981a)
Moghania macrophylla Sen *et al* (1987)
Monarda fistulosa L. Bee Balm (Goff & Tissot, 1932)
Penstemon hirsutum (L.) Willd. Beard tongue (Goff & Tissot, 1932)
Malvastrum coromandelianum Starý, 1981a)
Mammea americana L. Mammeeapple (Goff & Tissot, 1932)
Pittosporum tobira Ait. Pittosporum (Goff & Tissot, 1932); Starý, 1981a)
Pluchea sp. (Goff & Tissot, 1932)
Pluchea carolinensis Starý, 1981a)
Rauwolfia tetraphyla Starý, 1981a)
Riedlea corchorifolia (L.) DC (Goff & Tissot, 1932)
Ruellia sp. Starý, 1981a)
Ruellia paniculata Starý, 1981a)
Sesame indicum Moursi *et al* (1985)
Tridax procumbens Starý, 1981a)
Vitex negundo Starý, 1981a)
Waltheria americana Starý, 1981a)
Zinnia elegans (Inaizumi, 1981)