Host plant adaptation in the glasshouse whitefly

Promotor Dr. J. C. van Lenteren
Hoogleraar in de Entomologie
in het bijzonder de Oecologie der Insekten

David Crawshaw Thomas

Host plant adaptation in the glasshouse whitefly

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Aan de lijdende kerk, vooral mijn broeders and zusters in Albanië
Dedicated to the sufferring church, especially my bothers and sisters in Albania.

Stellingen

1 In designing experiments to test the susceptibility of plant cultivars against an insect pest, insect lines originating from different host plants should be compared so as to incorporate the effect of 'pre-conditioning' in the analysis, this improving the reliability of the test method concerned.

Beregovy, V. H., Starks, K. J. and Janardan, K. J., 1988. Environ. Entomol. 17, 59-62.
Lowe, H. B. J., 1973. Bull. ent. Res. 62, 549-556.
McCaulley, G. W. Jr., Margolies, D. C. Collins, R. D. and Reese, J. C., 1990. Environ. Entomol. 19, 949-954.
Schotzko, D. J. and Smith, C. M., 1991. J. Econ. Entomol. 84, 1083-1087.

2 Vague descriptions of the methods used to rear plant and insect material in published experimental studies, hinders the comparison of experimental results between publications, as such comparisons cannot accurately consider possible differences in the rearing methodologies used, that may have ultimately affected so well the quality of the data as the experimental values obtained.

this thesis
Thomas, D. C., 1992. Proc. Exper. & Appl. Entomol., N.E.V., Amsterdam 3, 201-207.
Mason, L. J., Pashley, D. P. and Johnson, S. J., 1987. Florida Entomol. 70, 49-58.

3 The lack of published studies assessing the suitability of different methods to test the probable durability of the resistance of newly released cultivars, may lead to the release of genetically engineered resistant cultivars where the costs of deployment are not recuperated before the resistance concerned is overcome.

this thesis
Anderson, C., 1992. Nature 355, 661.
Gibbons, A., 1991. Science 254, 646.

4 Unlike many previous studies of whitefly performance which were done upon the basis of a single generation, such studies should be conducted over several generations so as to account for the between generation found within laboratory populations, even under standardised conditions.

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Boxtel, W. van, Woets, J. and Lenteren, J. C. van, 1978. Med. Fac. Landbouw. Rijksuniv. Gent 43/2, 397-408.
Merendonk, S. van and Lenteren, J. C. van, 1978. Med. Fac. Landbouw. Rijksuniv. Gent 43/2, 421-429.
Sas, J. van, Woets, J. and Lenteren, J. C. van, 1978. Med. Fac. Landbouw. Rijksuniv. Gent 43/2, 409-420.
Nicholson, A. J., 1954. Quant. Biol. 22, 153-173

5 The assessment of an insect's preference for certain host plant species, should incorporate the use of insect lines 'pre-conditioned' upon the host plants being tested, as this allows a comparison between the effect of an insect choosing the plant from which it came and the plant upon which its subsequent performance is the highest.

this thesis
Courtney, S. P., Chen, G. K. and Gardner, A., 1989. Oikos 55, 55-65.

6 The suggestion that the deployment of isoenzyme electrophoretic techniques for the detection of genetic differentiation between insect populations is a reliable and easily applicable methodology, does not hold for the glasshouse whitefly.

this thesis
Wool, D., Gerling, D., Nolt, B. L. Constantino, L. M., Belotti, A. C. and Morales, F. J., 1989. J. appl. Ent. 107, 344-350.

7 Life history studies of insect performance on a host plant under no choice conditions, should differentiate between females not ovipositing and thus exhibiting non-preference for the host plant and females ovipositing and thus exhibiting preference for the host plant. This differentiation would reduce discrepancies in comparisons of tests of insect performance done under laboratory (often no choice) and glasshouse (often choice) conditions.

this thesis
Romanow, L. R., Ponti, O,. M. B. de and Mollema, C., 1991. Entomol. exp. & appl. 60, 247-259

8 Science proves nothing. It purely draws inferences from data obtained by experimentation which in turn is subject to certain limiting assumptions.

9 The notion of the World's being a great machine, going on without the Interposition of God, as a clock continues to go without the Assistance of a Clockmaker; is the notion of Materialism and Fate, and tends, (under pretence of making God a Supra-mundane Intelligence,) to exclude Providence and God's Government in reality out of the World.

Clarke's first reply cited in: Koyre, A. and Cohen, I. B., 1962. Newton and the Leibniz-Clarke Correspondence with notes on Newton, Conti, and Des Maizeau. Archives internationales d'histore des sciences 15, 63-126.

10 De mensen zijn nu eenmaal zo dwaas dat het op een andere manier dwaas zou zijn om niet dwaas te zijn.

Blaise Pascal. Gedachten over de Godsdienst. Kampen, Uitgeverij Kok. p. 40.

Stellingen behorende bij het proefschrift "Host plant adaptation in the glasshouse whitefly" door David Crawshaw Thomas.

Wageningen, 22 January 1993

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PREFACE

Coming to Wageningen to commence my PhD was my first time ever in the Netherlands. It is never easy adapting to a different country and that also includes work. The Dutch PhD system and universities are often very different in their workings, from their British counterparts. I now take the opportunity to thank all those who have helped during my studies.

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Many colleagues have given advice during my studies and are acknowledged accordingly by the chapters of this thesis. One colleague I particularly thank is Frans Dieleman. who has from the beginning of my studies, always been generous in giving me his time.

At this point I would like to thank Ans Klunder-Wind. Without her practical advice on all aspects of Dutch life and language, professional and otherwise, her sense of humour and her listening ear, then especially in my first year here in Wageningen, I might easily have given up and returned to the U.K. My time in Wageningen has been made very pleasant by the superb accommodation that I have enjoyed by Mrs. T. de Wilde van Buul. Learning Dutch was in the beginning like trying to do a good impersonation of Donald Duck. However this task was made much more enjoyable by sharing an office with two colleauges, Leentje den Boer and Nanda Kaashoek, who took it as pride and pleasure to teach me and have also become good friends. Since their departures, Andries (give me $2), Roel and Jaqueline have arrived in the office. Their humour and everyday help at work has been appreciated. John Stanley is thanked for the many times he has put me up in Germany, allowing me to get away from it all and to come back fresh and invigorated for the task ahead.

Work is but a part of life and outside of working hours I have had the privilege to enjoy much. I am grateful to and thank all the people I know and have known in Ichthus, Gemeente Immanuël and Gemeente Salem. Thank you Wim and Margaret Spronk for the 'Engelstalige Kring' without which I would not have become so at home here. Bert Smit, Seerp and Maaike Wigboldus, Rudi and Maaike Heling, Jan and Mineke Meiras, Jan Bernhard and Tineke Struik, Hans and Kitty van de Beek, Johan and Rickie Natergal, Conny Lampe and Gijsbert and Oda van Oeveren are especially thanked for their warm friendship, encouragement, listening ears, advice and sometimes plain talking which they have given me, all of which has helped me along the pilgrim's path. The 'Centrum Kring' are thanked for all their support and prayers. During my studies much extra-curricular opportunity has been afforded to me. Thanks to the staff of Youth With a Mission Heidebeek for challenging me with a mini Discipleship Training School in the Summer of 1991, the East European Mission (Oosteuropa Zending Nederland) for allowing me to participate in their first trip to Albania at Easter, 1992 and Horizons Britain for allowing me to participate in their Pioneer Trip to the Balkans in the summer of 1992. These activities so well as being fundamental in the shaping of my future, have also stimulated me in the furthering of my studies.

My final word of thanks is to my parents. They have seen my ups and downs in life and through thick and thin have always in the end been there. Their steadfast christian faith, their resoluteness in stimulating me and above all in accepting me for whom I am, are qualities which have moulded me and for which I am indebted to them.

WAARDPLANTAANPASSING IN DE KASWITTEVLIEG

OVERZICHT

Inleiding

Hoewel er veel onderzoek gedaan is naar de ontwikkeling en het begrip van waardplantresistentie en biologische bestrijding als plaagbestrijdingsstrategieën, zijn er maar weinig studies geweest die zich gericht hebben op de interaktie tussen deze twee bestrijdingsmethoden waar deze gecombineerd worden. Ecologisch onderzoek heeft echter een duidelijk raamwerk geleverd waarbinnen biologische bestrijding en waardplantresistentie in een tritrofische context kunnen worden bestudeerd. Zulk een raamwerk benadrukt dat de veranderingen in de reaktie van een plaag op haar waardplant, de dynamiek van de interaktie tussen de plaag en haar natuurlijke vijand kunnen beïnvloeden. Omgekeerd kan het gebruik van een natuurlijke vijand om de dichtheid van een plaag beneden een bepaald niveau te houden, de interaktie tussen de plaag en haar waardplant beïnvloeden. Binnen dit raamwerk moet rekening gehouden worden met het vermogen van de plaag om zich aan de waardplant aan te passen. Daar waar aanpassing plaats vindt, zal de resistentie van de waardplant voor de plaag minder worden. Ook kan de doeltreffendheid van het biologische bestrijdingsmiddel dat gebruikt wordt om de plaag te bestrijden beïnvloed worden. Deze tritrofische systemen moeten vanuit de evolutie-ecologie bestudeerd worden. Deze benadering onderstreept het aanpassend karakter van de interakties, meer dan een zuivere ecologische benadering die tot nu toe de basis geleverd heeft voor het bestuderen van de populatiedynamiek van plaagbestrijdingssystemen.

In verband met deze tritrofische benadering van plaagbestrijding is het systeem *Encarsia formosa* (parasiet) - *Trialeurodes vaporariorum* (plaag; kaswittevlieg) - waardplant als een model-systeem genomen. In dit proefschrift worden aspecten van de bi-trofische interaktie tussen de witte vlieg en haar waardplanten beschreven. Het systeem is onderwerp van voortgaande studie door de vakgroep Entomologie van de Landbouwuniversiteit te Wageningen. Dit onderzoek heeft zich geconcentreerd op het voorkeurs- en prestatiegedrag van wittevlieg-plant relaties (van Lenteren en Noldus, 1990), het parasiteringsgedrag en de parisiteringsefficiëntie van *E. formosa* (Noldus en van Lenteren, 1990), de verbeterde resistentie van waardplanten tegen witte vlieg (de Ponti et al., 1990), en de vermindering van de incompatibiliteitsproblemen van waardplantresistentie met betrekking tot het gebruik van *E. formosa* (van Lenteren en de Ponti, 1991). Deze studies hebben een fundament geleverd voor de verbetering van wittevliegbestrijding in kassen door *E. formosa* (van Lenteren en Woets, 1988). Eerdere studies van bijvoorbeeld van Boxtel et al. (1978) duidden aan dat de witte vlieg in staat is, binnen haar waardplant-bereik, zich aan te passen van de ene waardplant aan of naar de andere. De snelheid waarmee deze aanpassing plaats vindt en of er genetisch te onderscheiden soorten van de kaswittevlieg bestaan in verhouding tot dat proces, werd uit die studies echter niet duidelijk. Het vermogen van de witte vlieg om zich snel aan nieuwe waardplanten aan te passen, of het bestaan van verschillende stammen van de witte vlieg in relatie tot dat proces, kan gevolgen hebben voor de doeltreffendheid van wittevliegbestrijding door *E. formosa*.

Onderzoeksvragen en experimenten

Het onderzoek dat in dit proefschrift beschreven wordt had tot doel de volgende vragen te beantwoorden:

1. Hoe snel zal witte vlieg zich kunnen aanpassen wanneer ze worden overgeplaatst van de ene waardplant naar de andere (hoofdstuk 2) ?
2. Vinden 'trade-offs' plaats gedurende de aanpassing, met betrekking tot de oorspronkelijke waardplant van de witte vlieg (hoofdstuk 2) ?
3. Zou opkweek van witte vlieg op de ene waardplant zodanig kunnen gebeuren, dat ze een zodanige 'vooraanpassing' opdoen die aanpassing aan een andere waardplant vergemakkelijkt (hoofdstuk 3) ?
4. Beïnvloedt de waardplant waar de witte vlieg vanaf komt haar voorkeur voor andere waardplanten (hoofdstuk 4) ?
5. Bestaan er genetisch te onderscheiden stammen van de witte vlieg (hoofdstuk 5)?

De snelheid waarmee de witte vlieg zich aan de waardplant aanpast, werd onderzocht door de veranderingen in de parameters van de levensgeschiedenis over opeenvolgende generaties witte vlieg te meten. De relatieve bijdrage van genotypische en fenotypische variatie aan het aanpassingsproces werd niet onderzocht. Dit was een bewuste keuze, omdat een eenvoudige meting van veranderingen in ecologische parameters over opeenvolgende generaties witte vlieg een algehele indicatie zou geven van intra- en intergeneratie variabiliteit, die vervolgens gebruikt zou kunnen worden om uit te rekenen hoeveel herhalingen nodig zijn om nauwkeurig elke component van genetische variatie te kunnen vaststellen. Het leggen van eieren, de larvale mortaliteit en de juveniele ontwikkelingsduur werden onderzocht. Dit zijn indicatoren voor de fitness van een populatie met betrekking tot de netto reproductiesnelheid.

Het hoofddoel was om een methode te ontwikkelen waarmee de snelheid en mate van aanpassing van de witte vlieg aan de waardplant vastgesteld kan worden. Dit bracht met zich mee dat veel logistieke problemen met betrekking tot het kweken van insekten en plantmateriaal overwonnen moesten worden, om zodoende te zorgen dat het materiaal dat bij alle witte vlieg generaties gebruikt zou worden vergelijkbaar was. Alle experimenten werden uitgevoerd in een klimaatcel onder standaard omstandigheden van licht, temperatuur en relatieve luchtvochtigheid. De wittevliegkweken werden als discrete generaties gehouden. Bij elke generatie die getest werd, werden de witte vliegen verwijderd uit de betreffende kweken door een zuiger te gebruiken. Ze werden licht verdoofd met behulp van kooldioxide en een mannetje en een vrouwtje werden in een bladkooitje geplaatst dat aan de waardplant werd bevestigd. Er werden 20 tot 40 van zulke bladkooitjes per wittevliegpopulatie per onderzochte waardplant gebruikt. Na 24 uur werden de witte vliegen en de bladkooitjes verwijderd en werd het aantal gelegde eieren per witte vlieg vrouwtje geteld. De ontwikkeling van de eieren werd dan gevolgd, om larvale mortaliteit en de juveniele ontwikkelingsduur vast te stellen. De ontwikkelde methode werd gebruikt om de aanpassingssnelheid van de wittevliegpopulatie van gerbera naar vier komkommer cultivars vast te stellen. 'Trade-offs' met betrekking tot de oorspronkelijke waardplant (gerbera) werden gezocht nadat de aanpassing aan komkommer eenmaal vastgesteld was. Dezelfde methode werd gebruikt om vast te stellen of witte vlieg ertoe gebracht kon worden zich aan te passen aan een Nederlandse paprika-cultivar, en of de waardplant waar de witte vlieg oorspronkelijk vanaf kwam dit proces wel of niet beïnvloedde.

De voorkeur van de witte vlieg die opgekweekt was op drie verschillende waardplanten (komkommer, gerbera, en paprika), werd gemeten in een meerkeuze test, om vast te stellen of de waardplant waar de witte vlieg oorspronkelijk vanaf kwam de voorkeur voor andere waardplanten beïnvloedt met betrekking tot hun geschiktheid voor witte vlieg.

Uiteindelijk werd geprobeerd om een electroforetische techniek voor de kaswittevlieg te ontwikkelen. Hierbij werd gebruik gemaakt van zetmeel en polyacrylamidegelelectroforese methoden voor het vaststellen van de variatie in iso-enzymallelfrequenties. Met behulp van deze techniek zou het mogelijk kunnen zijn om het bestaan te testen van genetisch te onderscheiden stammen van wittevliegpopulaties, gebaseerd op de genetische afstanden.

Resultaten

Witte vliegen die op gerbera waren gekweekt en vervolgens op komkommer geplaatst werden, toonden aanpassing binnen één generatie. Daarna fluctueerden de parameters van de witte vlieg zowel tussen komkommer cultivars, als tussen opeenvolgende generaties. De mate van variatie was hierbij circa 50% voor het aantal eieren gelegd per vrouwtje per 24 uur, circa 10% voor de juveniele ontwikkelingsduur (in dagen) en circa 25% voor het algehele percentage juveniele mortaliteit. Er werden geen 'trade-offs' gevonden, maar deze studie onderzocht slechts één mogelijkheid, namelijk die tussen gerbera en komkommer. 'Trade-offs' zouden gevonden kunnen worden voor andere wittevliegpopulaties en andere witte vlieg - waardplant combinaties.

Het werken met witte vlieg op Nederlandse paprika gaf aan dat als witte vlieg voor één generatie op *Lycopersicon hirsutem* cv. glabratum was opgekweekt, vóór ze overgebracht werden naar paprika, hun prestatie veel beter was dan wanneer ze opgekweekt waren op gerbera, komkommer of tomaat. Alhoewel de plant waarop de witte vliegen waren opgekweekt vóór het overbrengen naar paprika de prestatie op deze waardplant beïnvloedde, leek dit verschijnsel niet gerelateerd te zijn aan de kwaliteit van de betreffende waardplant met betrekking tot de prestatie van de witte vlieg.

De voorkeurstest gaf aan dat de invloed van de waardplant zodanig was, dat de witte vlieg die oorspronkelijk van een gegeven waardplant kwam, een grotere voorkeur tentoonspreidde voor die waardplant dan andere wittevliegpopulaties. Er was onafhankelijk van welke waardplant een wittevliegpopulatie oorspronkelijk af kwam, een onverandelijke rangorde van voorkeur van komkommer > gerbera > paprika. Deze rangorde is dezelfde als die voor de geschiktheid van deze waardplanten voor witte vlieg.

De pogingen gedurende een aantal maanden om een betrouwbare electroforesetechniek voor de kaswittevlieg te ontwikkelen, waren niet succesvol. Er zijn echter nog steeds veel mogelijkheden voor verbetering; vanwege gebrek aan tijd heb ik deze niet verder ontwikkeld.

Conclusies

De problemen die men tegenkomt in het ontwikkelen van een geschikte methode voor het vaststellen van de aanpassing aan een waardplant, benadrukken het belang van consequent gebruik van sterk gestandardiseerd plant - en insekten - materiaal van hoge kwaliteit. De kaswittevlieg blijkt zich binnen enkele generaties goed te kunnen aanpassen aan planten binnen haar waardplantbereik. Op meer marginale waardplanten zoals bijvoorbeeld de paprika, is de aanpassingssnelheid lager. Het blijkt echter dat onafhankelijk van welke waardplant witte vlieg oorspronkelijk kwam, de rangorde van voorkeur en prestatie komkommer > gerbera > paprika is. Wanneer de kwaliteit van de waardplant waar witte vlieg oorspronkelijk vanaf komt afneemt, neemt de grootte van het verschil tussen waardplanten binnen de rangorde af. De parameters van de levensgeschiedenis konden goed gebruikt worden als indicatoren voor verschillen in de prestatie van witte vlieg op waardplanten. De snelheid waarmee een populatie zich aanpast aan een waardplant zoals gemeten met deze parameters, zou een goede indicatie kunnen zijn voor de duurzaamheid van de resistentie van de waardplant tegen witte vlieg. Al dit soort testen met betrekking tot prestatie van witte vlieg moeten echter over verschillende opeenvolgende wittevlieggeneraties uitgevoerd worden, om zodoende rekening te houden met de inter-generatie variatie, zelfs wanneer witte vlieg al aan de waardplant in kwestie aangepast is. In 'geen-keuze' testen van witte vlieg prestatie moet zorg besteed worden aan het onderscheiden van leggende en niet-leggende vrouwtjes, die respectievelijk de antibiose en antixenose aspecten van waardplant-resistentie aangeven. Tenslotte moet nog onderzocht worden of er wel of geen genetisch te onderscheiden stammen van de kaswittevlieg bestaan, en ook voor wat betreft de relatieve bijdrage van genetische en fenotypische variatie aan wittevliegprestatie en aanpassing.

Praktische implicaties

Alhoewel de relatie tussen waarnemingen uit mijn studie en hun toepasbaarheid in de praktijk nog vastgesteld moet worden, worden nu enkele suggesties gedaan. Als witte vliegen overgebracht worden van het ene gewas op het andere onder de omstandigheden die gelden in praktijkkassen, bijvoorbeeld door geïnfecteerd plantmateriaal of door witte vliegen die de kas binnenkomen via de ventilatie openingen (ramen), dan zullen deze witte vliegen zich binnen enkele generaties aan het betreffende gewas aanpassen, tenzij het gewas marginaal is voor witte vlieg, zoals bijvoorbeeld paprika. In zo'n geval zal de kans dat witte vlieg zich aanpast aan het gewas klein zijn. Wanneer de raamopeningen afgeschermd worden met horregaas en de hygiëne met betrekking tot het verplaatsen en weggooien van plantmateriaal strikt nageleefd wordt, dan zal de wittevliegverplaatsing tussen kassen afnemen. Daar waar meer dan één cultivar van een siergewas geteeld wordt in dezelfde kas, neemt de kans toe dat witte vlieg zich zal aanpassen aan één cultivar en zodoende 'voorbereid' wordt om zich aan te passen aan andere cultivars in de kas, waaraan zij zich anders niet zou hebben aangepast.

OVERVIEW

Introduction

Although much research towards the development and understanding of plant resistance and biological control as pest control strategies has been done, few studies have concentrated upon the interaction between these two control methods where they are combined. However, ecological research has provided a firm framework in which biological control and plant resistance can be studied within a tritrophic context. Such a framework emphasises how the changes in the response of a pest to its host plant, may consequently affect the dynamics of the interaction between it and its natural enemy. Conversely, how the use of a natural enemy to maintain pest density to below a certain level, may affect the interaction between the pest and its host plant. Within this framework, the pest's potential to adapt to the host plant, needs to be considered. Where adaptation occurs, the resistance of that host plant to the pest diminishes and also the efficacy of the biological control agent (s) used to control that pest may be affected. These tritrophic systems, should be studied from the viewpoint of evolutionary ecology. This stresses the adaptive character of the interactions, more than a pure ecological approach, which until now has provided the basis for studying the population dynamics of pest control systems.

In relation to this tritrophic approach to pest control, the system *Encarsia formosa* (parasitoid) - *Trialeurodes vaporariorum* (pest; common name, glasshouse whitefly) - host plant was taken as a model system. In this thesis, aspects of the bi-trophic interaction between whitefly and its host plants are described. This system is a subject of continuing studies at the Department of Entomology in Wageningen. Here, research has concentrated upon preference and performance aspects of whitefly-plant relationships (van Lenteren and Noldus, 1990), the parasitization behaviour and parasitizing efficiency of *E. formosa* (Noldus and van Lenteren, 1990), the improved resistance of host plants to whitefly (de Ponti et. al., 1990) and the reduction of incompatibility problems of host plant resistance with respect to the deployment of *E. formosa* (van Lenteren and de Ponti, 1991). These studies have provided a fundamental basis for the improvement of whitefly control in commercial glasshouses by *E. formosa* (van Lenteren and Woets, 1988). Earlier studies e.g. van Boxtel et. al., 1978, had indicated the potential of whitefly to adapt from one host plant to another, within its host range. However the rate at which adaptation would occur and whether or not genetically distinct races of the glasshouse whitefly exist in relation to this process was not clear from such studies. The ability of whitefly to adapt rapidly to new host plants, or the existence of distinct races of whitefly in relation to this process may have repercussions upon the efficacy of whitefly control by *E. formosa.*

Research questions and experiments

The studies described in this thesis, aimed to answer the following questions:

1 At what rate is a whitefly likely to adapt, when transferred from one host plant to another (chapter 2) ?

2 Do 'trade-offs' occur during adaptation with respect to the host plant from which whitefly originated (chapter 2) ?

3 Can the rearing of whitefly upon a certain host plant, 'pre-condition' them to adapt to another host plant (chapter 3) ?

4 Does the host plant from which whitefly originates influence its preference for other host plants (chapter 4) ?

5 Do genetically distinct races of whitefly exist (chapter 5) ?

The whitefly's rate of host plant adaptation was assessed by measuring changes in life history parameters over consecutive whitefly generations. The relative contributions of genotypic and phenotypic variation to the adaptation process were not assessed. This was a deliberate decision, because a simple measurement of changes in ecological parameters over consecutive whitefly generations would give an overall indication of intra and inter-generational variability, that could subsequently be used to calculate the degree of replication required, to accurately ascertain each component of genetic variation. Egg laying, immature mortality and immature development time, were assessed. These are all indicative of population fitness with respect to the net reproductive rate of the population.

The major objective was to develop a method for assessing the rate and extent of host plant adaptation by whitefly. This required the solving of many logistical problems related to the rearing of insect and plant material, so that the material used in all whitefly generations was comparable. All experiments were conducted in a climate cell under standardised conditions of light, temperature and relative humidity. Whiteflies were maintained as rearings with discrete generations. In each generation tested, whiteflies were removed from each respective rearing using an aspirator. They were lightly anaesthetized under carbon dioxide and a single male and female were placed in a leaf cage, that was clipped to the appropriate host plant. There were typically 20 to 40 such leaf cages per whitefly population per host plant tested. After 24 hours the whiteflies and leaf cages were removed and the number of eggs laid per female counted. The development of the eggs was then followed to assess immature mortality and development time. The method developed was used to assess the rate of adaptation of a whitefly population originating from gerbera, to four cucumber cultivars. 'Trade-offs' with respect to the original host plant gerbera were sought once adaptation to cucumber had been ascertained. The same methodology was used to assess whether or not whitefly could be induced to adapt to a Dutch cultivar of sweet pepper and whether the host plant from which whitefly originated influenced this process or not.

The preference of whiteflies reared upon three different host plants (cucumber, gerbera and sweet pepper), was assessed in a multiple choice test, to determine if the host plant from which whitefly originates influences its preference for other host plants with respect to their suitability for whitefly.

Finally it was attempted to develop an electrophoretic technique for the glasshouse whitefly using starch and polyacrylamide gel electrophoresis methods for assessing variation in isoenzyme allele frequencies. With this technique, it may be possible to conduct tests for the existence of genetically distinct races between whitefly populations, based upon the genetic distances between them.

Results

Whiteflies originating from gerbera and exposed to cucumber showed adaptation within one whitefly generation. Thereafter the whitefly performance fluctuated so well between cucumber cultivars as over successive whitefly generations. The degree of variation hereby was circa 50 % in the number of eggs laid per female per 24 hours, circa 10 % in the immature development time (in days) and circa 25% in the overall percentage immature mortality. No 'trade-offs' were found, but this investigation was quite cursory in nature and examined just one possibility i.e. that between gerbera and cucumber. 'Trade-offs' may well be detected for other whitefly populations.

The work with whitefly upon Dutch sweet pepper indicated that where whiteflies were reared for a single generation upon *Lycopersicon hirsutum* cv. glabratum prior to being transferred to sweet pepper, their performance was much better than where they had been reared upon gerbera, cucumber or tomato. Although the plant upon which the whiteflies were reared prior to being transferred to sweet pepper influenced their subsequent performance upon this host plant, this phenomenon did not appear to be related to the quality of the host plants concerned with respect to whitefly performance. Rather the specific secondary plant substances which they contained seems to be of importance.

The preference tests indicated that the influence of the host plant was such that whiteflies originating from a given host plant, exhibited a greater preference for that host plant relative to that of other whitefly populations. However independent of which host plant a whitefly population originated from, there was an invariate rank order of preference of cucumber > gerbera > sweet pepper. This rank preference, is the same as that of the suitability of these host plants with respect to whitefly performance.

The attempts over several months, to develop a reliable electrophoresis technique for the glasshouse whitefly were not successful. However there is still much scope for further improvements. I did not develop this further because of time constraints.

Conclusions

The problems faced in developing a suitable method for assessing host plant adaptation emphasised the importance of consistently using highly standardised plant and insect material of high quality. The glasshouse whitefly appears to adapt readily to plants in its host range, within a few generations. Upon more marginal host plants such as for example sweet pepper, the rate of adaptation appears to be lower than that upon better quality host plants and is influenced by the host plant from which the whitefly originates. Independent from which host plant whitefly originates, that its rank order of preference, so well performance will be cucumber > gerbera > sweet pepper. As the quality of the host plant from which whitefly originates decrease, then the magnitude of the difference between host plants within this rank order also decrease. Life history parameters could clearly be used to indicate differences in whitefly performance upon host plants. The rate at which a population adapts to a host plant measured by these parameters, may provide a good indicator as to the durability of a host plant's inherent resistance to whitefly. However all such tests upon whitefly performance should be conducted over several consecutive whitefly generations so as to account for the between generation variation, even where whitefly is already adapted to the host plant in question. In 'no-choice' tests of whitefly performance, care should be taken to differentiate between laying and non-laying females which indicate respectively antibiosic and antixenosic aspects of host plant resistance. Finally research must still be done to establish whether or not genetically distinct races of the glasshouse whitefly exist and also the relative contributions of genetic and phenotypic variation to whitefly performance and adaptation.

Practical implications

Although the relationship between observations made in my studies and their applicability in the commercial glasshouse situation has yet to be determined, some speculations are now made. If whiteflies are transferred from one crop to another under commercial glasshouse conditions, e.g. through infected plant material or through whiteflies migrating into a glasshouse through air ventilators, then these whiteflies would adapt to the crop concerned within a few whitefly generations, unless the crop was marginal with respect to whitefly use e.g. sweet pepper. In such a case, the chances of whiteflies becoming adapted to the crop are slight. If however air ventilators are covered with insect proof gauze and hygiene standards with respect to the movement and disposal of plant material are strictly maintained, the likelihood of whitefly movement between glasshouses will be reduced. Where more than one cultivar of an ornamental crop is grown in the same glasshouse, the possibility arises that whitefly will adapt to one cultivar and in thus doing become pre-conditioned to adapt to other cultivars in the glasshouse, to which it might not otherwise have adapted.

1 INTRODUCTION

Summary

Host plant adaptation is defined and its importance in relation to the integrated control of an insect pest, which relies principally upon the use of a natural enemy and plant resistance explained. An example of this is the control of the glasshouse whitefly (*Trialeurodes vaporariorum* [Westwood]) by the parasitoid *Encarsia formosa* Gahan. Despite many previous investigations on the ecology and behaviour of the glasshouse whitefly, few studies as to the potential of whitefly to adapt from one host plant to another within its host range had been done. My studies examine the process of host plant adaptation in the glasshouse whitefly and suggest the significance of my findings in relation to whitefly's integrated control. Accordingly, the last two sections of this introductory chapter explain the need to study host plant adaptation in the glasshouse whitefly and my specific research objectives.

1 What is host plant adaptation ?

Host plant adaptation is the process whereby the performance of a population of a phytophagous insect upon a particular sort of host plant improves over successive successive generations, due to the selection pressure exerted by the plant. More specifically it may be defined as an increase in the net reproductive rate of an insect population, as a result of continued selection pressure upon it by a given host plant. Such an increase in the net reproductive rate is indicative of a general increase in population fitness (Rougharden, 1983). Thus host plant adaptation is a micro-evolutionary process (a vague term for slight evolutionary changes within a species [Futuyma, 1985]) and a study of it can lead to insights as to the selective forces of the plant upon the phytophage concerned. Various aspects of the host plant adaptation process may be studied, e.g. the genetic variation present, the rate at which the adaptation process occurs and the underlying biochemical and physiological mechanisms. Past studies have often focused upon analyzing the relative contributions of genetic and phenotypic variation to an insect population's fitness upon different host plants (see review of Via, 1990). The motivation for this was to assess possible constraints on this evolutionary relationship (Thompson, 1988). Fewer studies have as mine focused upon the demographic changes which an insect population undergoes over successive generations when transferred from one host plant to another, thereby assessing how rapidly such a population can adapt to a specific host plant. Similar studies have for example been done by Gould (1979) and Fry (1989 and 1990) investigating *Tetranychus urticae*. Knowledge of the physiological and biochemical mechanisms involved in adaptation processes is also scanty (e.g. review of Gould, 1988a).

2 Why combine plant resistance and biological control in an integrated control program ?

Before explaining the significance of plant resistance and biological control in an integrated control program, some definitions relating to these concepts are given in the subsequent two paragraphs.

Host plant resistance is defined by Painter (1951) as: 'the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect. In practical agriculture it represents the ability of a variety to produce a larger crop of good quality than do ordinary varieties at the same level of insect population.' Host plant resistance may be expressed by the plant as an antixenosis or an antibiosis property. Antixenosis is where the plant influences the insect's behaviour (Smith, 1991), e.g. whitefly exhibiting non-preference for *Lycopersicon hirsutum* due to the sticky exudate upon its leaves (Gentile, et. al., 1968). Antibiosis is where the host plant reduces insect fitness e.g. through inflicting mortality on population or reducing female fecundity. A plant resistance mechanism may constitute both antixenosic and antibiosic properties. Also properties that act to compensate for or reduce the damage which, the plant suffers as a result of pest attack, may be present. This last mechanism is termed plant tolerance. The degree of resistance a plant may exhibit to a pest may vary from very susceptible to a partial resistance through to an absolute resistance. Absolute resistance is where total mortality of an insect population upon the host plant occurs e.g. Renink et al. (1989). Susceptibility of a plant cultivar is where on average more damage consequent of pest attack under standardised test conditions occurs, than the level of damage found on average within that crop (Painter, 1951 and Smith, 1991). Partial resistance in a plant cultivar is where a level of resistance is expressed intermediate to that of susceptible or absolutely resistant cultivars. Cultivars expressing partial resistance are often sought in integrated control programs combining the use of plant resistance and biological control.

Biological control in an ecological sense is definable as the regulation by natural enemies of another organism's population density at a lower average than would otherwise occur (e.g. DeBach, 1974). It is an established practice under glasshouse crops (van Lenteren and Woets, 1988). This success is partly due to the use of plant cultivars conducive to the control of pest species by their natural enemies e.g. the breeding of semi-glabrous cucumber varieties to improve whitefly control by *E. formosa* (van Lenteren and de Ponti, 1991). This consideration of how one aspect of pest control may influence another is an important aspect of integrated pest management (IPM), under which the combined use of plant resistance and a natural enemy in an integrated control program, may form one aspect. IPM may be defined as: 'a reduction of pest problems by actions selected after the life systems of the pests are understood and the ecological so well as economic consequences of these actions have been predicted as accurately as possible, to the best interests of mankind' (Rabb, 1970). This definition emphasises the need to understand ecological interactions e.g. between plant and natural enemy (e.g. Bergman and Tingey, 1979 and Price et al., 1980) and states that the control aim is a reduction in pest density and not pest elimination. This last aspect is important as it was the idea of pest elimination that often led to excessive pesticide application in the period 1940 to the mid 1960s which exacerbated problems of pesticide resistance (Wheatley, 1987). In practice IPM is considered in relation to the integration of various control tactics: chemical, biological, plant resistance, cultural and other (e.g. Kogan, 1988). More recently IPM has come to emphasise the use of control tactics other than pesticides (Anon., 1980), pesticides supplementing other tactics for effective control to be maintained (e.g. Gruys, 1980). This is very important in countries who have strict environmental regulations e.g. the Netherlands (Meerjarenplan voor Gewasbescherming, 1991).

Integrated control may be termed a complimentary pest control strategy. For example, the resistant host plant may reduce the density of the pest to a level at which the natural enemy can more effectively control it (Starks et al., 1972 and 1974), or may prolong the pest's development time, thus increasing the chance of the pest being attacked by a natural enemy (Price, 1986). Also the natural enemy compliments the plant's resistance by suppressing pest density, thus reducing pest selection pressure against the plant (van Emden, 1990). This complimentary action is the foundation for combining plant resistance and biological control within an integrated control program.

Also integrated control may be viewed tritrophically, the host plant (first trophic level) and natural enemy (third trophic level) controlling the pest (second trophic level). This tritrophic approach has been adopted by van Emden (1986) who assessed the effect of biological control in enhancing plant resistance, and van Lenteren (1991) who considers biological control within a tritrophic context where the host plant may enhance or diminish the efficacy of a natural enemy.

The augmentation of plant resistance by a natural enemy has been modelled by van Emden (1986 and 1990). His models illustrated the percentage reduction in pest density that could be achieved using various levels of partial plant resistance and a natural enemy, relative to a very susceptible cultivar where no natural enemies were deployed. The results showed that deploying a natural enemy allowed partial and not absolute resistance to be used for effective pest control. Partial resistance exerts less selection pressure upon a pest than absolute resistance, possibly improving the durability of the resistance (van Emden, 1990). These results have been confirmed in field trials e.g. Gowling (1988), Kaneda (1986), Orr and Boethel (1985) and Schalk and Creighton (1989). However this approach is not always effective, as the newly selected host plant may in some way be unsuitable for the natural enemy concerned. For example the pest may sequestrate plant products harmful to the natural enemy (see review of Duffey, 1980) or the plant structure may hinder the searching efficiency of the natural enemy (see review of Obrycki, 1986 and van Lenteren, 1991). Such obstacles may be overcome by conducting plant breeding programs that improve resistance to a pest, whilst minimising the negative effects upon natural enemies currently used to control it e.g. de Ponti (1980).

3 Why is host plant adaptation detrimental to a tritrophic integrated control program ?

An integrated control program utilising host plant resistance and biological control is in a state of flux over time, which is partly due to the potential of the pest to adapt to the host plant. It should therefore be viewed from an evolutionary ecology perspective. This not only considers the interrelationships between parameters but also emphasises more than an ecological approach, how these might change over time, as a result of selection pressures upon the genetic variation they contain (Charlesworth, 1984 and Bradshaw, 1984). Where the pest adapts to the resistant host plant and its density increases, it may be necessary to increase the density of natural enemy released, for effective control to be maintained. If this is unsuccessful pesticides may be applied to reduce the pest back to a level below its economic threshold (Onstad, 1987). This is obviously a factor of increased cost and inconvenience for the grower concerned, and is detrimental within the context of an IPM program (sensu Rabb, 1970).

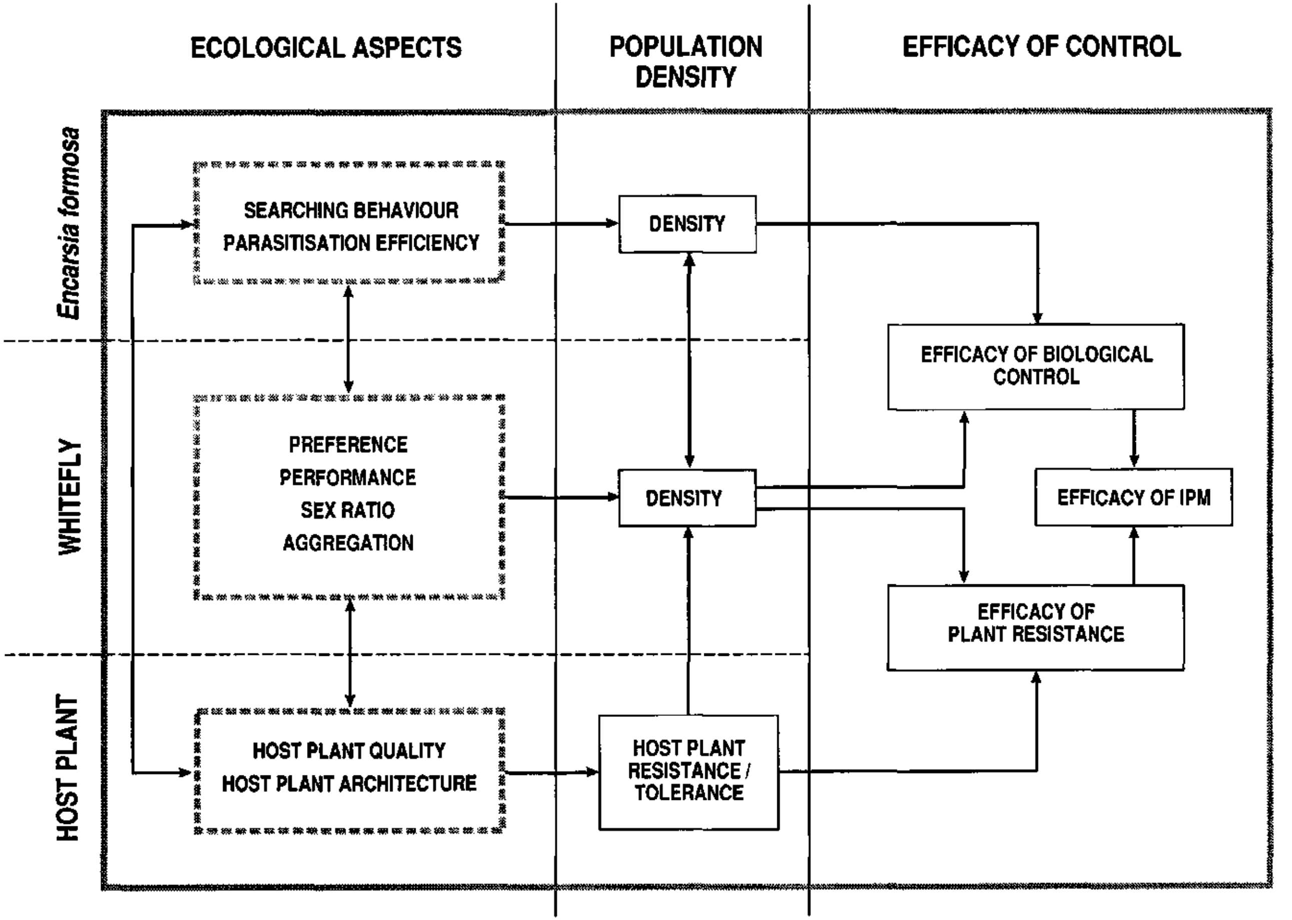
For example the greenbug (*Schizaphis graminum*) is a serious pest of sorghum in the United States. The deployment of sorghum varieties resistant to this pest gave in 1989 a net benefit of circa $ 14 US per acre, compared with the deployment of susceptible varieties (Teetes et al., 1989). However greenbug can rapidly develop resistance to new sorghum cultivars. In 1988 there were eight known greenbug biotypes (Putkera et al., 1988), compared with three in 1968 (Reese, 1990). Furthermore biological control by a natural enemy is not very effective. High density releases of the commonly used natural enemy are ineffective in reducing greenbug population density to below its economic threshold (Starks et al., 1966). However, where a resistant cultivar is deployed, biological control is complimentary, and enhances the level of greenbug control (Starks et al., 1972 and 1974). Thus, unless an improvement in the biological control agent is found, new resistances must continually be developed for satisfactory control to be maintained. Otherwise growers will have to resort to a more frequent use of pesticides which is unfavourable economically, and can lead to an upsurgance of secondary pests (Peters and Starks, 1981).

4 The tritrophic system: 'Host plant - whitefly - *Encarsia formosa*'

To place the effect of host plant adaptation within a tritrophic context of integrated control, an appreciation of the ecological interactions occurring between the components of the control system is requisite. A generalised assessment of interactions between plant genotypes and biological control was made by Bergman and Tingey (1979), upon the basis of several different pest species. Such an analysis is now done for the system 'host plant - whitefly - *E. formosa*'. This system was chosen for a study of host plant adaptation, for the reasons given in the next section. Much fundamental an applied research has been conducted upon this system as reviewed by van Lenteren and Noldus (1990) and Noldus and van Lenteren (1990) and research on fundamental aspects of whitefly control continues e.g. its biological control by *E. formosa* on gerbera (e.g. Sütterlin et al., 1990, Sütterlin et al., 1991, Sütterlin et al., 1992 and Bouwman et al., 1992) and the development of methods to detect cultivars resistant to it (e.g. Romanow et al., 1991).

The system is depicted in figure 1. The ecological aspects detailed to the left of the diagram are sequentially described in this section, in the order host plant, whitefly, *Encarsia formosa*. These ecological aspects in turn effect the population density of each level. The efficacy of control depicted to the right of the diagram where plant resistance and a natural enemy are combined has already been outlined in section 2, a specific case study for whitefly being given in van Lenteren (1991).

FIG 1 TRITROPHIC INTERACTIONS BETWEEN HOST PLANT, WHITEFLY AND *Encarsia formosa*



Host plant

Plants vary in their quality for whitefly. Of the commercially grown crops in The Netherlands, sweet pepper is of the lowest quality. Whiteflies on this crop exhibit a high mortality (van Boxtel et al., 1978, Merendonk et al., 1978, van Lenteren et al., 1989 and Thomas 1992b) and die out within a few whitefly generations (Thomas 1992b). Aubergine is the most suitable host plant (van Boxtel et al., 1978 and van Merendonk et al., 1978), whitefly mortality being very low and fecundity being high. Between these two extremes there is a rank order of suitability of aubergine > cucumber = gherkin = melon > gerbera > tomato > sweet pepper (van Lenteren and Noldus, 1990) based upon the data of van Boxtel and al. (1978), van Merendonk et al. (1978), van Sas et al. (1978) and Verschoor van der Poel and van Lenteren (1978), concerning fecundity, immature mortality and immature development time. The effect of host plant quality on whitefly performance occurs not only between plant species, but also within plant species e.g for sweet pepper (e.g. Laska et al., 1982 and 1986), tomato (e.g. van Gelder and de Ponti, 1987 and Romanow et al., 1991) and cucumber (e.g. Zabudskaya, 1989 and this thesis (chapter 2)). These differences are related to host plant chemistry. For tomato the differences seem to be related to the variation in alpha tomatine content between cultivars (van Gelder and de Ponti, 1987). Also different whitefly populations may perform differently upon the same host plant cultivars e.g Dutch and Hungarian whiteflies upon sweet pepper (van Lenteren et al., 1989).

Host plant quality also affects whitefly preference. The pre-alighting phase of this is not mediated by leaf shape, structure or odours (Woets and van Lenteren, 1977) reflected light from plant leaves being the sole influencing factor (Vaishampajan et al., 1975 and Affeldt et al., 1983). Post-alightive preference is affected by host plant quality (Noldus et al., 1986b), which the whitefly determines by probing the leaf apoplast (Jansen et al., 1989). This post-alightive preference has a rank order corresponding to that of the host plant suitability for whitefly (van Lenteren and Noldus, 1990). This preference is invariate independent of which host plant the whiteflies originate from (chapter 4).

In general host plant quality does not significantly affect whitefly sex ratio (van Roermund and van Lenteren, 1992). However few detailed studies of this phenomena have been made and the data of Boiteau and Singh (1988) showing a male biased whitefly sex ratio on potato have not been further confirmed.

Whiteflies aggregate upon the youngest leaves of a plant for both rosette (Sütterlin et al., 1991) and non-rosette (Noldus et al., 1985) forms. Under greenhouse conditions leaf hairs do not affect glasshouse whitefly aggregation on a plant (van Lenteren and Noldus, 1990). However in cotton fields, the cotton whitefly (*Bemisia tabaci*) prefers moderately haired leaves (Pollard and Saunders, 1956) due to microclimatic effects (Mound, 1965).

The host plant may also directly affect the searching efficiency of *E. formosa*. This is primarily due to the presence of leaf hairs impeding the walking of the parasitoid upon the leaf surface (Hulspas-Jordaan and van Lenteren, 1978), the walking speed being inversely proportional to leaf hairiness. Hairy plant cultivars, also trap more honeydew excreted by whitefly larvae than glabrous cultivars. Where *E. formosa* walks into honeydew droplets she drowns in them or spends much time preening this reducing searching efficiency (van lenteren, 1991). Biological control on cucumber has been enhanced by breeding semi-glabrous varieties, that promote the searching efficiency of *E. formosa* (van Lenteren and de Ponti, 1991). Effects of the host plant mediated through the whitefly upon *E. formosa* parasitization e.g. whitefly sequestrating plant substances have not yet been demonstrated.

Whitefly

The whitefly may affect the host plant by adapting to it, this potential having being indicated by van Boxtel et al. (1978) and is detailed further in this thesis (chapters 2 and 3). Whitefly has a high reproductive capacity. The simulation model of Hulspas-Jordaan and van Lenteren (1989), showed that in the absence of natural enemies and other limiting factors, whitefly population growth on tomato was exponential and was only limited when the whitefly density resulted in the deterioration and death of the host plant. Commercial glasshouse experience where control measures are not applied, generally confirms this scenario (van Lenteren and Noldus, 1990). In a commercial glasshouses whitefly distribution is highly aggregated (Eggenkamp et al., 1982) and these aggregated patches may be distributed at random throughout a glasshouse (Yano, 1983). This aggregative settling of whiteflies influences the searching behaviour of *E. formosa*.

Encarsia formosa

Since its first application by Speyer (1927 and 1929), *E. formosa* has proved to be an effective natural enemy against the glasshouse whitefly under glasshouse conditions (van Lenteren and Woets, 1988).

The searching behaviour exhibited by *E. formosa* is a form of area restricted search (Kareiva and Odell, 1987) whereby a parasitoid alights upon a plant at random and searches upon the leaf at random, its search remaining restricted to that plant if unparasitized hosts are available and encountered. This behavioral pattern results in a net aggregation of the parasitoid in areas of high host density. E. *formosa* cannot detect whitefly patches prior to alighting upon a plant (van Lenteren and Noldus, 1990). After alighting, the time duration a parasitoid spends on a leaf is increased where unparasitized whitefly larvae are present, relative to an uninfested leaf (van Eck-Borsboom, 1979). Further the presence of larvae upon a leaf increases the relative amount of time that the parasitoid spends walking on the leaf surface (van Lenteren et al., 1976). Both of these effects increase the probability of the parasitoid encountering and thus possibly parasitising whitefly larvae (van Roermond, in prep.). This effect of whitefly larvae upon E. *formosa* searching behaviour is also mediated through a kairomone present in whitefly honeydew (e.g. Carter and Dixon, 1984 and van Vianen and van der Viere, 1988) and by direct contact with the whitefly larvae self (van Roermond, in prep.).

The parasitization efficiency of E. *formosa* upon whitefly is influenced by several factors. Host quality is important. Third and fourth instar larvae are preferred for parasitization (e.g. Nell et al., 1976 and Nechols and Tauber, 1977), second instar larvae being used for host feeding where a surplus of hosts is available (e.g. Nell, et al., 1976). Host feeding increases with increased host density (Fransen and van Montfort, 1987). Superparasitism may occur at low host parasitoid ratios (Xu et al., 1987) and reduces searching efficiency. At high whitefly densities E. *formosa* fecundity becomes a limiting factor (van Vianen and van Lenteren, 1986 and van Lenteren et al., 1987). Finally the parasitization efficiency is limited by temperature (Burnett, 1949).

5 Why study host plant adaptation in the glasshouse whitefly ?

There were three main reasons for choosing the glasshouse whitefly as a study subject.

Firstly, as described earlier, much is already known about whitefly ecology and behaviour, this providing a basis for ecologically orientated studies of whitefly host plant adaptation. Furthermore, specific studies had indicated that adaptation of whiteflies occurs when transferred from one host plant to another or as a result of geographic segregation. For example, preliminary investigations of van Boxtel et al. (1978) had shown that whiteflies originating from a particular host plant showed a higher oviposition frequency upon that host plant, than whiteflies originating from other host plants. This indicated adaptation by whitefly populations to specific host plants that resulted in increased whitefly performance.

Also, investigations by van Lenteren et al. (1989) which compared Dutch and Hungarian whitefly populations, had shown that Hungarian whiteflies performed better upon both Dutch and Hungarian sweet pepper cultivars than Dutch whiteflies. These results hinted the possibility of Dutch and Hungarian whiteflies, due to their geographic separation, having become distinct races (Jaenike, 1981).

Secondly, much research on whitefly - host plant and whitefly - parasitoid relationships has already been conducted at the Department of Entomology, Wageningen Agricultural University and this is also an area of ongoing research. This has resulted in the accumulation of much technical expertise regarding whitefly rearing and the conduction of behavioral and ecological studies. This was advantageous to the inception of my experimental studies.

Thirdly, the glasshouse whitefly is a serious worldwide pest, found upon several hundred plant species (Mound and Halsey, 1978). Therefore research aimed at improving its control is of economic significance. As host plant adaptation may affect the efficacy of integrated control programs, a study host plant adaptation in whitefly which, may lead ultimately to its improved control, is of potential economic importance.

My studies pursue earlier whitefly work (van Boxtel et al., 1978 and van Lenteren et al., 1989) by investigating the likelihood of host plant adaptation occurring in the glasshouse whitefly and the rate at which this happens. Also factors limiting host plant adaptation were studied. It is considered that these studies would provide a basis for future investigations assessing the influence of host plant adaptation by whitefly on its biological control by E *formosa* and the durability of host plant resistance against whitefly.

6 What were the specific aims and objectives of my research ?

The primary objective was to find an experimentally realisable method for assessing host plant adaptation in the glasshouse whitefly, based upon the measurement of life history parameters. Any experiment conducted over several generations of an insect, where comparisons between insect generations are to be made, entails many risks and experimental difficulties which need to be overcome. The details of the methodology developed and the problems encountered are described in chapter 2.

Once an appropriate method had been developed, an experiment was conducted to assess the rate of adaptation of whitefly originating from gerbera to cucumber cultivars of differing resistance to mildew. It was hypothesized that mildew resistance may be correlated with resistance to whitefly (chapter 2). This hypothesis was based upon observations made during the development of the methodology to assess host plant adaptation, where it was observed that whiteflies upon the partially mildew resistant cucumber cultivar Santo, performed less well than those upon the mildew susceptible cultivar Lange Groene Giganta. That the resistance of a plant to a disease, can influence the performance of an insect population upon it, has been shown for example by Karban et al. (1987) and Lewis (1979). The rate of adaptation was assessed over several consecutive whitefly generations. 'Trade-offs' (Rausher, 1988) resultant of the whiteflies adapting from gerbera to cucumber with respect to the original host plant gerbera were also sought.

The research of van Lenteren et al. (1989), had already shown that Hungarian whiteflies performed much better upon sweet pepper than Dutch whiteflies. I hypothesized that this difference is the result of Hungarian whiteflies having been 'pre-conditioned' (Schotzko and Smith, 1991) on other cultivars than Dutch whiteflies. This difference has been shown by Laska et al. (1982 and 1986). Their comparative tests of central european and western hemisphere sweet pepper cultivars have shown that central european cultivars are more susceptible to whitefly damage than western cultivars, these two groups of cultivars having different breeding histories. Research was thus done (chapter 3) to assess if the performance of Dutch whiteflies upon sweet pepper was at all related to the suitability of, or the secondary plant substances contained within the host plants from which they originated (chapter 3).

All previous studies of whitefly preference except for that of van Boxtel et al. (1978), had not experimentally considered the host plant from which the whiteflies originated. Van Boxtel et al.'s (1978) data had demonstrated an effect of host plant origin upon the number of eggs a female laid upon a given host plant. In relation to this I hypothesised that the host plant from which the whiteflies originated, may also influence the magnitude of preference they exhibit in a choice situation for different host plants (among which the original host plant is present). Chapter 4 presents a study that tested this hypothesis and seeks to explain the significance of the whiteflies preference behaviour, in relation to its polyphagous habit and its ability to adapt to different host plants.

An electrophoresis study of the glasshouse whitefly is presented in chapter 5. This study was done with the aim of developing an electrophoresis method for the glasshouse whitefly, to assess upon the basis of allele frequencies the genetic distance between different whitefly populations. The genetic distance can indicate how genetically distinct populations are and whether or not they are distinct enough to be termed races or sibling species (Feder et al., 1990). This information would also be useful in comparing Dutch and Hungarian whitefly populations to test if they are genetically distinguishable as races (Jaenike, 1981).

Chapter 6 summarises the main conclusions of my studies and places them in the context of current commercial glasshouse situation e.g. the disposal of old plant material, cropping practices, migration of whitefly through glasshouse ventilators and the new regulations governing plant movements with in the European Community with effect from January 1993. The importance of host plant adaptation with respect to the breeding of durable plant resistance is also described. Finally the possible effects of natural enemies and whitefly sex ratio as limiting factors upon host plant adaptation are discussed.

2 REARING A GERBERA STRAIN WHITEFLY UPON FOUR CUCUMBER CULTIVARS: RATE AT WHICH ADAPTATION OCCURS AND A SEARCH FOR RESULTANT 'TRADE-OFFS'[1]

Summary

Although much is known about the preference and performance aspects of whitefly-host plant relationships, little is known about the rate at which a whitefly population can adapt from one host plant to another. In pilot studies a method had been developed to assess host plant adaptation in the glasshouse whitefly (*Trialeurodes vaporariorum* [Westwood]), by following the demographic changes (egg laying, immature mortality and immature development time) of populations on specific host plants, the populations all originating from the same parent line. This study was specifically aimed at assessing the rate of adaptation of a gerbera line of whitefly to four cucumber cultivars. It was hypothesised that the rate of adaptation to and performance of the whitefly lines upon these cultivars might vary in relation to how resistant these cultivars were to powdery mildew (*Sphaerotheca fuliginea*). A preliminary investigation was also made to assess if 'trade-offs' arose when the cucumber lines were reverted to their parent host plant gerbera.

The results obtained indicated that whitefly adapted from gerbera to cucumber within one whitefly generation. The subsequent variation in the mean number of eggs laid per female, the immature mortality and the immature development time was non consequent for both gerbera and cucumber, although the performance of the whiteflies upon cucumber, was clearly higher than that upon gerbera. The mean number of eggs laid per female per host plant was not correlated to the subsequent development time of these eggs. The whitefly performance was higher upon the mildew resistant than the mildew susceptible cucumber cultivars tested, although the mildew resistance cannot be implied as the causal factor in this observation. No indication for a 'trade-off' was found when the cucumber lines were reverted to the original host plant gerbera.

The study emphasised the need for tests upon host plant suitability for an insect to be conducted over several insect generations where the variation demonstrated by the pest is high. This variation can lead to a false ranking of host plant suitability, which may vary from one generation to the next where differences between cultivars are small. Also the data illustrate the need to differentiate between antixenosic and antibioisic properties of

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[1] submitted to Entomol exp. appl.

egg laying under no-choice conditions. Finally experiments such as these may be used to provide data for simulation models that predict the durability of plant resistance.

Introduction

This study was done to gain an insight into population dynamic aspects of host plant adaptation of the glasshouse whitefly. First it will be outlined, why such a study was found to be necessary. Subsequently the methods considered and tested for this investigation and the specific aims of this study on cucumber are discussed.

The glasshouse whitefly (*Trialeurodes vaporariorum* [Westwood])is a serious problem in many parts of the world. It has a wide host range encompassing several hundred plant species (Mound and Halsey, 1978). Its status as a pest species is still on the increase. For example it has within the last few years become a pest upon tamarillos in New Zealand (Sale, 1987) and strawberries in Japan (Maeda et al., 1988). Numerous studies have been done on the life history of this species upon various host plants of commercial horticultural importance. Many of these have been summarised by van Roermond and van Lenteren (1992). Upon the basis of previous studies, that had used various host plant strains van Lenteren and Noldus (1990) stated that there was a rank order of performance in glasshouse whitefly of Dutch origin of eggplant (aubergine) > gherkin > cucumber > gerbera > melon> tomato > sweet pepper. However until now little is known about changes in performance that may occur when a whitefly population is transferred from one host plant to another, as the subsequent development upon the new host plant has seldom been monitored for several consecutive whitefly generations. The experiments described here were aimed at measuring adaptation to a host plant at the antibiosis level. Antixenosis effects are mentioned in more detail in a separate experiment (chapter 4).

In initiating this study various methods of assessing host plant adaptation were considered. An electrophoresis study was initiated (chapter 5) but yielded limited results. This approach was thus set aside to concentrate upon a life history study. Morphological methods of analysis were considered in relation to a life history study, but to date the only investigation which I know of for whitefly is that of van Vianen (1990), where pupal size was not correlated to host plant quality. So a morphological method was rejected and I decided to concentrate upon the measurement of demographic parameters. Consideration was given to the use of quantitative genetic techniques, for example sib analyses, as espoused in a review of Via (1990). As a detailed sib analysis is logistically very complex, I first performed ecological life history observations over several consecutive whitefly generations. This would give a firm basis for a genetic study, and would indicate the random variation between successive whitefly generations. Such information is needed to account for random variation in a sib analysis, to ensure an appropriate amount of replication.

I define host plant adaptation as an increase in the net reproductive rate of a population as a result of continued exposure to a given host plant. Such an increase in the net reproductive rate is indicative of a general increase in population fitness (Rougharden, 1983). In this study the number of eggs laid per female in a 24 hour period was measured (as an indicator of fecundity) and the per stage mortality and total immature development time were determined. An increase in fecundity (egg laying), a decrease in mortality and a decrease in immature development time are all indicators of adaptation to a host plant, because they result in a higher reproductive rate of the population.

As the investigation was conducted over several consecutive whitefly generations, all experimental conditions had to be strictly standardised to enable the comparison of data between generations. Host plant rearing was regulated so as to limit the variation in plant phenological effects (e.g. changes in fertiliser regime [Barbour et al., 1991] and differences in leaf age [e.g. Noldus et al., 1986b]. Contrary to other studies (e.g. Gould, 1979 and Fry, 1989) the whitefly rearings were maintained as discrete and not overlapping generations. Possible selection processes that could occur in the rearing are thus eliminated, such as age related processes (Charlesworth, 1973).

It was decided to use a laboratory whitefly rearing as the basis for this study. There is the risk that such a population will be more inbred than a field population, although the data collected by van Roermond and van Lenteren (1992) do not indicate that the population is any less able to adapt to plants within its host range than other whitefly populations studied. Furthermore this laboratory population has the advantage of a long known (20 years) demographic history. This is important for standardising the experiment as it is known that the demographic history of an insect population in relation to host plant usage may affect the populations demography on subsequent host plants (e.g. McCauley et al., 1990).

I examined the adaptation of a whitefly population originating from gerbera to various cucumber cultivars. The biological control of whitefly upon cucumber is an example of how plant breeding has facilitated biological control. By breeding for cucumbers with semi-glabrous leaves, biological control by the whitefly parasitoid *Encarsia formosa* Gahan was greatly enhanced (Hulspas-Jordaan and van Lenteren, 1978, Li et al., 1987 and van Lenteren and de Ponti, 1990), as on the hairy cultivars, leaf hairs interfered with the searching behaviour of *E. formosa*. This breeding in relation to *E. formosa* and whitefly was developed in relation to other breeding work to improve resistance to *Tetranychus urticae* and powdery mildew (*Sphaerotheca fuliginea*) (de Ponti, 1980). Powdery mildew control now heavily relies upon fungicides that tend to impede biological control (Mol, 1991). A possibly important question in relation to the continued success and development of integrated pest and disease control upon cucumber is whether cultivars express a consistent level of resistance to a pest for which no specific resistance has been selected. In some preliminary investigations, it was observed for two cucumber cultivars, Santo and Lange Groene Giganta (LGG), that the performance of whitefly upon Santo seemed to be less than that upon LGG. Further, it was known that there might be a difference in the level of mildew resistance expressed by the two cultivars, Santo being a newer and possibly more resistant cultivar than LGG. Recent publications indicate an association between plant resistance to a disease and the susceptibility of the same plant line to an insect pest (e.g., Karban et al., 1987 and Lewis, 1979).

It was aimed to test several hypotheses during this study. The first hypothesis was that as cucumber is a high ranking plant with respect to whitefly performance (van Lenteren and Noldus, 1990), it is expected that adaptation to this host plant would be rapid and would occur within a few whitefly generations. Secondly if differences in resistance between the cucumber cultivars tested exist, it is expected that there would be clear and consistent differences in whitefly performance upon and rate of adaptation to the cucumber cultivars over several consecutive whitefly generations. Thirdly it is expected that whitefly performance will be lower upon the more mildew resistant cultivars than mildew susceptible cultivars if mildew resistance is associated with a negative effect upon whitefly performance. Finally if the adaptation process is typical for that of a colonising species (MacArthur and Wilson, 1967), then it would be expected that fecundity would be negatively correlated with immature development time.

A preliminary search was made to detect 'trade-offs' resultant of the whiteflies having adapted to cucumber and then being transferred to their host plant of origin, gerbera. A 'trade-off' may in general be defined as; 'a negative covariance between the characters in question at the genotypic or phenotypic level' (Pease and Bull, 1988). With respect to insect-plant relations it may be more specifically defined as; ' a loss of adaptation to one host plant in conjunction with increased adaptation to another' (Rausher, 1988). No 'trade-offs' are expected to be detected upon reverting a cucumber line back to gerbera. The adaptation to cucumber should not result in a loss of genetic variation for adaptation to gerbera, as this is not directly selected against in the adaptation process, as cucumber is a more suitable host plant for whitefly than gerbera.

Materials and methods

Host plants

The plants used were gerbera cv Fame (from Terra Nigra BV) and cucumber cv's Cordoba (from Rijk Zwaan BV), Santo (from Zaadunie BV), Corona (from De Ruiter Zonen CV) and Lange Groene Giganta (from Zandbergen BV). Cordoba and Santo are new cultivars and Corona and Lange Groene Giganta (LGG) old cultivars on the Dutch market. Cordoba appeared on the Dutch market in the 1985 as one of the first cultivars with almost total resistance against mildew. Also Santo appeared that year on the Dutch market and was originally thought to have absolute resistance to mildew through three genes, although this resistance has proven in practice to be only partial. Mildew resistance leads to necrosis of the plant foliage under low light conditions, so these cultivars are only suitable for planting in the summer months. Corona was first introduced on the Dutch market in 1977 and was in the first few years thereafter the most important cultivar, despite having no proven mildew resistance. It still held a fair proportion of the market in 1991. LGG has been on the Dutch market for circa 10 years and its level of mildew resistance is unknown.

In a pilot study prior to this, several problems were encountered with the methodology used. In summary these were:

* problems in maintenance of rearings	- possible inbreeding effects
	- infestation from other pest species
	- diseased plant material
* problems in the detection of trends	- insufficient number of replicates

With respect to these problems improvements to the methodology were made for this study. The problems from insufficient replication were the result of a lack of whitefly material (problems in the rearing or plant material becoming infested by a pest or disease during the course of an experiment). In the pilot study certain of the plants were particularly susceptible to mildew (tomato cv Moneymaker) and aphids (aubergine). To reduce such problems, all cucumber plants in this study were sprayed on a weekly preventative basis against mildew. Four fungicides were used on a rotational basis to reduce the likelihood of fungicide resistance occurring (active ingredients: chloothalonil, bupirimaal, bitertanol and fenarimol). The plants can be used by whiteflies 48 hours after spraying. The gerbera plants were sprayed against aphids on an intermittent basis, using dichloorvos. Otherwise throughout this study, biological control against all pest species that were a potential hazard was used on a preventative weekly basis, so well in the plant and whitefly rearings as on the plants in the experiments. The agents used were were: *Amblysieus cucumeris* against *Thrips tabaci*, *Phytoseiulus persimilis* against *Tetranychus urticae* and *Aphidioletes aphidomyza* against *Myzus persicae*. Further preventative measures against *Thrips tabaci* were taken by hanging blue sticky cards up and against *Trialeurodes vaporariorum* by hanging yellow sticky cars up above the plants.

The plant rearing was done, with the following stringent conditions being applied:

- plants were potted up and fertilised in a manner which maintained adequate growth without 'forcing' the plants.
- biological control agents were used as pesticides may have a possible effect upon host plant suitability.
- in selecting experimental material from the rearings, a zero tolerance of pest and disease infestation was enforced (thus much more material was reared than required).
- in selecting plant material young plants were chosen.

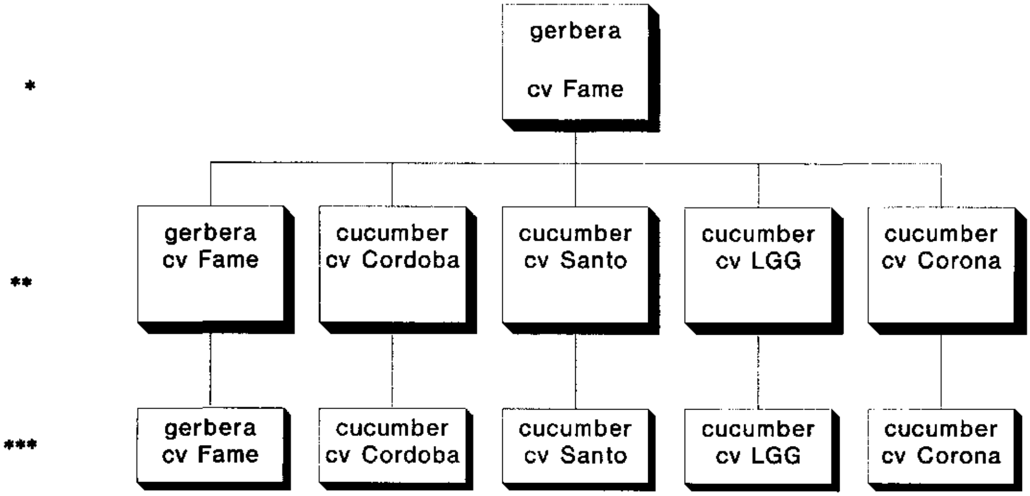
The plants were reared in a heated glasshouse, where the temperature was 18 ^{0}C ± 3 ^{0}C with a relative humidity between 60% and 80%. Throughout a standard compost was used for sowing and potting the plants. It contained 95% peat and 5 % clay. To this was added per cubic metre, 7kg of chalk containing 10 % magnesium and 1.5 kg of fertiliser (12N:14P:24K). Supplementary lighting at 850 lux, was given to maintain a photoperiod of 16L:8D. For experiments cucumber plants were taken in 18cm pots at the 4 or 5 leaf stage. The gerbera plants obtained as plugs from Terra Nigra BV were transferred to 18 cm pots and reared for at least 8 weeks prior to use, to ensure that no active pesticide residue on the leafs remained from the spraying of the plugs at Terra Nigra's nurseries. Plants were used when they had 4 or 5 medium sized (Sütterlin et al., 1990) leafs.

Whiteflies

Whiteflies were reared in heated glasshouse maintained at 22°C ± 1°C with a relative humidity of 65% to 75%. The stock population for the adaptation so well as the 'trade-offs' experiment was a longer term rearing on gerbera cv Fame which had already been maintained in our department for 18 months, prior to the start of this study. The whiteflies from this stock rearing originated from the 20 year old rearing on tomato cv Moneymaker (van Lenteren et al., 1989). For each rearing line, two rearings were maintained in separate glasshouse compartments under the same conditions. From the stock population leaves with pupae on them were placed upon the floor of a wooden framed cage (60*60*100 cm) covered with fine gauze (mesh size 0.4*0.4mm), in which the new host plant stood. The whiteflies emerged from the pupae and flew up to the new host plant. Fourteen days after the leaves with pupa on had been introduced, they were removed, any whiteflies required for experimental work being taken within this 14 day period. All whiteflies were then aspirated from the host plant. The larvae were allowed to develop, until the majority were in the pupal stage. At this stage the leaves were removed from the plant and placed in the bottom of a clean cage with a new host plant, the rearing cycle thus being completed. For experiments whiteflies were selected equally from both rearings held. For each whitefly generation, whiteflies from each line were reciprocally transferred between rearings (adults aspirated into a vial and then released) to reduce possible inbreeding effects. The precise host plant transfer sequence of the whiteflies for the adaptation experiment is given in figure 1 and that for the 'trade-offs experiment in figure 2. For the 'trade-offs' experiment reversion lines were begun from the ninth whitefly generation upon cucumber.

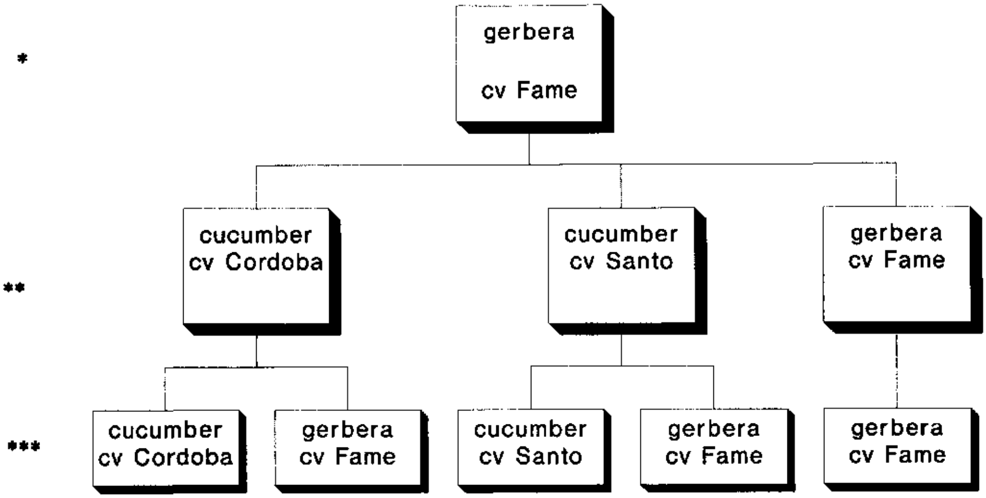
For so well the adaptation experiment and the 'trade-offs' experiment, a climate cell at 21 °C and 70% RH with supplementary lighting at 8000 lux (16L:8D) (provided by mercury vapour lamps), was used. Plants were arranged at random in the area under the mercury vapour lamps. Whiteflies from the rearings, were lightly anaesthetized under carbon dioxide and a single male and female transferred to leaf cages (2.5 cm diameter). Xu (1983) had showed that a single whitefly pair per leaf cage forestalled density dependent effects. After 24 hours the leaf cages and whiteflies were removed, the position of each cage being circled with a felt pen that gave no phytotoxic effects. During the first four generations of the adaptation experiment, immature mortality and immature development time were only observed from leaf cages where three or more eggs were laid. This was resultant of the compromise between maximising the degree of replication with respect to the egg laying

Figure 1 Host plant transfer sequence of whiteflies for adaptation experiment



* stock populaton, ** rearing populations, *** experimental populations

Figure 2 Host plant transfer sequence of whiteflies for'trade-offs' experiment



* stock population, ** parent lines, *** reversion lines

and the available manpower to record the subsequent development of the eggs. In each experiment there were no more than 5 cages per plant. Young plants between the 3 and 6 leaf stage were used. No observations were made between the fifth and eighth generations. Thus the data as collected were intended to indicate any adaptation process that may be occurring in the initial generations. The concluding observations in the ninth generation might indicate the maximum level of adaptation, assuming that adaptation to cucumber occurs within several whitefly generations. In the 'trade-offs' experiment observations were made for all host plants when the reversion lines on gerbera were in the second generation. This was done to negate possible maternal effects arising in the first generation. No observations from the first generation could be made due to logistical constraints. Per whitefly population 30 to 40 adult pairs were distributed on 7 to 10 plants. All experimental plants were between the 4 and 6 leaf stage. The experiment has a double control as the reversion lines are compared with the initial population on gerbera, so well as their parent lines on cucumber (figure 2). Only data relating to egg laying and immature survivorship were collected.

Statistical testing was done using the software package 'Statistix' from Analytical Software, St. Paul, Minnesota, USA.

Results

The results are presented in tables 1 to 5 and figures 3 to 14. In analyzing and interpreting the results, general patterns and trends consistent over several whitefly generations were sought. To facilitate this the results from the cucumber cultivars are often additionally pooled and presented as the average result for cucumber so as to negate specific varietal affects. The results are presented and analyzed in the following order: egg laying, survivorship / mortality, immature development time, rank order of suitability of the cultivars tested with respect to whitefly, the correlation sought between fecundity and immature development time and a search for 'trade-offs'.

Egg laying

Table 1 lists per host plant the number of females observed in each whitefly generation, the percentage thereof which did lay eggs and the total number of eggs laid by the ovipositing females. There are more ovipositing females upon the cucumber cultivars than upon gerbera, except in the first generation. That the percentage of non-ovipositing females

Table 1 Number of eggs laid and number of laying and non laying whitefly females per host plant per generation

Host plant :- cucumber cv Cordoba

whitefly generation	number of females observed	% laying	total no. of eggs laid
1	30	53.3	59
2	35	100	331
3	29	86.2	238
4	43	95.3	318
9	25	88.0	121

Host plant :- cucumber cv Santo

whitefly generation	number of females observed	% laying	total no. of eggs laid
1	36	66.7	124
2	36	86.1	188
3	26	84.6	172
4	41	73.2	156
9	18	89.9	57

Host plant :- cucumber cv LGG

whitefly generation	number of females observed	% laying	total no. of eggs laid
1	31	61.3	52
2	38	97.4	243
3	36	77.8	208

Host plant :- cucumber cv Corona

whitefly generation	number of females observed	% laying	total no. of eggs laid
1	37	78.4	161
2	44	95.5	355
3	37	70.3	206
4	45	86.7	261
9	26	46.2	53

Host plant :- cucumber (average / sum for all cultivars)

whitefly generation	number of females observed	% laying	total no. of eggs laid
1	134	64.9	396
2	153	94.8	1117
3	128	79.7	824
4	129	85.1	736
9	69	74.7	231

Host plant :- gerbera cv Fame

whitefly generation	number of females observed	% laying	total no. of eggs laid
1	12	91.7	41
2	36	69.4	47
3	21	14.3	8
4	31	87.1	157
9	36	44.4	60

in the first generation upon cucumber is so high, is possibly due to maternal effects upon female preference. High variation between females in non-preference exhibited upon gerbera exists. Figure 3 shows the frequency distribution of the number of eggs laid per female whitefly per generation averaged for all the cucumber cultivars and for gerbera cv Fame. It can be seen that over successive whitefly generations, the mean number of eggs laid per female decreases, less females lay more than 10 eggs per 24 hour period and the data remains non-normally distributed. Upon gerbera the frequency distribution shows no clear trend. The distribution remains random and the oviposition in the ninth generation seems to be lower. However the range of the distribution is less than that upon cucumber and the average number of eggs laid thus lower. Figure 4 illustrates the mean number of eggs laid per female per host plant per generation in a 24 hour period. In calculating this mean, non-ovipositing females were excluded. Thus antixenosic and antibiosic effects were differentiated between. It can be seen that for all host plants there is no clear upward or downward trend over time, although there is a considerable amount of fluctuation in the mean value over successive generations. Furthermore the mean number of eggs laid in the ninth generation is for all cultivars much lower than in the previous generations. The variation per host plant within any one generation is also considerable (co-efficient of variation lies between 30 and 50%). The between generation fluctuations in the mean appear to be random in nature and give no indication that an adaptation process is occurring upon cucumber. However, as in general the mean number of eggs laid on each cucumber cultivar is higher than that upon gerbera, it may be concluded that adaptation possibly occurs within the first generation upon cucumber.

Immature survivorship

Figures 5 and 6 show the overall immature survivorship per host plant per generation. It can be seen from figure 5 that just as with the egg laying data, there is considerable between generation variation present within and between cultivars. However, as emphasised in figure 6 the immature survivorship is much higher on cucumber than on gerbera. The level of immature survivorship between cucumber cultivars is not consistent over successive whitefly generations (figure 5). For example in the first generation the survivorship upon Corona is higher than that upon Cordoba, whereas in the third generation the opposite is true. Figure 7 shows the per stage immature mortality per host plant per whitefly generation. For the cucumber cultivars the highest mortality is clearly

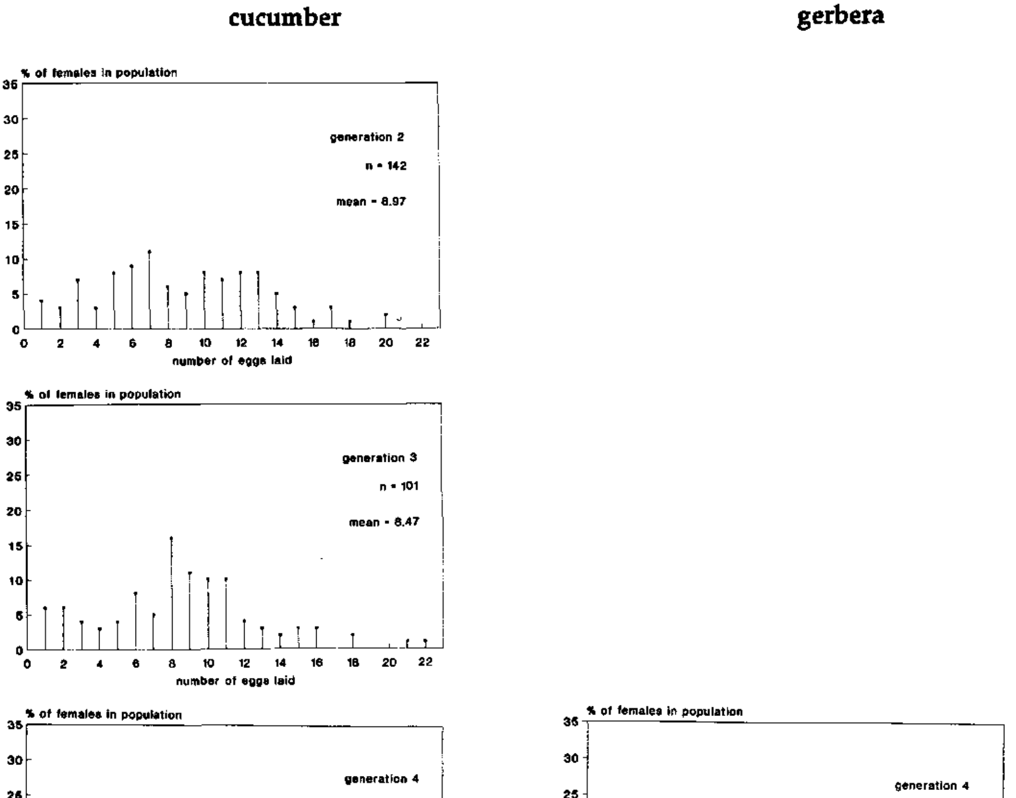


Figure 3 Frequency distributions of the number of eggs laid per whitefly

Figure 4 Mean number of eggs laid per female per whitefly generation on cucumber and gerbera

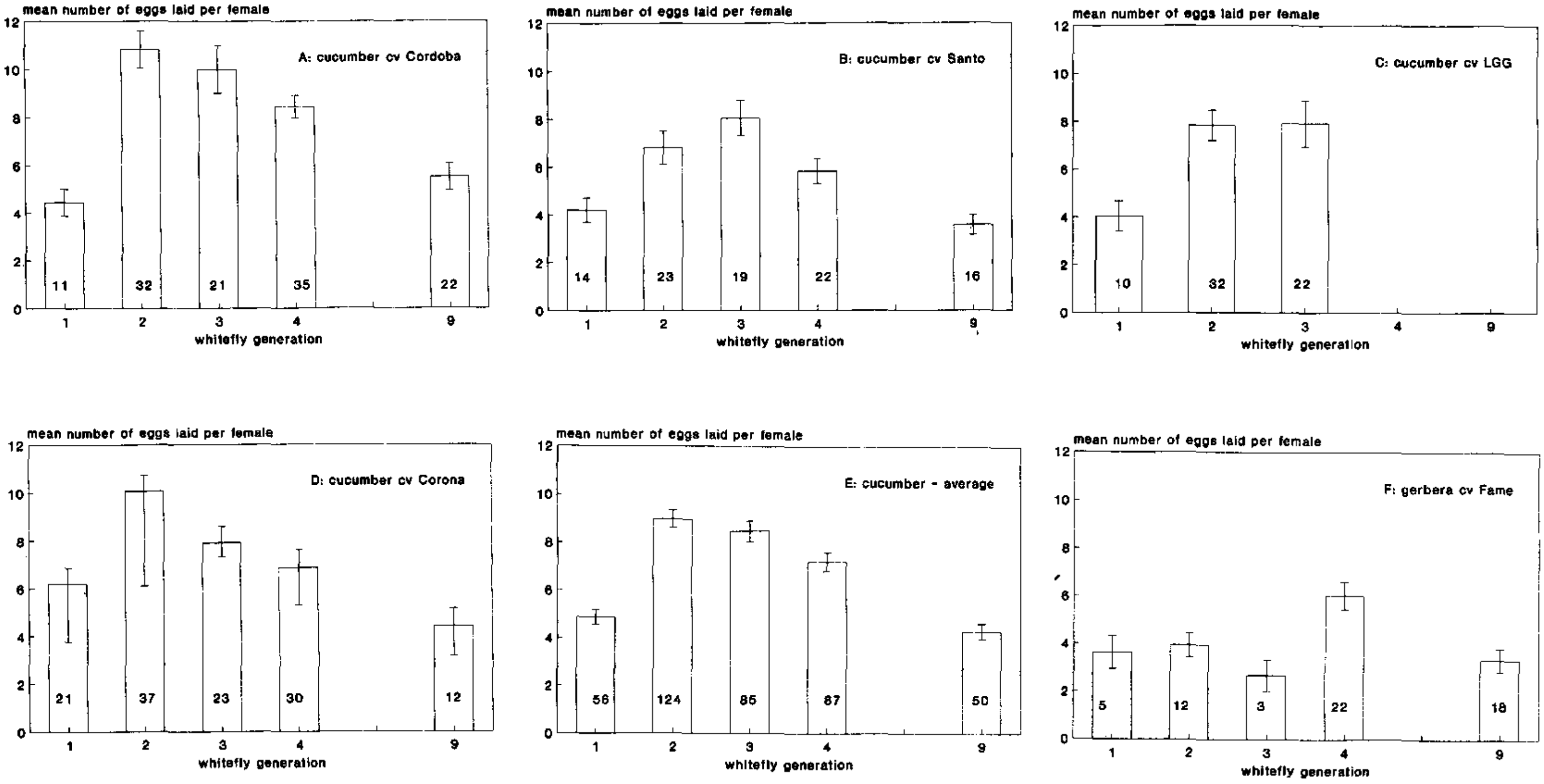
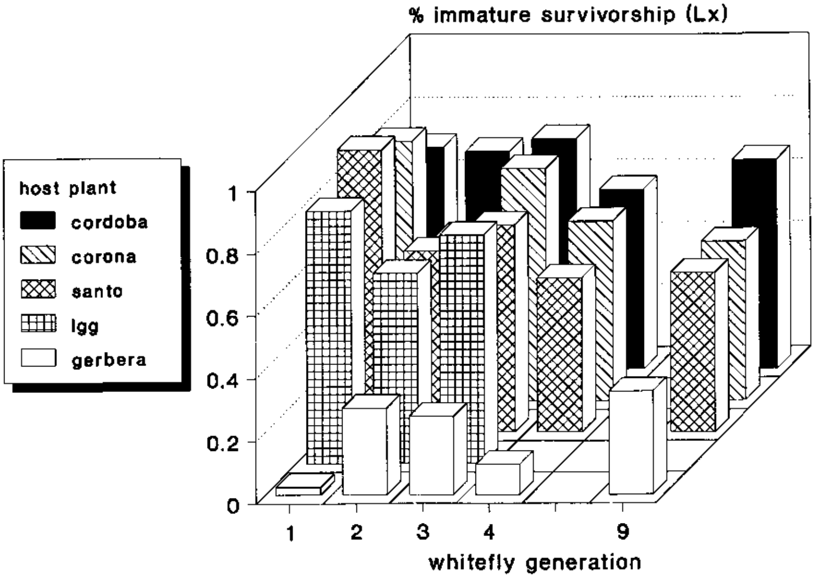


Figure 5 Percentage immature survivorship for whitefly on cucumber and gerbera over successive whitefly generations



population on LGG extinct after gen. 3

Figure 6 Average trend in whitefly immature survivorship from all cucumber cultivars and gerbera over successive whitefly generations

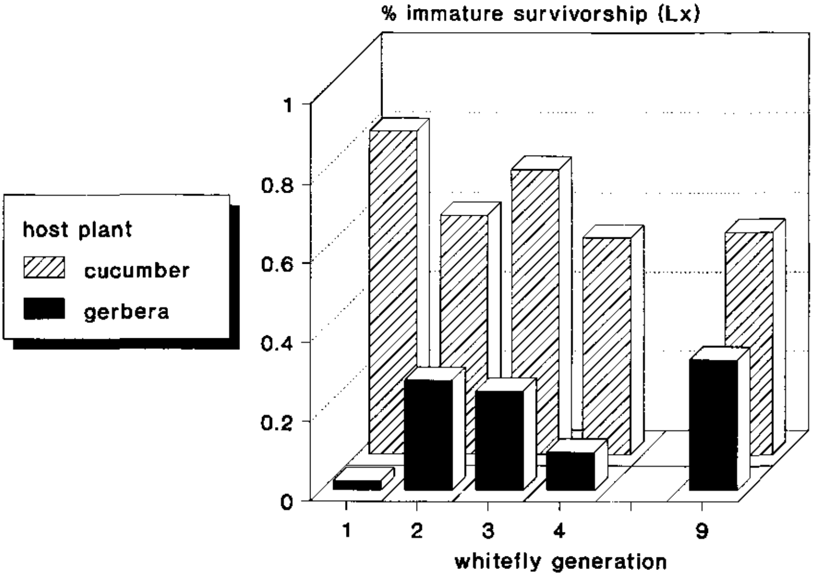
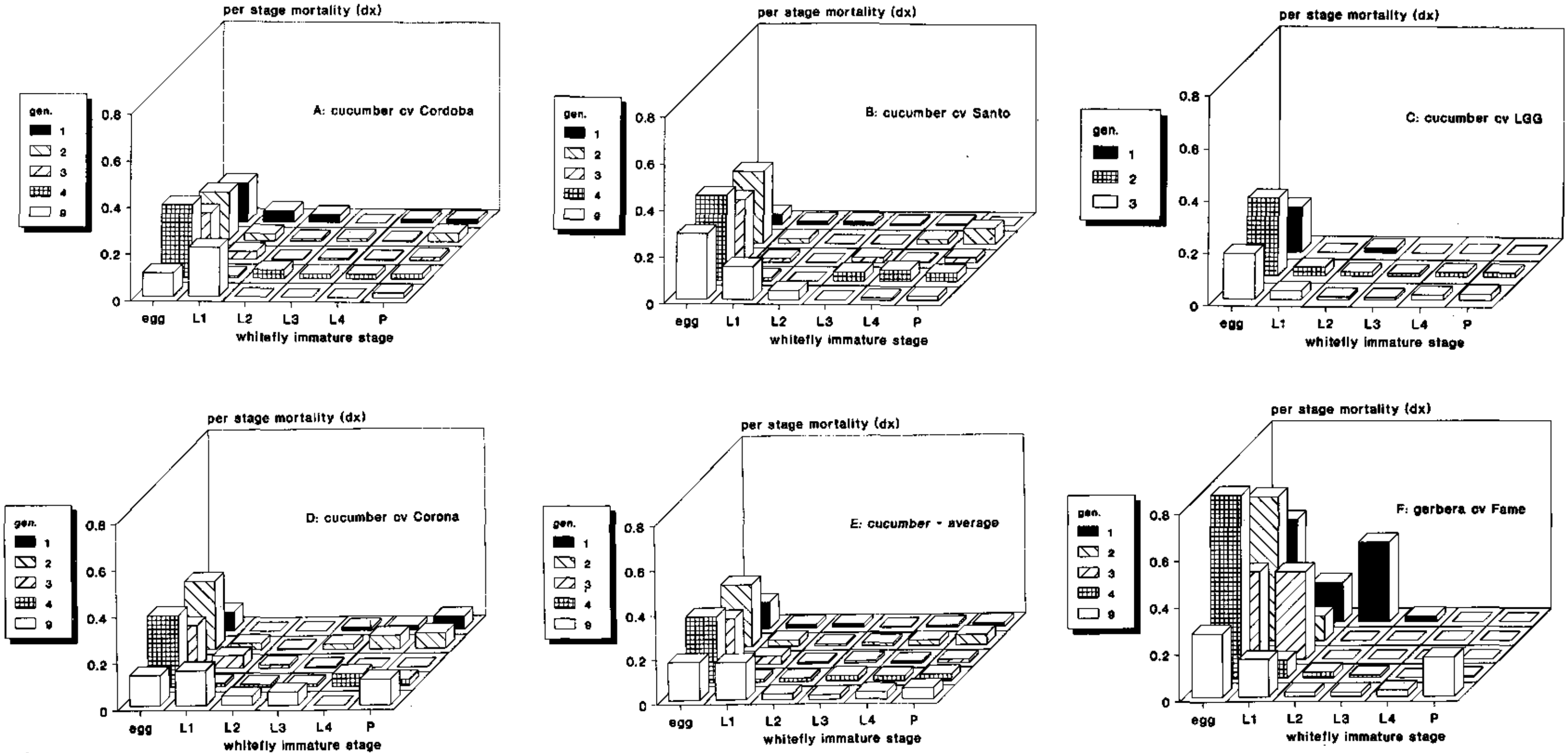


Figure 7 Per stage immature mortality of whitefly upon cucumber and gerbera per whitefly generation



values are average per generation from
the cumcumber cultivars tested

in the egg stage, the remainder falling mostly in the L1 stage. Very little mortality occurs in the immature stages. For gerbera the highest mortality is also in the egg stage but there is relatively more mortality in the L1 stage than is the case by cucumber. Like cucumber the mortality in the other immature stages is very low. Just as with the egg laying data, the mortality data indicates adaptation to cucumber in the first generation.

Immature development time

Figure 8 shows the frequency distribution of the development time per host plant per whitefly generation. The range of the distribution is for the cucumber cultivars no more than 8 days and for gerbera no more than 5 days. Fewer females were tested by gerbera than cucumber. No clear trend over whitefly generations could be seen for the cucumber cultivars the distribution remaining random and fluctuating in skewness. For gerbera sufficient data to graph a distribution was only available for the fourth and ninth generations. In these two generations a random distribution is observed. Figure 9 shows the mean immature development time per host plant per whitefly generation. The variation between generations for a given cultivar is much less than that seen by the egg laying and survivorship data. Differences between cucumber cultivars and between cucumber and gerbera are slight and non consistent over successive whitefly generations. Within each whitefly generation, the variation per host plant is small (co-efficient of variation lies between 5 and 15%), this being in sharp contrast to the egg laying data. This contrast is also reflected in other studies of whitefly (van Roermond and van Lenteren, 1992).

Rank order of host plant suitability for whitefly

As no consistent differences were found in life history parameters between cucumber cultivars over successive whitefly generations, it was decided to qualitatively rank the data indicating the antibiosic properties of the host plants for each whitefly generation to see if an overall trend for host plant suitability could be detected. This method has the advantage that it is easy to see changes in relative rankings between generations and how the ranking in any one given generation, compares with the average ranking based upon the rankings from all the generations observed. Table 2 presents the rankings for the egg laying data, the immature survivorship data and the immature development time data. Figure 10 shows for each of these three indices the average ranking over all generations

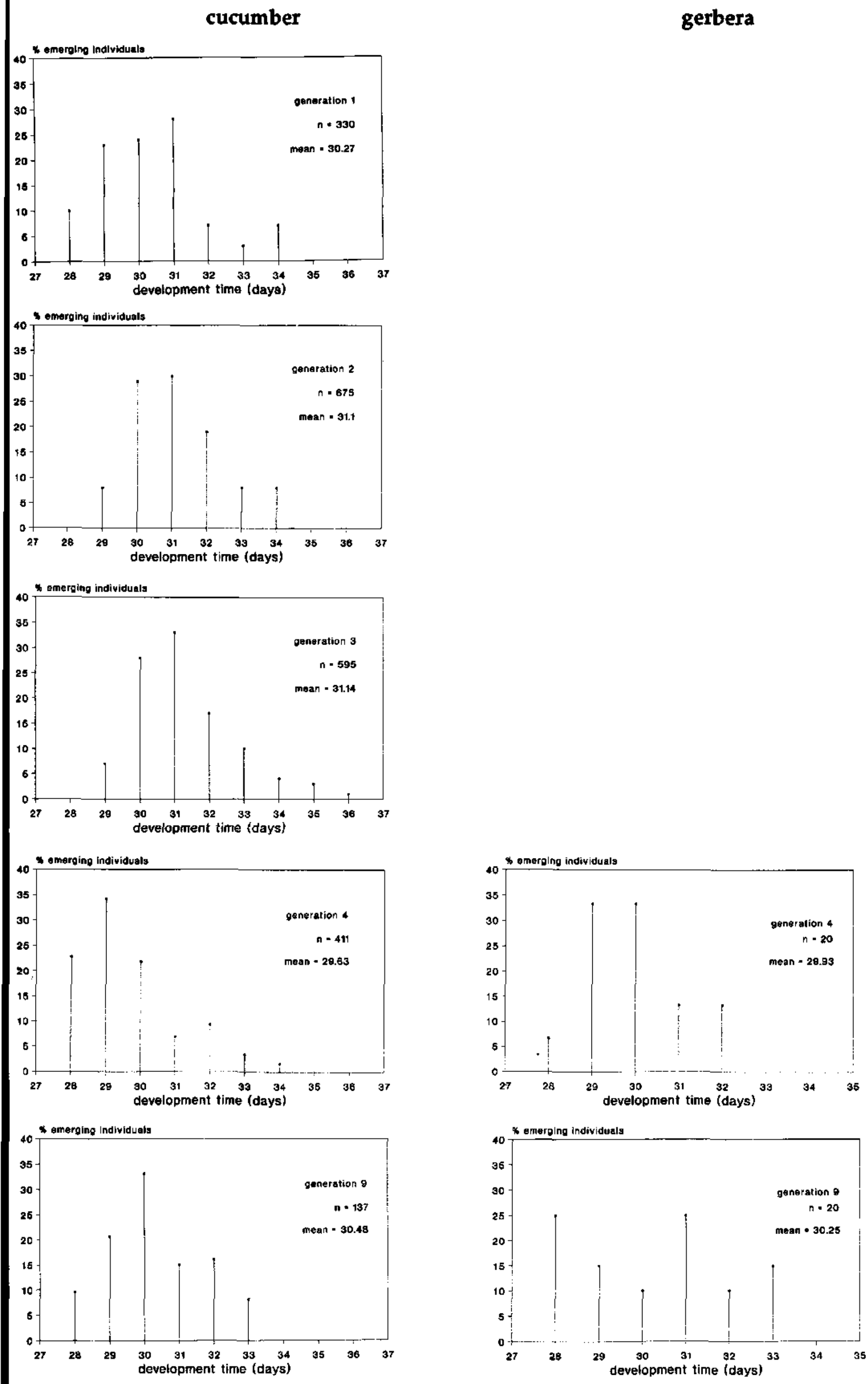


Figure 8 Frequency distributions of immature development time per whitefly generation

Figure 9 Mean immature development time per whitefly generation upon cucumber and gerbera

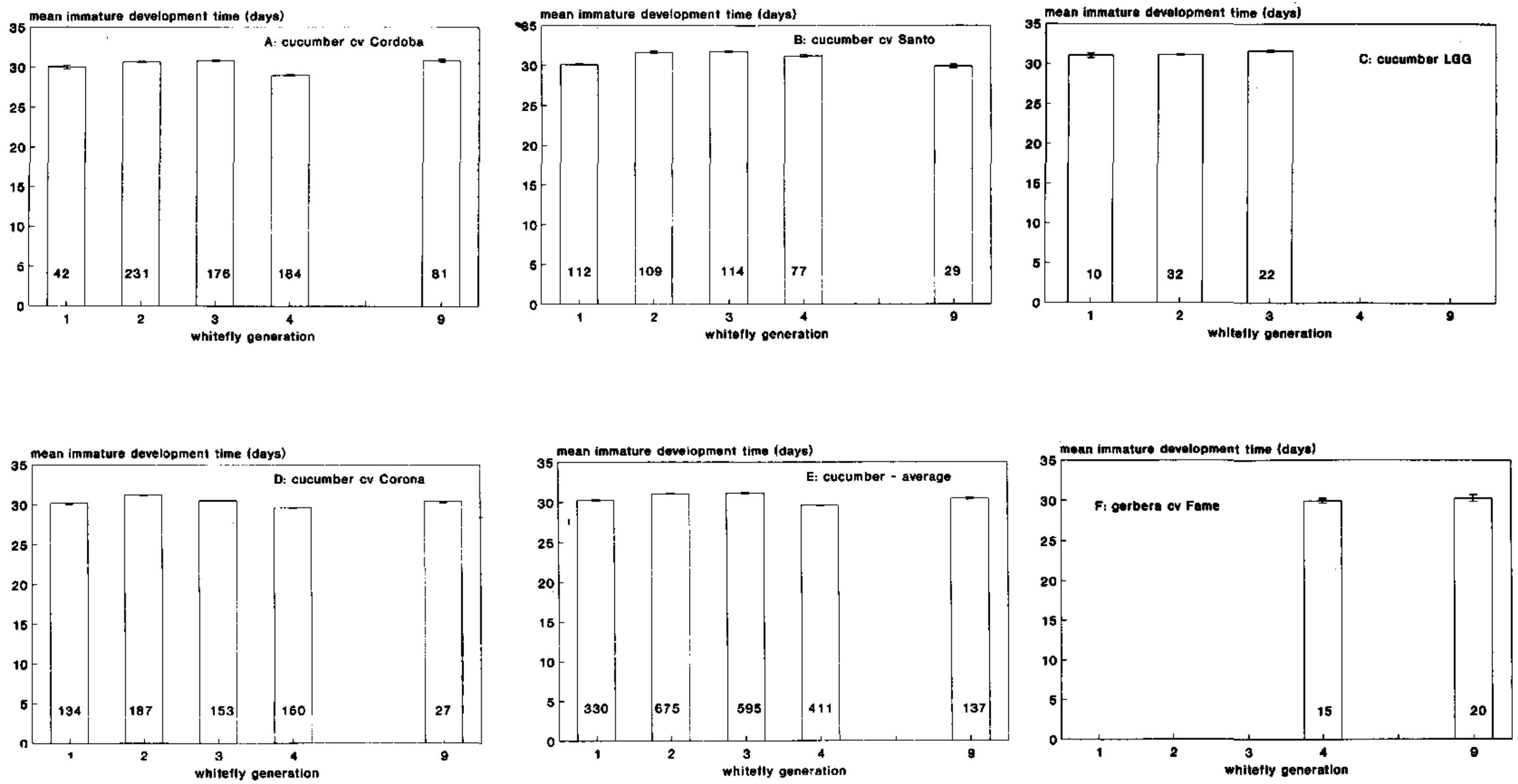


Table 2 Rank order of host plant suitability per generation.

A. based upon the mean number of eggs laid

	whitefly generation				
host plant	1	2	3	4	5
cuc. Cordoba	2	1 a	1 a	1 ac	1a
cuc. Santo	3	4 b	2 a	4 bc	3a
cuc. LGG	4	3 b	4 a		
cuc. Corona	1	2 a	4 a	2 b	2a
gerb. Fame	5	5 c	5 a	3 bc	4a

B. based upon immature survivorship

	whitefly generation				
host plant	1	2	3	4	5
cuc. Cordoba	4	1	2	1	1
cuc. Santo	1	3	4	3	2
cuc. LGG	3	2	3		
cuc. Corona	2	4	1	2	2
gerb. Fame	5	5	5	4	4

C. based upon the whitefly immature development time

	whitefly generation				
host plant	1	2	3	4	5
cuc. Cordoba	1	1	2	1	3
cuc. Santo	2	4	4	4	4
cuc. LGG	4	2	3		
cuc. Corona	3	3	1	3	2
gerb. Fame				3	1

notes:-

- number indicates ranking (1 = high and 5 = low)
- rearing on LGG extinct after 3rd generation
- first 3 generations on Fame too few data to make a ranking in table 2C
- where no statistical testing done, this because non-parametric testing gave tied values to more than 90% of the values in each pair of data sets tested
- letters indicate differences between means at p <.05 using the Mann Whitney U test with the Bonferroni correction applied
- no testing could be done on data from 1st generation as original data sheets lost, only means and standard deviations available

Table 3 Rank order of host plant suitability per generation, based upon the percentage of non-ovipositing females in each population (data in table 1).

	whitefly generation					
	2	3	4	9	average (generations 2-9)	1
host plant						
cordoba	1	1	1	2	1.25	5
santo	4	2	4	1	2.75	3
LGG	2	3			2.5	4
corona	3	4	3	3	3.25	2
Fame	5	5	2	4	4.0	1

notes :-

- population on LGG extinct after 3rd generation
- numbers give ranking (1 = high acceptance, 5 = low acceptance)

Figure 10 Net ranking averaged from all generations, of host plant suitability based upon egg laying, immature mortality and immature development time

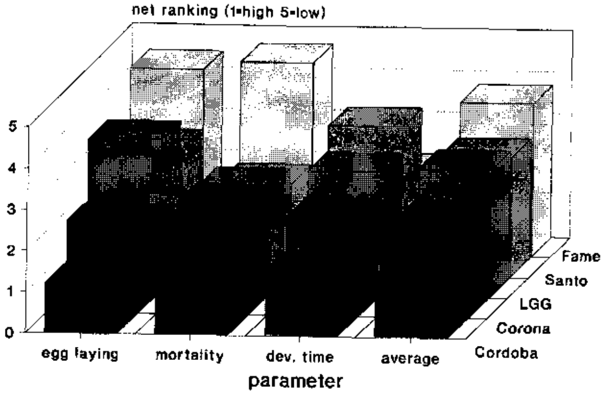


Table 3 Rank order of host plant suitability per generation, based upon the percentage of non-ovipositing females in each population (data in table 1).

	whitefly generation					
host plant	2	3	4	9	average (generations 2-9)	1
cordoba	1	1	1	2	1.25	5
santo	4	2	4	1	2.75	3
LGG	2	3			2.5	4
corona	3	4	3	3	3.25	2
Fame	5	5	2	4	4.0	1

notes :-

- population on LGG extinct after 3rd generation
- numbers give ranking (1 = high acceptance, 5 = low acceptance)

Table 4 **Net ranking (weighted average from all generations) of host plant suitability based upon the mean eggs laid per female per 24 hrs., immature survivorship (Lx) and immature development time (days) data. (average given, with rank in parentheses)**

host plant	egg laying	immature survivorship	immature development	overall average rank
cuc. Cordoba	8.44 (1)	0.669 (2)	30.28 (2)	1.67
cuc. Santo	5.89 (4)	0.633 (3)	31.08 (4)	3.67
cuc. LGG	7.29 (3)	0.680 (1)	31.29 (3)	2.33
cuc. Corona	7.68 (2)	0.629 (4)	30.47 (3)	3.0
gerb. Fame	4.44 (5)	0.163 (5)	30.11 (1)*	3.67

* based on two values and thus ranking possibly biased

Correlation between egg laying and immature development time

Where data for all five generations were available, a non weighted linear regression of mean immature development time against mean number of eggs laid was made for each cultivar. Each observed generation formed a paired data point. Of the three cucumber cultivars tested, Cordoba, Santo and Corona, only the regression for Santo was significant (table 5). The overall regression for cucumber was non significant. The regression lines obtained were all positive. This is contrary to the expectation of a negative correlation resultant of a colonisation strategy (McArthur and Wilson, 1967). It may be concluded from these data, that the mean number of eggs laid per host plant is not a strong predictor of the subsequent development time of those same eggs. However if a more accurate measurement of fecundity was made, a stronger correlation may well be detected.

Table 5 Non weighted linear regression of mean immature development time against mean number of eggs laid per cultivar over successive whitefly generations

cultivar	R^2	p value
cucumber Cordoba	0.014	0.851
cucumber Santo	0.939	0.007
cucumber Corona	0.323	0.318
cucumber (average)	0.233	0.410

notes:-

- R^2 is the co-efficient of determination
- result for cucumber is mean using grouped data from all cucumber cultivars tested

'Trade-offs'

With regards to the investigation for 'trade-offs', figure 11 illustrates the mean number of eggs laid per female whitefly per generation for each whitefly line. The sample size for each line lay between 10 and 20 females. The standard error bars indicate the amount of variation present. The coefficient of variation lay between 20% and 40%. Comparisons made with the Mann Whitney U test, showed that significantly more eggs were laid by the cucumber cv Cordoba strain whiteflies than the other strains. There were no differences between the strains cucumber cv Santo and the two cucumber reversion lines upon gerbera. The strain from gerbera cv Fame had the lowest mean oviposition although this was not significantly different from that of the reversion line from cucumber cv Cordoba. The percentage of non- ovipositing females (figure 12) was highest for the stock line upon gerbera and lowest for the two parent lines upon cucumber. The reversion lines on gerbera were intermediary between the gerbera and cucumber lines. The immature survivorship (figure 13) was clearly higher upon the two cucumber lines than upon the lines on gerbera. For the gerbera lines the stock gerbera line showed a similar survivorship to the reversion line from Cordoba. The survivorship on the Santo reversion line was lower. An examination of the per stage immature mortality (figure 14) indicated that for all lines respectively, the egg and pupal mortality were approximately equal and much

Figure 11 Comparison of mean number of eggs laid per female for each whitefly population

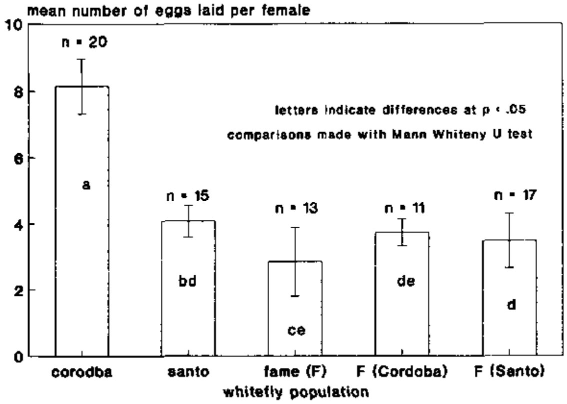


Figure 12 Percentage of females in each population that did not oviposit

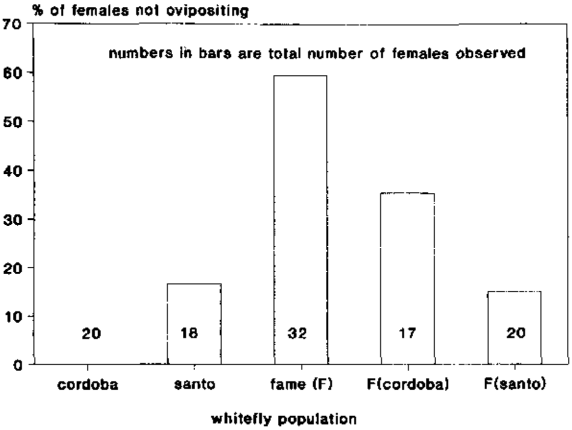


Figure 13 Percentage immature survivorship of the different whitefly populations

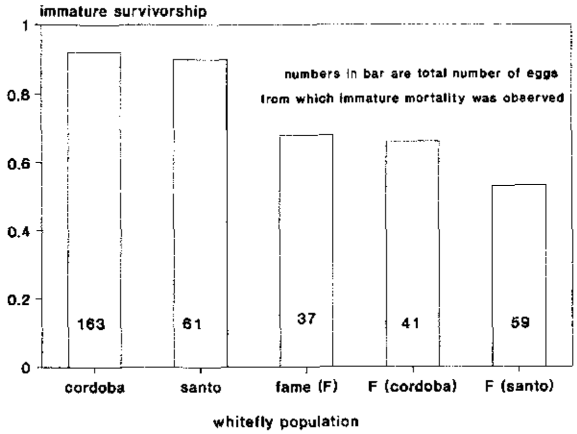
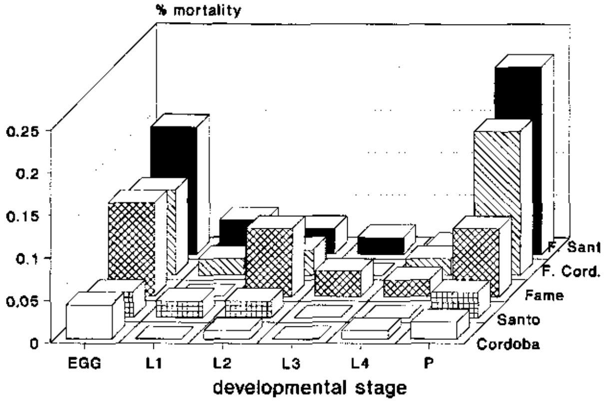


Figure 14 Per stage percentage mortality for the different whitefly populations



higher than the mortality in the other immature stages. Indeed for the two reversion lines the pupal mortality was higher than the egg mortality. There were no significant differences between lines in the distribution of the per stage immortality. The high pupal mortality is atypical in comparison with the data obtained elsewhere in this study (figure 7) and other data for whitefly on these two plant species (see van Roermond and van Lenteren, 1992). This suggests that these results are possibly an experimental anomaly.

In summary it can be concluded that the two cucumber reversion lines upon gerbera demonstrate a lower performance upon gerbera than the parent lines upon cucumber. In comparison with the stock population upon gerbera the two cucumber reversion lines show a lower acceptance for gerbera (figure 12), a slightly higher (though in the case of cucumber cv Cordoba not significant) number of eggs laid (figure 11) and the immature survivorship was the same as for the reversion line from cucumber cv Cordoba and higher than the reversion line from cucumber cv Santo. As the differences in egg laying between the original gerbera line and the reversion lines upon gerbera are approximately negated by the differences demonstrated in immature mortality, the presence of 'trade-offs' is not indicated by this study.

Discussion

Mildew resistance is not associated with whitefly resistance in cucumber

That one of the mildew resistant lines appears to be more suitable for whitefly than the mildew susceptible lines, underlines the care that needs to be taken in breeding programs, so that resistance against one pest or disease does not, albeit indirectly, facilitate the performance of a second pest or disease upon the host plant concerned. Whether the differences in whitefly suitability noted between the cucumber cultivars, accurately reflects differences under commercial greenhouse conditions and thus possibly adjustment of *Encarsia formosa* numbers needed to be released for effective whitefly control, requires further investigations to be made. This is important where it is desirable to release mildew resistant cucumber cultivars as part of an integrated control program, thus hopefully promoting biological control and reducing fungicide dependency (Mol, 1991).

Rate of whitefly adaptation

This study demonstrates a rapid adaptation of whitefly within one generation from gerbera to cucumber. In the pilot study previous to this the adaptation of whiteflies originating from tomato cv Moneymaker to two gerbera cultivars, Parade and Fame, was clearly reflected in a gradual and approximately asymptotic decrease in the immature mortality. This trend was not reflected in the egg laying data or immature development time data, both of which demonstrated a random fluctuating pattern over consecutive whitefly generations. However that particular study must be repeated to confirm the result as too many complicating factors were present as outlined in the introduction to this article. In a third study upon sweet pepper described in chapter 3 of this thesis, an examination of the per stage immature mortality data indicated a limited adaptation of a population conditioned on *Lycopersicon hirsutum* cv. *glabratum*. The per stage mortality decreased in the earlier larval stages and increased in the later larval stages. The overall immature mortality remained fairly constant. Thus whitefly seems to adapt rapidly to more suitabile plants within its host range and much slower to marginal host plants such as sweet pepper.

Comparisons with previous whitefly data

When my data are contrasted with previous studies of Dutch whitefly performance upon cucumber and gerbera (van Merendonk and van Lenteren, 1978; van Boxtel, et al., 1978; van Sas et al., 1978; and Dorsman and van de Vrie, 1987), it was noted that previous studies had only been conducted for a single whitefly generation, although the study of van Boxtel et al. (1978) had considered the effects of whitefly host plant origin (see importance of this in relation to 'pre-conditioning' described in chapter 3). More importantly the whiteflies had been reared on a second (control) host plant and then placed upon the host plants to be tested, without previous experience upon these plants. The data from this first generation were used to assess whitefly performance upon them. This methodology has several drawbacks. Firstly by examining solely the performance of the whiteflies in the first generation upon the new host plant the possibility of maternal effects cannot be excluded. Secondly, as was found in this study the number of non-ovipositing females is higher than in the subsequent generations. This possibly gives rise to a misleading impression of the fecundity of the whitefly upon the host plant concerned. This is especially so where non-ovipositing females are included in the calculation of the mean number of eggs laid per female per day. (In the forementioned studies, although the number of dead and living females in a leaf cage after 24 or 48 hours was differentiated, it is not necessarily the case that all living females will have laid in that period if some had a non-preference for the host plant concerned. This should be differentiated as in my study where data for females laying no eggs is not included in calculating the mean number of eggs laid.) Finally, measurement of a single generation, does not consider the between generation variability that may be present and thus where host plants tested are of a similar resistance, a biased conclusion may be drawn as to their rank order of suitability for whitefly.

Upon making comparisons between this and other studies, the development time cannot readily be included, due to the previous studies being conducted at different temperatures to this one. The egg laying data is only approximately comparable due to differences as outlined between this and the previous studies in its measurement. The study of van Boxtel et al. (1978) showed a mean number of eggs per living female of circa 10 per 24 hours, which is slightly higher than in this study, the discrepancy possibly being due to the different cultivars used. Van Merendonk et al. (1978) give a value of 7.7 eggs per living female per 24 hours and van Sas et al. (1978) give a value of 7.5 eggs per living female per 24 hours, which are of the same magnitude as this study. For gerbera the average number of eggs laid at 20°C grouped from several cultivars was 5 per living female per day, which is slightly higher than my data. The mortality data of van Sas et al. (1978), whiteflies originating from tomato cv Moneymaker, gave a total immature mortality of 1% for cucumber (based upon 211 eggs) and 60 % for gerbera (based upon 245 eggs). The result for gerbera is comparable to the data for this study but that for cucumber is extremely low. The data of van Merendonk and van Lenteren (1978) using whiteflies that originated from tomato cv Moneymaker but conditioned for the first 10 days after emergence upon cucumber gave an immature mortality upon cucumber of 10.6 % which is 70 % lower than the data obtained in this study. In the study of Dorsman and van de Vrie (1987) using whiteflies sampled from and tested upon gerbera, the mortality was between 10 and 16 % at 20 °C (a temperature comparable to this study). This is much lower than the result obtained in this study. This lower immature mortality, may in part due to differences in the cultivars used between this study and previous studies and also differences in the precise origin of and in the rearing methodology for the whiteflies used.

Between generation variation in whitefly performance

It is difficult upon the basis of this study to ascribe causal factors for the variation in performance seen between successive whitefly generations. Such fluctuations are typical of laboratory rearings even under optimal conditions (e.g. Nicholson, 1954).The whitefly females used to lay eggs in all generations were of similar age. The experiments were all conducted in a climate cell with a constant lighting regime and very little variation in temperature and relative humidity. Although the rearing of the plant material was highly standardised, phenological effects cannot be excluded. We cannot differentiate whether the cause of the variation is more attributable to the plants or the whiteflies. A sib analysis designed to detect the components of genotypic and phenotypic variation (e.g. Via, 1984) would be a suitable approach. Adopting such an approach, needs serious consideration of the experimental design especially with regards to the amount of replication required to detect within and between generation differences, considering that the magnitude of between generation fluctuations observed in this study are circa 30% By assessing genetic and phenotypic components of variation over consecutive whitefly generations for the gerbera - cucumber system studied, several questions may be answered. Firstly the level of phenotype plasticity present in the different lines may be assessed, phenotype plasticity playing a potentially important role in selection processes (eg Stearns, 1989) and in maintaining population fitness under unfavourable conditions with respect to the genotypes in the population concerned (Thompson, 1991). Also by examining especially the additive component of the genetic variance over consecutive generations, it could be assessed if the lines maintained were undergoing a more stabilising or a more disruptive selection process (Mather, 1953). A disruptive selection process could be causal of population fluctuations and will tend to maintain genetic variation within a population which is advantageous, where a population has to adapt to a new environment.

'Trade-offs' by host plant adaptation of whitefly

No 'trade-offs' were detected as a result of whiteflies originating from gerbera, adapting to cucumber. This result may be expected upon the basis of the hierarchy threshold model (Courtney et al., 1989). In chapter 4 of this thesis, this model was used to explain the results obtained from tests of whitefly host plant preference. Prediction 11 of the hierarchy threshold model reads: 'genetic variance for rank order low in the hierarchy is not subject to direct selection, and should be maintained in populations. Insects may therefore exhibit genetic variance for acceptance of hosts that they do not use in nature.' This prediction is realised in the result I obtained. Cucumber is a higher ranking host plant for whitefly than gerbera. Therefore selection against variation for cucumber should not have occurred during the rearing of the gerbera strain whiteflies on cucumber. Consequently, upon being returned to gerbera, the variation for this host plant was still present in the whitefly populations, no 'trade-offs' being observed. However 'trade-offs' may be expected upon transferring whitefly reared on a high ranking plant, cucumber, to a low ranking plant, sweet pepper and then reverting them back to cucumber. Here variation for a higher ranking host may be selected against, when the population is upon a lower ranking host, if population fitness upon this host is to be maximised. Such 'trade-offs' have yet to be sought in whitefly.

Precision and consistency in measurements of host plant adaptation

If a study is to be conducted over several generations of an insect pest then much care needs to be taken in the rearing and maintenance of insect and plant material. In a review outlining the genetic constraints upon laboratory populations, Mason et al. (1987), state: 'It is ironic that large amounts of time and money are often spent on experiments utilising laboratory insects, but little time is spent on maintaining their quality'. In that review the genetic aspects of laboratory rearings is emphasised, especially problems associated with inbreeding. However another aspect of quality is the maintenance of rearings under standardised conditions, controlling for phenological and other effects as outlined in the introduction to this article. Such attention to the quality of insect and plant material requires much plain hard work. Although this is undoubtedly done by most researchers, precise details of rearing methods used, are not always apparent in scientific publications (Thomas, 1992a). Although I accept that a certain amount of variation will always exist between studies consequent of the fact that populations of living organisms are themselves inherently variable, differences in the quality of rearings still tends to hinder the comparison of different studies, even where the same insect and host plant species were used. Poorly maintained rearings tend to yield results aberrant to those found in general, this being compounded where studies are made based on a single generation of the insect population concerned. Therefore, in scientific publications, researchers should clearly state the methods and conditions they used, so as to facilitate the exact duplication of experiments by a third party. If a trend in adaption to a host plant is detectable upon the basis of immature mortality and fecundity data, these parameters clearly need to be measured more accurately than in this study. To account for the stochastic nature of the daily number of eggs laid per female and also for the influence of the females age, the fecundity schedule must be accurately determined as for example was done for whitefly by Romanow et al. (1991). As differences between host plants may be small for development time (a day or less), an accurate detection of differences between lines would require that emergence of whitefly pupa was checked for every six hours. Precise measurements of fecundity and development time are much more laborious than the more indicative measurements made in this study. A more accurate measurement of the whiteflies' fecundity may reveal whether the tendency of females to lay less than 10 eggs per 24 hours over successive whitefly generations as observed in this study, is actually resultant of a change in the whitefly's fecundity schedule and not purely a stochastic affect in daily egg laying.

Determining the resistance of plant cultivars to whitefly

The testing of cultivars for resistance against insect pests often uses life history parameters as indicators of plant antibiosis. Studies vary in which life history parameters are measured and how precise such measurements are. Certain improvements may be made upon the basis of this study. Not all studies measure immature mortality at the per stage level, although this may reveal important differences between cultivars. For example two cultivars may exhibit the same overall level of immature mortality but for one cultivar the mortality may fall predominantly in the egg stage and in the other it falls more uniformly over all immature stages. In the second case the potential damage to the plant caused by feeding of the immature stages is much greater than in the first. Fecundity measurements are often made over a 24 or 48 hour period on a single generation. This does not account for the highly stochastic nature of a female's daily oviposition behaviour thus possibly leading to a false assessment of lines where differences between lines are small. This can be overcome by assessing the fecundity schedule over the female's entire lifespan as done in earlier studies e.g van Boxtel, et al. (1978), van Sas et al. (1978) and more recently by Romanow et al., 1991 in comparing different tomato lines for resistance against whitefly. Also where insects are confined to a plant in a no choice situation, the calculation of the mean number of eggs laid per female does not always differentiate between laying and non laying females the measurement thus combining the antibiosic and antixenosic properties of a plant. This can result in leaf cage experiments indicating different levels of resistance than greenhouse tests where a choice situation exists (Romanow et al., 1991). I suggest upon the basis of this study that more care needs to be taken in the selection of breeding lines for the development of resistant cultivars, especially to account for between generation variation of the pest species and also in differentiating between antixenosic and antibiosic properties of resistance. The ranking of the suitability of the four cucumber cultivars based on data from several consecutive generations would seem to be a good method of reliably determining the level of resistance.

Simulation models of host plant durability

Between generation variation as observed in this study, should be considered in determining the base values of parameters for whitefly simulation models. Such models have to date calculated parameters upon the basis of studies done on single whitefly generations and used data originating from different whitefly populations, tested on different cultivars of the same host plant (Hulspas-Jordaan and van Lenteren, 1989, and Yano et al, 1989a and b). Further, the model of Yano et al.(1989b) compared two different whitefly populations, one Hungarian and one Dutch, on Dutch and Hungarian sweet pepper cultivars, thereby simulating the results of van Lenteren et al. (1989). Such a comparison of differences between different cultivars of the same host plant for different whitefly populations, is needed in plant breeding studies where the efficacy and durability of the resistance needs to be determined. Indeed few models have been built to determine the durability of a resistant line. Of the two I know, that of Gould (1986) assessed durability in terms of a quantitative genetics model considering general changes in general population fitness but not specific population demography. The review of Kennedy et al. (1987) considers various factors of importance but also does not detail specific demographic changes. Models will have to consider between generation variation and also the effects of 'pre-conditioning' on various host plants in relation to a pests ability to adapt to the cultivar being tested. If simulation models on the biological control of whitefly upon different host plants, were to consider data upon the basis of which plants the whitefly had been conditioned upon, then a valuable insight as to the possible role of a 'pre-conditioning' plant on the subsequent pest-parasitoid dynamics, would be gained.

3 CAN A DUTCH STRAIN OF WHITEFLY ADAPT TO A DUTCH CULTIVAR OF SWEET PEPPER ?[1]

Summary

A previous study by van Lenteren et al. (1989), indicated that whiteflies originating from Hungary, performed much better upon sweet pepper than whiteflies originating from Holland. As yet it is not precisely known whether or not these observed differences are a result of the two whitefly populations being genetically differentiated from each other, to the extent that they are parapatric strains or host races of the same species. It was thought that the differences between whitefly populations in their performance on various host plants could be due to the very different host plants that the populations had been previously exposed to in their respective histories. Upon the basis of this premise a series of experiments was conducted using Dutch whitefly populations of known but different rearing histories, to test whether 'pre-conditioning' of a particular whitefly population on a particular host plant could (in anyway) facilitate the adaptation of the populations to sweet pepper. In the experiments several parameters of whitefly performance were measured: egg laying, survivorship and development time. From the results it could be seen that of the various host plants used as 'pre-conditioning', *Lycopersicon hirsutum* cv. glabratum definitely facilitated adaptation to sweet pepper in comparison with *L. esculentum* cv. Moneymaker, this facilitation perhaps being related to the alpha tomatine present in this former host plant. The performance of whiteflies that were 'pre-conditioned' on gerbera and cucumber was not significantly different, tentatively indicating that host plant quality may be of secondary importance in the 'pre-conditioning' process. Overall it can be concluded that, even where 'pre-conditioning' of the whiteflies does occur, sweet pepper remains a poor quality host plant for Dutch whiteflies. This is predominantly due to the high level of mortality that occurs between the egg and L1 stages of the whitefly.

Introduction

At present the glasshouse whitefly (*Trialeurodes vaporariorum* [Westwood]) is not considered to be a pest upon glasshouse crops of sweet pepper (*Capsicum annuum* L.) in The Netherlands. This is in contrast with the situation in central european countries e.g. Czechoslovakia, (Laska et al., 1986), Hungary (van Lenteren et al., 1989) and Moldavia

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[1] accepted for publication in J. appl. Ent.

(Zabudskaya, 1989) where the whitefly has a variable pest status, dependent upon the origin of the whiteflies and the sweet pepper cultivars tested. For example in the tests of Zabudskaya (1989), the net reproductive rate of a whitefly population tested on 8 sweet pepper cultivars varied between 1.34 on one cultivar through to 25.92 on another cultivar. Furthermore it is clear from the work of van Lenteren et al. (1989), that this variability in performance upon sweet pepper is not just due to differences between sweet pepper cultivars in their resistance to whitefly, but also to the difference was between the whitefly populations themselves. To assess whether or not there are genetic differences between Dutch and central european whiteflies with respect to their ability to adapt to different host plants, crossing experiments between the whiteflies from different locations would need to be done similar to those for example of Hsiao (1982), for the colorado potato beetle. From such experiments it could be determined if the different whitefly populations were compatible (could interbreed) and also if the performance characteristics of each population are genetically inheritable and transferable between populations.

As it was desired to minimise the potential risk of importing a different strain of a pest species, this study was limited to a Dutch whitefly population. During the course of my research on the ability of whiteflies to adapt to different host plants, the idea arose that the pre-eminent ability of the Hungarian strain whiteflies to adapt to sweet pepper could be because they are (due to the crops etc. grown in Hungary) 'pre-conditioned' in a different way than Dutch whitefly. I therefore tested whether it was possible to 'pre-condition' Dutch whiteflies, such that they would adapt to sweet pepper. A 'pre-conditioning' treatment is where the performance of the whiteflies tested upon the experimental plants in question, is affected by the host plants upon which they have previously been reared. This effect has already been demonstrated for the russian wheat aphid by Schotzko and Smith (1991) and for *Myzus persicae* by Lowe (1973).

Schotzko and Smith (1991), took two wheat cultivars, 'border oats' which is partially resistant to russian wheat aphid and 'stephens', a susceptible cultivar. Aphids 'pre-conditioned' for five generations upon 'stephens', were used as a standard population. Over the subsequent three generations aphids were transferred from one cultivar to the other each generation. Thereby host plant sequences were established e.g 'stephens'-'border oats' - 'stephens' or 'border oats'- 'stephens'-'border oats', eight permutations being tested. It was shown that where in the previous generation a population had been 'pre-conditioned' upon 'border oats', its performance upon 'stephens' was lower than a population previously 'pre-conditioned' on 'stephens'. A population 'pre-conditioned' in a previous generation on 'stephens' showed a better performance upon 'border oats' than a population 'pre-conditioned' on 'border oats' in the previous generation. In summary aphids 'pre-conditioned' upon a susceptible cultivar performed better upon a partially resistant so well as a susceptible cultivar than aphids 'pre-conditioned' upon a partially resistant cultivar.

Lowe (1973), took a stock population of *Myzus persicae*, reared on chinese cabbage for two and a half years. From this stock, lines were initiated upon sugar beet and broad bean. When these lines were approximately a year old, tests on aphid performance and settling behaviour were done. Aphids originating from chinese cabbage settled least on sugar beet and those originating from broad bean settled more on sugar beet, than the sugar beet line. This trend was the same for aphid performance (number of offspring per female). In general, clones collected from various field locations showed a more enhanced performance on sugar beet when pre-conditioned upon broad bean, than upon chinese cabbage.

In order to assess whether it is all possible for whitefly to adapt to sweet pepper I conducted three experiments. Experiment 1 was a preliminary trial, designed to assess the overall immature survivorship of whiteflies from a long standing laboratory rearing on tomato (*Lycopersicon esculentum*, cv. Moneymaker) upon sweet pepper. From this experiment it was clear that the survivorship of this population on sweet pepper was so low, that a viable second generation could not be raised on sweet pepper. Therefore it was decided to 'pre-condition' the whitefly on another *Lycopersicon* species, *L. hirsutum* cv. glabratum, a species used earlier to transfer partial resistance to whitefly to commercial tomato varieties (de Ponti et al., 1983). This 'pre-conditioning' proved to facilitate the adaptation process and the performance of these 'pre-conditioned' whiteflies upon sweet pepper was followed for 3 generations. In a third experiment, I tested whether the quality (acceptance of and performance upon with respect to the whitefly) of the host plant in anyway affected the subsequent performance of that whitefly population upon sweet pepper. This experiment also gave an indicat ion as to the egg laying capacity of whiteflies upon sweet pepper.

With respect to the methods used in these experiments, that for experiment 3 was a fairly standard procedure (in the same vein for example as van Lenteren et al., 1989) using leaf cages and following the progress of each individual from egg to adult. However due to the very high mortality whitefly exhibits in the early immature stages when on sweet pepper, it was decided for the first two experiments, where it was desired that the whitefly performance could be reasonably followed over several generations, to sample directly the mortality on a sweet pepper rearing with non-overlapping generations.

The measure obtained in experiment 3 of the mean number of eggs laid per female over a 24 hour period is only an indicator of the actual fecundity of the populations in question. Whitefly fecundity is dependent upon the age of the females used and for any specific age is still highly variable between females. The females used in experiment 3 were all between 5 and 10 days old, the period in which fecundity is at a peak (van Lenteren et al., 1980 and Romanow et al., 1991).

Materials and Methods

Rearing of plant material

The following plant species were used; *Cucumis sativus* (cucumber) cv.'s Cordoba (from Rijk Zwaan B. V.) and Santo (from Zaad Unie B. V.), *Lycopersicon esculentum* (tomato) cv. Moneymaker, *Lycopersicon hirsutum* cv. glabratum, *Gerbera jasemonii* (gerbera) cv. Fame (from Terra Nigra B. V.) and *Capsicum annuum* (sweet pepper) cv. Westlandse zoete. The plants were all reared as described in chapter 2 of this thesis. The sweet pepper plants used were taken (unless otherwise stated) at the 6/7 leaf stage in 13cm pots.

The whitefly rearing

The material and rearing methods are as described in chapter 2 of this thesis.

Experiment 1

This experiment was conducted in April 1990, in a heated glasshouse compartment, with an average temperature of 22 C ± 1 C, a relative humidity of 70% ± 15% and supplementary lighting of 6800 lux as necessary to give a photoperiod of 16 L and 8 D. Biological control agents were used against other phytophagous insects on a weekly basis throughout this experiment. Leaves with whitefly pupa on were taken from the rearing on tomato cv. Moneymaker, and placed in the bottom of a wooden cage containing a single 10 week old sweet pepper plant. The whiteflies were allowed to emerge and lay eggs on the sweet pepper plant. Ten days after the tomato leaves had been placed in the cage they were removed as were the adult whiteflies on the sweet pepper plant. Once all adults had emerged the leaves were removed and the number of pupae remaining on all the leaves was counted (eggs not counted as the eggs had already fallen from the leaves).

Experiment 2

This experiment was conducted in the period May to August 1990 in a heated glasshouse with a mean temperature of 24°C ± 3°C, a relative humidity of 55 % ± 25%, and supplementary lighting of 6800 lux to give a photoperiod of 16 L and 8 D. As in the first experiment biological control was applied on a weekly preventative basis. Leaves with whitefly pupae were taken from the rearing on tomato cv. Moneymaker and placed in a cage with a *L. hirsutum* plant which was 2 months old and had 8 true leaves. The whiteflies were allowed to emerge and lay eggs, the whiteflies and the tomato leaves being removed from the cage 10 days after the tomato leaves had been placed in the cage. When pupae appeared on the *L. hirsutum* plant, the leaves were removed and placed on the bottom of a second cage which contained a 10 week old sweet pepper plant. The pupae were allowed to emerge from the *L. hirsutum* leaves. These were then removed and the number of each larval stage present on a random sample of 6 leaves was assessed. The *L. hirsutum* leaves and the adult whiteflies from the sweet pepper plant were then removed. The eggs were allowed to develop until they reached the pupal stage. The leaves were removed and placed in the bottom of a cage with a fresh sweet pepper plant. The pupae were allowed to emerge and the whiteflies and leaves were removed after 10 days. The leaves were analyzed as before. This process was repeated also for the third generation on sweet pepper. The rearing is illustrated in figure 1.

Experiment 3

This experiment was conducted in November 1991, in a climate room held at 21°C and 70% RH, with a photoperiod of 16L and 8D the light concentration being 8000 lux. Six different whitefly populations were used with their respective host plants, the lineage of each population being illustrated in figure 2. The basic methodology was as described for the adaptation experiment in chapter 2. Additionally, at 10 and 20 days after the experiment started, a level teaspoon of fertiliser (19N: 6P: 20K) was added to the water in each tray (45*30*8 cm) wherein the sweet pepper plants (2 per tray) sat.

From these data the mean number of eggs laid per female over a 24 hour period was calculated for each of the populations. The immature mortality was calculated in the form of standard life history parameters (A_x, L_x and d_x) as given by Gradwell and Varley (1970). The total immature development time was also calculated per population (for the populations where immature development was completed). Further with relation to the identification of different whitefly stages I chose for convenience not to differentiate between the pupal and pre-pupal stages, both of these stages being referred to as the pupal stage.

Statistical testing

Overall differences between data sets were assessed at the $p < 0.05$ level, using a Kruskal - Wallis one way analysis of variance. Where an overall difference between populations was found or apparent, the respective populations were then tested on a paired basis, using a Mann Whitney U test, using the Bonferonni correction. All tests were performed using the computer software package Statistix, version 3.1 from Analytical Software, St. Paul, Minnesota, USA.

Figure 1 Rearing sequence of whiteflies in experiment 2

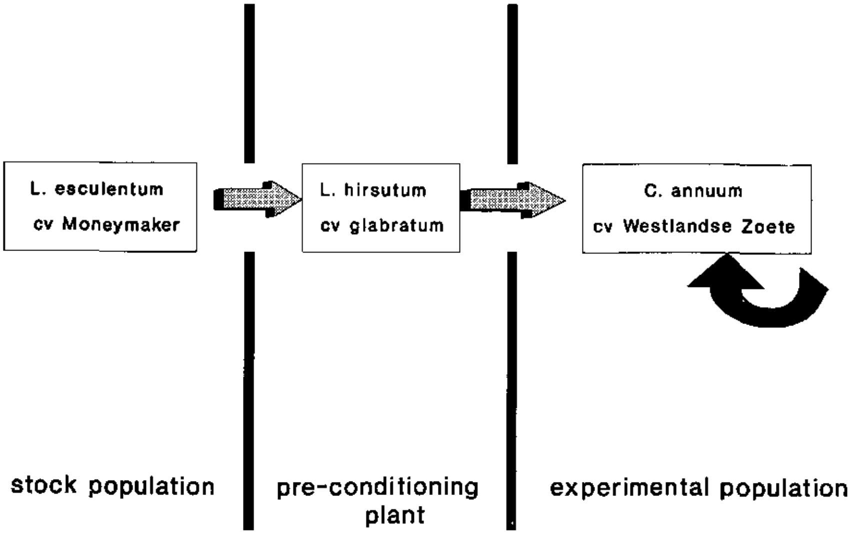
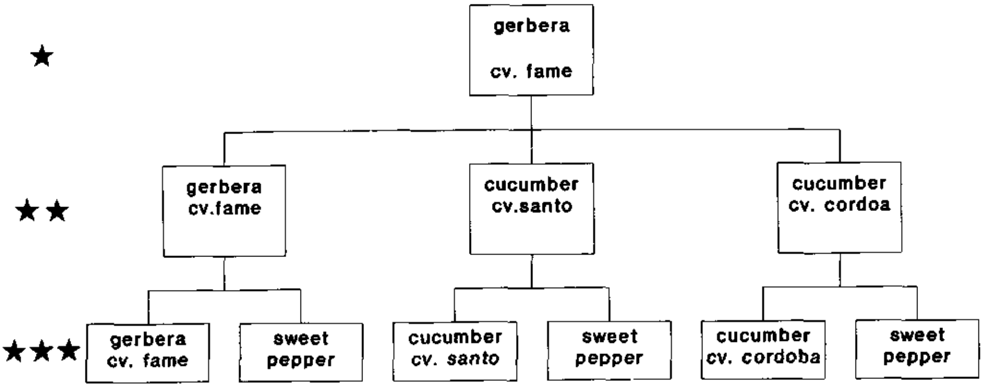


Figure 2 Rearing sequence of whiteflies in experiment 3



* stock population
** preconditioning plants
*** experimental populations

Results

Experiment 1

In this experiment, where the whiteflies had been transferred from *L. esculentum* cv. Moneymaker to sweet pepper, only 40 pupa were found of which only 6 had emerged as adults, of the estimated several thousand eggs laid.

Experiment 2

The whitefly counts from all the replicates were summed to give a 'population total' (table 1). Counts of immatures are for individuals not emerging as adults. Generation 0 is the result from the control population on *L. hirsutum*. Generations 1, 2 and 3 are consecutive generations on sweet pepper. There was an overall significant difference in the distribution of the mortality between the generations tested. The trend between generations 1 and 3 on sweet pepper was a decrease in mortality in the L1 stadium and a corresponding increase in mortality in the later larval stages. The mortality distribution of the third generation is not significantly different from the control (table 2), although this is misleading as the percentage of emerging adults was much higher upon the control than on sweet pepper. This trend is illustrated in figure 3.

Table 1 The total number of individuals per stage observed on a random sample of 6 leaves, after all adults had emerged

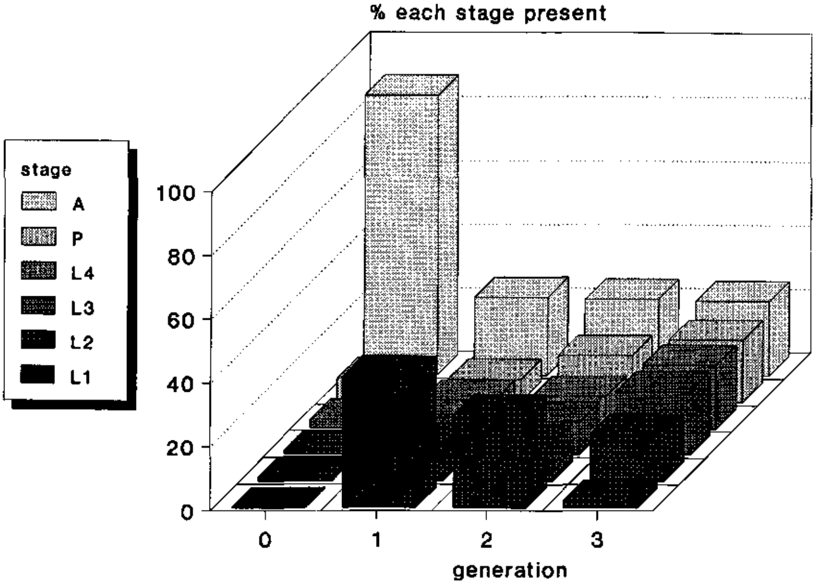
	generation			
stage	0	1	2	3
L1	0	370	167	6
L2	5	108	67	38
L3	4	57	59	51
L4	10	79	57	51
P	27	63	83	50
A	328	220	137	60

Table 2 Probability values obtained from Mann Whitney U test comparing distribution of number of individuals recorded per development stage between generations.

	generation		
generation	0	1	2
1	.0453		
2	.0656	.6310	
3	.1282	.0082*	.0131

* significant at $p < 0.05$ level (with Bonfferoni correction)

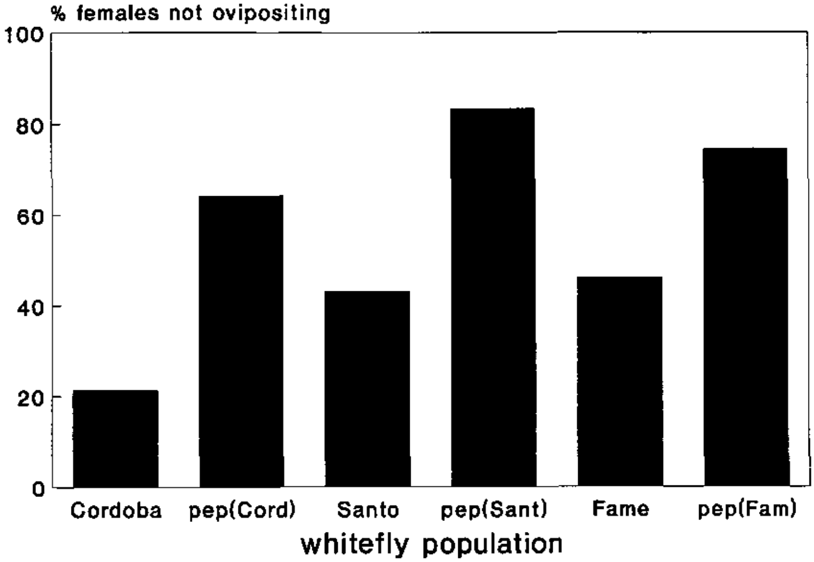
Figure 3 Percentage of all individuals present in each developmental stage



Experiment 3

Figure 4, shows the percentage of females laying no eggs per population. Approximately twice so many females laid eggs upon the two cucumber cultivars and

Figure 4 Percentage of females in each population not ovipositing



gerbera, than upon sweet pepper. The mean number of eggs laid per laying female are presented in figure 5. There was an overall difference between the populations in the mean number of eggs laid per female. From further testing (table 3), it was clear that populations on different host plants significantly differed from each other. The sweet pepper populations were significantly different from the two cucumber populations and from the population on gerbera. However the two cucumber populations were not significantly different from each other and also the three sweet pepper populations were not significantly different from each other.

The survivorship data are presented in table 4 as A_x values. The A_x, is the number of individuals observed in each larval stage. For ease of interpretation the survivorship data are also presented in the form of d_x values in table 5. The d_x, is the proportion of the original number of eggs laid dying within each larval stage.There was an overall difference found (table 6) between the populations in the distribution of the mortality between the different larval stages. It was found (as with the egg laying data) that there were significant differences between populations from different host plants but not between populations reared on the same host plant species. Each of the populations reared on sweet pepper was different from its parent population except for the population from gerbera cv. Fame, where the sample size on sweet pepper was small and this possibly accounted for the non significant difference between it and the parent population on gerbera.

Table 3 Probability values obtained from the Mann Whitney U test upon the egg laying data to assess for differences between whitefly populations

			population		
population	cordoba	santo	fame	paprika (cordoba)	paprika (santo)
santo	.5601				
fame	.0011*	.0002*			
p. (cord.)	.0000*	.0000*	.0002*		
p. (sant.)	.0001*	.0001*	.0011*	.4014	
p. (fame)	.0000*	.0000*	.0007*	.5805	.8280

* significant at $p < 0.05$ level (with Bonfferoni correction)

Figure 5 Frequency distribution of eggs laid per laying female within a 24 hour period

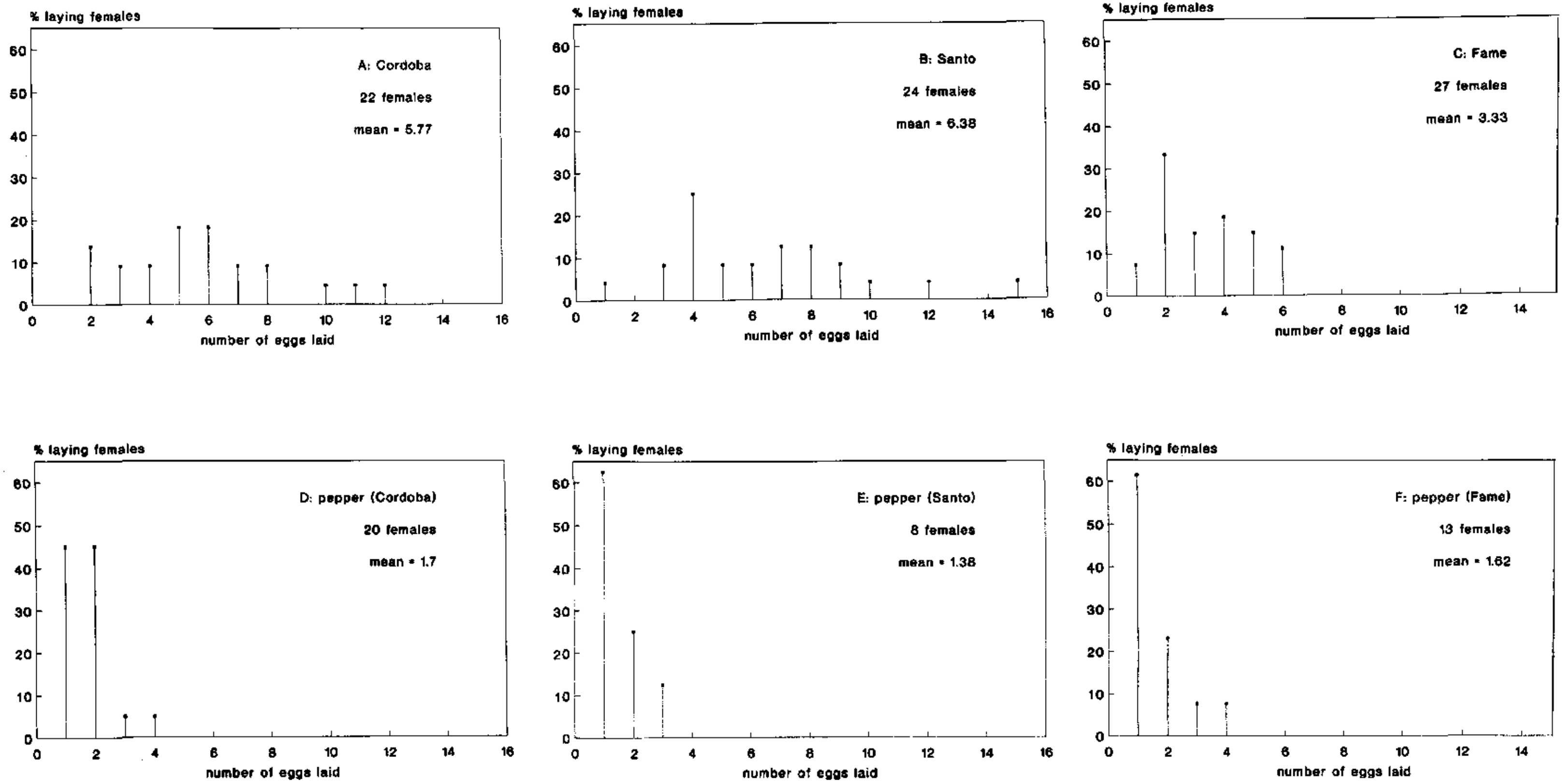


Table 4 Total number of whitefly individuals surviving to each developmental stage (A_x) per host plant

	whitefly population					
stage	cordoba	santo	fame	paprika (cordoba)	paprika (santo)	paprika (fame)*
egg	127	153	90	34	11	21
L1	97	129	63	3	10	8
L2	94	129	49	1	3	4
L3	91	127	48	0	0	1
L4	91	127	48	0	0	1
Pupa	91	126	48	0	0	1
Adult	88	124	46	0	0	1

* name in parentheses indicates parent population of sweet pepper whiteflies

Table 5 The immature mortality in each of the whitefly populations expressed as 'd_x'

	whitefly population					
stage	cordoba	santo	fame	paprika (cordoba)	paprika (santo)	paprika (fame)
egg	0.24	0.16	0.30	0.91	0.09	0.62
L1	0.02	0.00	0.16	0.06	0.64	0.19
L2	0.02	0.01	0.01	0.03	0.27	0.14
L3	0.00	0.01	0.00	-	-	0.00
L4	0.00	0.00	0.00	-	-	0.00
Pupa	0.03	0.02	0.02	-	-	0.05

'-' in table indicates that no more individuals were present in the population i.e. it had died out.

Figure 6 Frequency distribution of the development time of all emerging adults

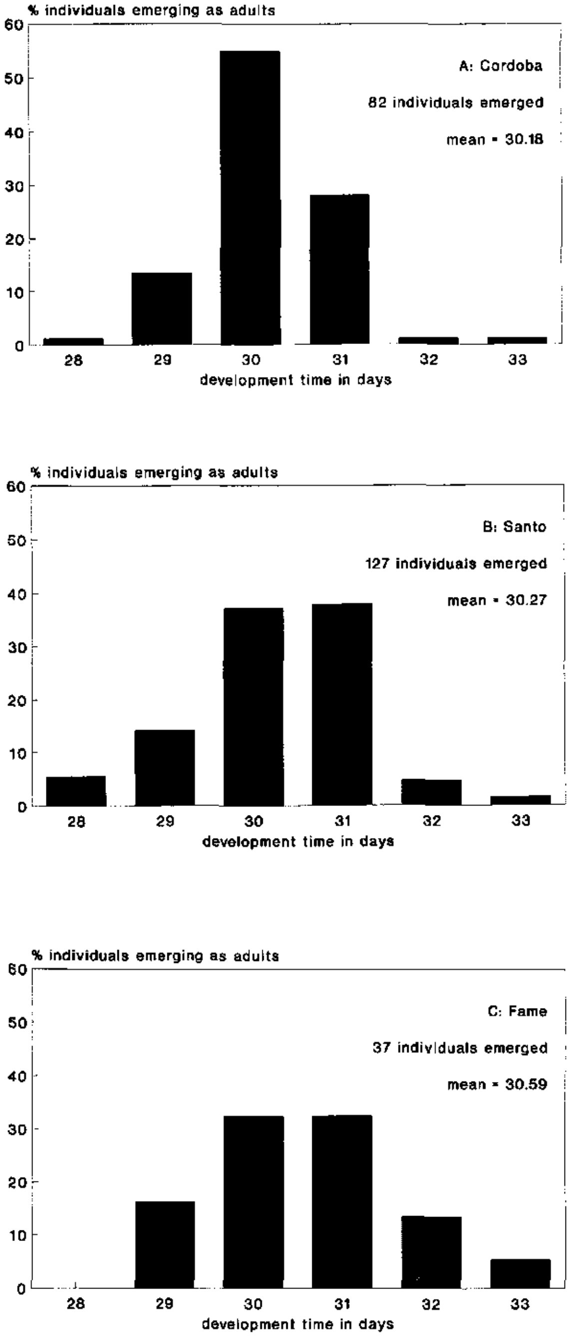


Table 6 Probability values obtained from Mann Whitney U test to compare per stage survivorship (A_x) distributions between the populations tested

	population				
population	cordoba	santo	fame (cordoba)	paprika (santo)	paprika
santo	.0073*				
fame	.0033*	.0022*			
p. (cord.)	.0022*	.0022*	.0022*		
p. (santo)	.0022*	.0022*	.0022*	.9491	
p. (fame)	.0022*	.0022*	.0022*	.1599	.3067

* significant at p <.05 level (with Bonfferoni correction)

The development time data are presented in figure 6. No significant differences were found (Kruskal Wallis; p = 0.125). No development time data for sweet pepper is available, as only one individual upon sweet pepper emerged (from cucumber cv Santo population on sweet pepper).

Discussion

From these experiments it is clear that sweet pepper is a poor quality host plant for whitefly (low number of eggs laid, high immature mortality), in relation to gerbera and cucumber. This poor host quality of sweet pepper correlates with the findings of van Boxtel and van Lenteren (1978) and van Lenteren et al. (1989).

On the basis of experiment 3 it is clear that the highest mortality on sweet pepper is between the egg and first larval stage. That the majority of the immature mortality occurs in the early larval stages is favourable to the plant, as less damage is done to it, the overall herbivore fitness remaining invariate (Billington et al., 1989). In experiment 2 it was observed that a greater proportion of whiteflies were surviving to the pupal stage and that the L1/L2 mortality clearly decreased over the three generations. This is hard to explain in terms of the overall fitness of the whitefly population, as there was no increase in the number of whiteflies developing to adults over the three generations. That the population died out so quickly is possibly not solely due to the mortality rate outstripping the 'birth rate', but may further be enhanced by a male biased sex ratio. (Thomas, unpublished observations).

In these experiments there is an indication that the plant used to 'pre-condition' the whiteflies may have an effect upon their subsequent performance upon sweet pepper. The study of Gould (1979) with *Tetranychus urticae*, demonstrated that the ability of a phytophage to adapt to one or another host plant, does not necessarily bear much relation to the taxonomic affiliations between the potential host plants concerned. In this study whitefly pre-conditioned on *L. esculentum* cv. Moneymaker showed very poor adaptation to sweet pepper. However on the taxonomically closely related species *L. hirsutum* cv. glabratum the adaptation was more pronounced. This may be due to the fact that *L. hirsutum* cv. glabratum contains circa a thousandfold more alpha tomatine than *L. esculentum* (van Gelder and de Ponti, 1987), this substance possibly facilitating adaptation to sweet pepper. This hypothesis could be tested by 'pre-conditioning' the same whitefly population on different *Lycopersicon* spp. accessions containing different amounts of alpha tomatine under standardised conditions, and then assessing the performance of whitefly from each accession on a sweet pepper cultivar. If this hypothesis is justified then it would demonstrate that care needs to be taken in the selection of accessions for breeding programs, so as to ensure, that resistance of the one crop to whiteflies does not promote its adaptation to another, e.g. *L. hirsutum* cv. glabratum was used in the breeding of tomato varieties that were partially resistant to whitefly, as a means of promoting its biological control (de Ponti et al., 1983).

The results show that although the performance of the populations on sweet pepper was significantly poorer than that upon the 'pre-conditioning' host plant, to which they had been adapted for at least 7 generations, no difference was found between the three populations present upon sweet pepper. Therefore, it would appear that the quality of the host plant used (with respect to the whitefly) does not seem to determine the subsequent performance of the population on sweet pepper. (Cucumber is a better quality host plant than gerbera for whitefly (van Lenteren and Noldus, 1990)).

In relation to the differences between central european and Dutch whiteflies performance on sweet pepper, I suggest that a factor which might have influenced this are differences in cropping conditions. For example in Czechoslovakia sweet pepper is sometimes intercropped with cucumber (Jarosik and Plíva, 1989). Under such conditions there will always be an infection source of whitefly for the sweet pepper crop. With such continual cross infection sufficient adaptation may occur over years to allow whitefly to sustain itself on sweet pepper in the absence of an infection source. If such a scenario is possible then perhaps caution needs to be exercised in relation to the use of intercropping techniques as a means of promoting the efficacy of biological control. In Hungary the numerous whitefly populations found upon field crops of sunflower, often invade greenhouses housing sweet pepper crops, the sunflowers providing over the summer months a sustained infection source of whiteflies for the sweet pepper crops affected, thus furthering adaptation to this crop.

4 PLANT OF ORIGIN AFFECTS HOST PLANT PREFERENCE OF WHITEFLIES[1]

Summary

A multiple choice preference test was conducted with females from three whitefly populations for each of the three host plants upon which they were respectively reared. The host plants were cucumber, gerbera and sweet pepper. At 24 hours the distribution of the whiteflies showed a significant rank order of preference, cucumber > gerbera > sweet pepper, for all three populations tested. However, the specificity of acceptance was dependent upon the host plant from which the whitefly population originated. A 'generalised linear interactive model' (GLIM) analysis of the data demonstrated that whiteflies express a significant preference for the plant from which they originated although this effect was less in magnitude than the effect of preferring the most suitable plant available. The results suggest thus a strong correlation between preference and performance in the glasshouse whitefly. The mechanisms underlying the results are discussed in relation to the polyphagous host plant use of whitefly.

Introduction

Previous studies upon the host plant preference of the glasshouse whitefly (Trialeurodes vaporariorum [Westwood]) indicated a rank order in the preference of certain plant species (van Sas et al., 1978 and Verschoor van der Poel and van Lenteren, 1978). For Dutch populations of whitefly this order is eggplant > gherkin > cucumber > gerbera > melon > tomato > sweet pepper (van Lenteren and Noldus, 1990). However in both studies upon Dutch whitefly only one population was tested in a choice experiment, a population held upon Lycopersicon esculentum cv. Moneymaker since the early 1970s (van Lenteren et al., 1989). After studies on the adaptation of whiteflies (chapter 2) over several generations, it was tested whether these respective populations showed a consequent increase in preference for the host plants to which they had adapted. Three populations were tested, a population reared on cucumber (a high ranking plant), a population from gerbera (a middle ranking plant) and a population from sweet pepper (a low ranking plant). As a result of adapting to a lower ranking host, it was expected that a population will show an

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[1] submitted to Oecologia

increased acceptance for this host, and thus a decrease in the relative preference (although not the absolute acceptance) of a higher ranking host under the conditions of a multiple choice preference test (Courtney et al., 1989).

Preference - performance studies can take many forms. Recently, Thompson (1988) has pleaded that studies of preference - performance relationships need to concentrate more upon the genetic characteristics of this correlation so that the selective dynamics of insect plant relationships may be better understood. Such information can be attained through sibling analysis studies as reviewed by Via (1990). In order to maximise the accuracy of such studies at the individual level, an ecological study such as the one presented in this article is first necessary, so that the overall processes occurring at the population level can be assessed, especially how variable such processes are. Thereafter, studies of individuals can be compared with the overall population, so as to check for example that the number of individuals studied is enough to account for the overall patterns of variation seen in the population as a whole. Also this study demonstrates how important certain behavioral mechanisms are at the population level. These mechanisms are difficult to observe in experiments done with individual whiteflies, due to the high level of variability they demonstrate in the acceptance of host plants.

Based on an ecological approach just defended, this study aims to interpret the observations made in light of two models that describe host plant location and selection by an insect. These models are the hierarchy threshold model (Courtney et al., 1989) and a model of random host plant searching (Morris and Kareiva, 1991). The hierarchy threshold model of Courtney et al. (1989) describes factors pertaining to host plant selection at the level of the individual insect. As I examine the net response of a group of insects, it is necessary to extrapolate prepositions of this model to the population level. In synopsis the model suggests the following:

1 There is a rank order of host plant preference which is invariate throughout the individual's lifetime.

2 Host range is flexible throughout an individual's life history.

3 Female fecundity and egg load affect diet breadth.

4 Adult experience upon different host plants may affect host plant specificity but not acceptability.

By 'acceptability', is meant that a plant is sufficiently suitable for an insect to demonstrate a preference for it. By 'specificity' is meant the range of host plant species an insect exhibits preference for, i.e the more specific an insect the fewer the number of host plant species it prefers.

The 'non-random settlement' model of Morris and Kareiva (1991), assumes a constant rate of random movement with no taxis. The rate of settlement is related to the quality of the plant(s) encountered. Morris and Kareiva 's simulations demonstrated the 'non random settlement' method of host plant location to be extremely effective for polyphagous insects. Over a period of several days, the average quality of the host plant found is only slightly less than where purely orientated searching is used.

Materials and methods

The methodology was that of a multiple choice preference test. Preference was defined as a non-random choice (Singer, 1986). Pre- and post-alighting preference are differentiated as follows:

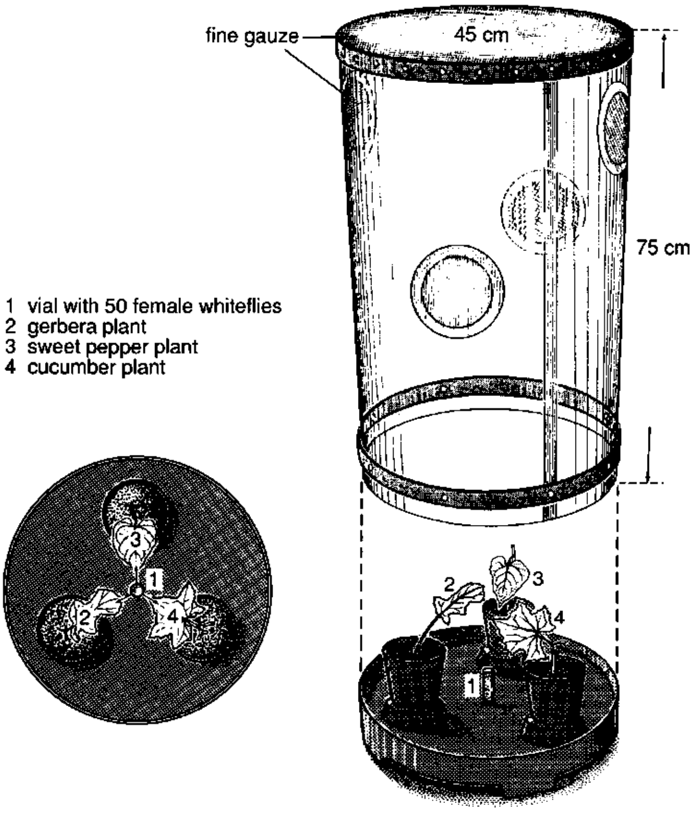
* pre-alighting behaviour is the movement of the whiteflies upon emerging from the central release point until they alight upon a plant. The net outcome of this behaviour forms the basis of the result seen at one hour after the whiteflies were released.

* post-alighting behaviour follows after the first landing upon a plant and includes settling upon the plant of initial choice and also, when this plant is rejected, the subsequent re-alighting and re-settlement upon a different plant. The net outcome of this behaviour is the distribution of the whiteflies seen 24 hours after their release. Earlier research by Verschoor van der Poel and van Lenteren (1978), had shown that this 24 hour interval was therefore sufficient.

Preference is then the number of whiteflies found on a specific plant after an elapsed period of time. In each experiment the preferences of the populations were assessed simultaneously in the same glasshouse compartment. The compartment had a temperature of $21^0C \pm 1^0C$ and a relative humidity of 70 ± 10 %. Throughout the 24 hour period of each experiment, and independent of the natural lighting available, artificial lighting was continuously provided by mercury vapour lamps (6800 lux per lamp), one lamp above each experimental cage. To minimise the effect of oblique lighting upon the flight orientation of the whiteflies the side walls of the glasshouse compartment were covered in black heavy duty PVC, so that light could only come from directly above the host plants.

For each of the three populations the experimental set up was as detailed in figure 1. Young host plants that were pest and disease free were reared and selected for in accordance with Thomas (1992a). Cucumber plants were in the 2 or 3 leaf stage, gerbera plants in the 4 or 5 leaf stage and the sweet pepper plants had between 12 and 15 leaves. From each plant, all but one of the leaves (so far as possible the youngest) were removed such that the area of the leaf which remained, was for each of the three plants per cage

Figure 1 Experimental set up for host plant preference test



approximately the same. In practice the area of the leaves used differed by no more than 20 %. The plants were then positioned in the cages such that all the leaves were at the same height above so well as equidistant from the central release point.

The whiteflies all originated from gerbera cv. Fame, which was also the control. A population coming from cucumber population had been reared upon this plant for 8 consecutive generations. The population on sweet pepper originated from both the gerbera and cucumber populations. It had been present upon this plant for only one generation. As the mortality was circa 90%, it was assumed that all surviving individuals, by virtue of their survival, were to some extent adapted to this host plant. From each whitefly population a random sample of about 200 whiteflies was taken and 50 females sexed under light anaesthetize from carbon dioxide, and retained in a glass vial sealed with a rubber stopper. Whiteflies were between 3 and 15 days old. For sweet pepper, fewer whiteflies were present and therefore details of the origin and number of females used are given in table 1. The vials containing the whiteflies were opened at the position shown in figure 1. At 1 and 24 hours after release, the number of whiteflies per leaf per cage was counted. This was done carefully by removing the top of the cage and lifting each plant up in turn, to assess the number of whiteflies present upon the underside of each leaf. The experiment was conducted seven times.

Table 1 **The numbers and origin (parent generation) of the whiteflies used for the sweet pepper population.**

experimental number	origin and number of whiteflies sampled			total no. females used in preference test
	cucumber cv Santo	cucumber cv Cordoba	gerbera cv Fame	
1	20	4	7	7
2	29	2	10	17
3	27	2	8	15
4	15	0	5	10
5	10	2	5	10
6	51	26	37	15
7	26	0	6	14

For the data obtained both at 1 and 24 hours, the relative contribution and significance of the factors influencing whitefly host plant preference were assessed using the computer software package 'GLIM'. GLIM is an abbreviation for 'general linear interactive modelling (GLIM). Two models were constructed. The first of these considered factors influencing the number of whiteflies not being found back upon a plant after their release and the second considered factors influencing the distribution of the whiteflies upon the respective host plants available. The general principles of GLIM are detailed by Healy (1988) and Aitkins et al. (1989). GLIM analyses the probable outcome of events in an experiment. The data in the form of relative preferences are transformed to logit values (Snedecor and Cochran, 1980). These logit values are the basis needed for the logistic modelling which GLIM performs. GLIM begins an analysis with a null model, where the probabilities of all events are equal to each other and the influence of various factors upon the outcome of a model are excluded. Analysis proceeds, by adding possible experimental factors to the model and observing by how much the scaled deviance decreases and with how many degrees of freedom. The scaled deviance indicates how accurately the model fits the observed experimental data. A scaled deviance of zero indicates a perfect fit. The p-value for a factor added in the model is calculated in two steps. Firstly, the deviance change is divided by the change in degrees of freedom. This value is in turn divided by the remaining deviance that had been divided by the remaining degrees of freedom. This second step in the calculation adjusts for the unaccounted deviance remaining. The value obtained through these two steps approximates to an F-value from which a p-value may be read under the appropriate degrees of freedom.

Results

Table 2 shows the number of females not found back upon a host plant after 1 hour, per whitefly population, per replicate and figure 2 the number of whiteflies from each population upon each host plant after 1 hour. This was analyzed using GLIM (table 3). The difference between replicates was significant ($p < 0.05$). This effect was particularly due to the data from replicates 1 and 5 (table 2), where the percentage of individuals not found upon a host plant was, unlike other days, about the same for all three populations tested. There was a significant effect of the host plant origin of the whitefly ($p < 0.025$). Further analysis showed this effect to be virtually entirely due to the population originating from

Table 2 **The number of released females not found back upon a host plant 1 hour after release. In parentheses is the percentage of the released number of females.**

	whitefly population originating from		
replicate	cucumber	gerbera	pepper
1	28 (56)	28 (56)	4 (57)
2	26 (52)	4 (8)	8 (47)
3	42 (84)	26 (52)	8 (53)
4	16 (32)	6 (12)	1 (10)
5	45 (90)	42 (84)	8 (80)
6	42 (84)	15 (30)	12 (80)
7	23 (46)	21 (42)	12 (86)

Figure 2 **Number of whiteflies from each population upon each host plant at 1 hour**

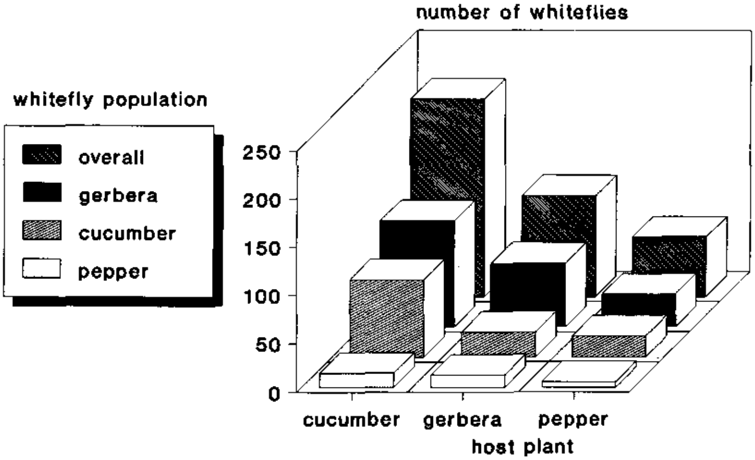


Table 3 **GLIM analysis to assess the significance of factors affecting whiteflies released not being found back upon a host plant 1 hour thereafter.**

model	scaled deviance	deviance change	d.f	change d.f	p
null model (1)	227.07	-	20	-	
1 + effect of replication (r)	94.18	132.9	14	6	< 0.05
1 + r + effect of whiteflies' host plant of origin (o)	43.62	50.6	12	2	< 0.025
1 + r + effect of whiteflies originating from gerbera (g)	43.71	50.47	13	1	< 0.005

gerbera ($p < 0.005$).

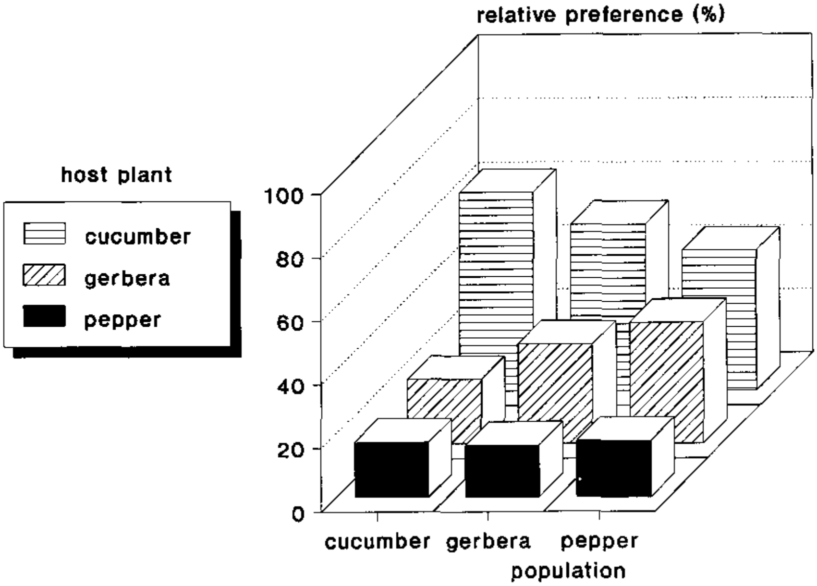
The GLIM analysis of whitefly distribution between host plants at 1 hour is presented in table 4. This showed a significant effect of the host plants available influencing whitefly

Table 4 **GLIM analysis to assess the significance of factors affecting whitefly distribution per host plant 1 hour after the whiteflies had been released (model restricted to whiteflies found back on a host plant after 1 hour)**

model	scaled deviance	deviance change	d.f.	change d.f.	p
null model (1)	199.64	-	42	-	
1 + effect of host plants influencing whitefly distribution (h)	114.40	85.24	40	2	0.00002
1 + h + effect of replication (r)	64.73	49.67	28	12	0.123
1 + h + r + effect of whiteflies' host plant of origin (o)	57.85	6.87	24	4	0.592
1 + h + r + effect of whiteflies preferring host plant from which they originate (z)	61.21	3.52	27	1	0.238

distribution (p = 0.00002). Therefore an element of preference had been demonstrated at 1 hour. This had also been demonstrated in the results of Verschoor van der Poel and van Lenteren, 1978). As seen by the relative preference values given in figure 3, the rank order of preference is cucumber > gerbera > sweet pepper for all three whitefly populations. This preference was not significantly different between replicates (p = 0.123). The host plant from which the whitefly originated had no significant effect (p = 0.592) and there was also no significant effect of whitefly exhibiting a preference for the host plant from which they originated (p = 0.238)

Figure 3 The relative preference of each whitefly population 1 hour after release



When after a period of 24 hours the whiteflies have settled upon their preferred host plant, the net preference does not further change over time (van Sas et al., 1978). Table 5 lists the number of females not found back on a host plant after 24 hours, per whitefly population, per replicate and figure 4 the number of whiteflies per population found upon each host plant after 24 hours. This data was analyzed by a GLIM model presented in table 6. Unlike the data at 1 hour, there were no significant differences between replicates (p = 0.12). Like the data at 1 hour, the whiteflies' host plant of origin was significant (p < 0.01). Whiteflies originating from gerbera accounted for most of this host plant effect (p < 0.01). Differences upon a day to day basis in the number of whiteflies found back, may be expected if whitefly flight contains a largely random component (Vaishampayan et al.,

Table 5 The number of released females not found back upon a host plant 24 hours after release. In parentheses is the percentage of the released number of females.

	whitefly population originating from		
replicate	cucumber	gerbera	pepper
1	32 (64)	13 (26)	4 (57)
2	18 (36)	4 (8)	8 (47)
3	36 (72)	11 (22)	4 (27)
4	14 (28)	10 (20)	0 (0)
5	31 (62)	27 (54)	7 (70)
6	26 (52)	12 (24)	10 (67)
7	8 (16)	5 (10)	12 (86)

Figure 4 Number of whiteflies from each population upon each host plant at 24 hours

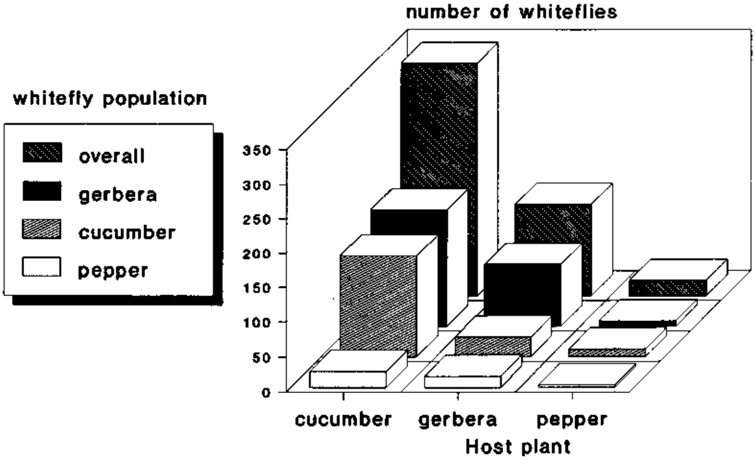


Table 6 GLIM analysis to assess the significance of factors affecting whiteflies released not being found back upon a host plant 24 hours thereafter.

model	scaled deviance	deviance change	d.f	change d.f	p
null model (1)	172.31	-	20	-	
1 + effect of replication (r)	112.52	59.8	14	6	0.12
1 + r + effect of whiteflies' host plant of origin (o)	54.54	58.0	12	2	< 0.01
1 + r + effect of whiteflies originating from gerbera (g)	55.47	57.05	13	1	< 0.01

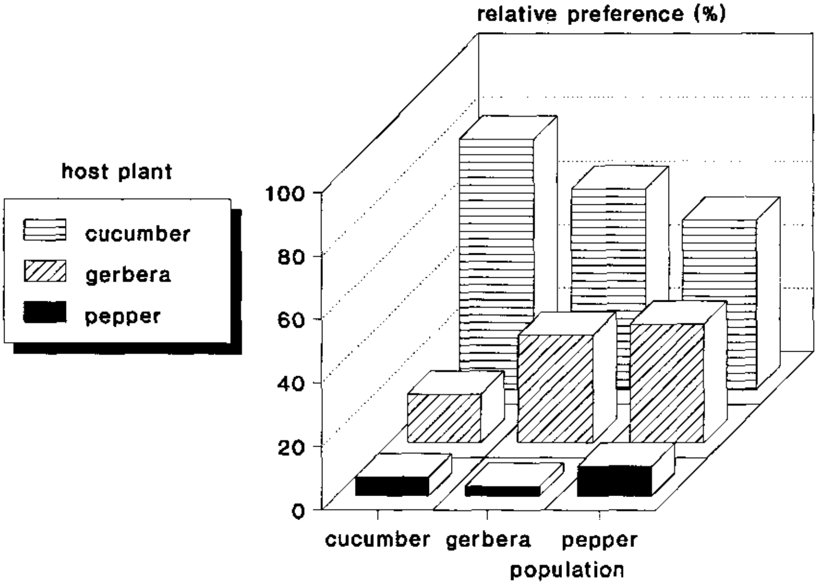
1975). However that whiteflies originating from gerbera were consistently found back upon a host plant more than the other two populations is a phenomenon for which no clarification can yet be given.

The GLIM analysis of whitefly distribution between host plants after 24 hours, is presented in table 7. As found with the data at 1 hour, the most significant factor affecting whitefly distribution was the host plants. As can be seen by the relative preference values (figure 5) there is a rank order of preference of cucumber > gerbera > sweet pepper, for all three populations. This same rank order was present at 1 hour (figure 3), but the differences in preference exhibited between host plants was less than at 24 hours (compare figures 4 and 5). The second significant factor is that the whiteflies exhibited a preference for the host plant from which they originated ($p < 0.03$), this effect not being observed at 1 hour. However, as the relative preference remained invariately cucumber > gerbera > sweet pepper, this second effect is clearly of less magnitude than the first. This effect of whiteflies preferring the plant from which they originate is seen in figure 5 by the relative preference for the highest ranking plant cucumber. This decreases as the ranking of the plant from which the whiteflies originate also decreases, i.e. relative preference exhibited for cucumber is less for 'pepper whiteflies' than 'gerbera whiteflies' than 'cucumber whiteflies.'

Table 7 GLIM analysis to assess the significance of factors affecting whitefly distribution per host plant 24 hours after the whiteflies had been released (model restricted to whiteflies found back on a host plant after 24 hours)

model	scaled deviance	deviance change	d.f.	change d.f.	p
null model (1)	472.33	-	42	-	
1 + effect of host plants influencing whitefly distribution (h)	137.89	334.44	40	2	< 0.01
1 + h + effect of replication (r)	84.66	53.23	28	12	0.14
1 + h + r + effect of whiteflies' host plant of origin (o)	63.67	21.0	24	4	0.13
1 + h + r + effect of whiteflies preferring host plant from which they originate (z)	70.91	13.7	27	1	< 0.03

Figure 5 Relative preference of each whitefly population 24 hours after release



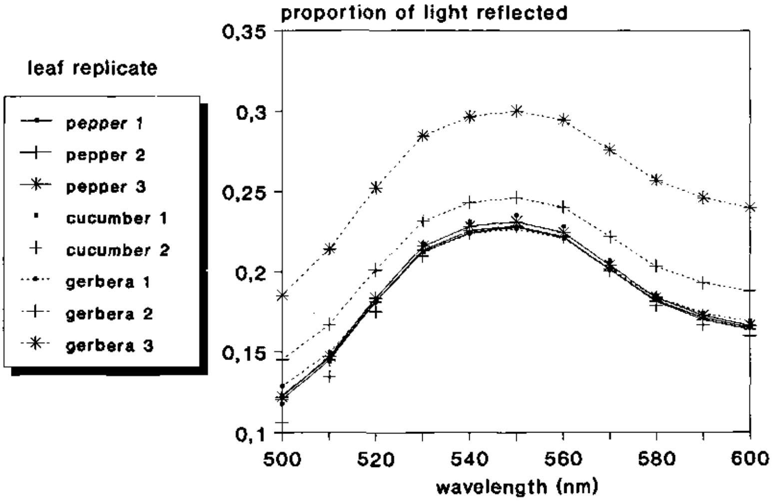
Discussion

General remarks

The results obtained in this study of some preference being exhibited at 1 hour and a definitive preference being observed at 24 hours, are in accordance with other studies (Verschoor-van der Poel and van Lenteren, 1978 and van Sas et al., 1978). In these studies different host species were used. Differences may, however, also exist between cultivars of the same plant species. Data from Veldhuis (1991) indicate that differences in performance for a Dutch strain of whitefly upon Dutch cucumber cultivars are small and not consistent over successive generations of the whitefly. Insufficient data are available from multiple choice preference tests to draw conclusions as to how the preference and performance of these populations on cucumber cultivars is correlated. However from other studies it is also known that the performance of a whitefly population on a variety of cultivars of the same species can vary considerably (eg. Zabudskaya, 1989 en van Lenteren et al., 1989). Therefore it would seem that within a given host plant species performance is closely related to the specific quality of the cultivar tested.

The data at 1 hour, (effect of host plant influencing whitefly distribution), indicated that some preference had been exhibited by the whiteflies. I thought this was due to differences in the reflective spectrum of the host plants, whiteflies being attracted to yellow light (Lloyd, 1921). However an examination of the reflected yellow / green spectrum (500-600 nm), showed that gerbera emitted more light than cucumber, which emitted about the same as sweet pepper as seen in figure 6. This rank order is not the same as the order of preference exhibited by the whiteflies at 1 hour. Therefore I suggest that pre-alighting flight was random, and one hour after being released, some whiteflies have demonstrated a rejection of gerbera and sweet pepper and an acceptance of cucumber. Verschoor-van der Poel and van Lenteren (1978), also observed differences in preference by whiteflies after 1 hour for the host plants tomato, eggplant, cucumber and sweet pepper. This result can occur, because a whitefly upon probing a plant makes a choice to accept or reject within a few minutes after the beginning of the probe (Jansen et al., 1989), rejection often resulting in the individual re-alighting upon a different leaf or host plant (van Sas et al., 1978 and Verschoor van der Poel and van Lenteren, 1978).

Figure 6 Reflective light spectra for gerbera, cucumber and sweet pepper.



How whiteflies select a host plant

The initial whitefly distribution between host plants is random, but after 1 hour some preference has been shown, which after 24 hours is more distinct. These two observations are consequent of how whiteflies search for a host plant, which can be detailed as a series of events:

1 Upon emergence, whiteflies reside upon the leaf of emergence for several hours unfurling their wings and forming a wax layer on their bodies (Hargreaves, 1914).

2 Nine light hours after emergence (Noldus et al., 1986a), the whiteflies generally depart from the leaf of emergence and fly upwards, being attracted to the blue light of the sky (400 nm) but if they further detect yellow green light (550 nm) reflected from a leaf surface, they fly preferentially towards this (Affelt et al., 1983).

3 This pre-alighting movement is except for the orientation towards certain light spectra, random. Whiteflies do not respond to visual or olfactory cues from the plant (Vaishampayan et al., 1975).

4 Upon thus having orientated towards and alighting upon a leaf, the whitefly undergoes a behavioral series of walking and probing upon the leaf surface as described by Noldus et al. (1986b) and van Vianen et al. (1988a).

5 Upon probing rejection occurs during the first few minutes of the probe. This rejection is based upon a reaction to a substance (substances) in the apoplast, just under the leaf surface (Jansen et al., 1989).

6 The higher the rank preference of a host plant, the less probable it is to be rejected and the greater the percentage of time that is spent on the same leaf and in the same position (van Sas et al., 1978 and Verschoor-van der Poel and van Lenteren, 1978).

7 Where the acceptability of a plant is low, the whitefly demonstrates a very unsettled behaviour pattern, flying between leaves and spending in comparison with a more high ranking plant much less time feeding and ovipositing upon the leaf (Verschoor-van der Poel and van Lenteren, 1978). Upon leaving a leaf the flight is again random.

This sequence of events described parallels closely the conditions of the 'non random settlement' model of Morris and Kareiva (1991), summarised in the introduction to this article.

With respect to whiteflies, the assumption of 'no taxis', in the model of Morris and Kareiva (1991), would need to be modified, such that light of certain frequencies elicit a taxile response, that is non host plant specific. This mechanism which the whiteflies have results in them tending, due to strong upwards orientation, to concentrate upon the youngest leaves of a plant, which have a higher nutritional quality (Noldus et al., 1986b). This occurs, regardless of the type of architecture that the host plant has, rosette (Sütterlin et al., 1991) or non rosette (Noldus et al., 1986b). The post-alighting probing of leaves leads to a rapid acception or rejection of a leaf, resulting in a preference within a day after emergence of a whitefly. This is advantageous to the female as a clear preference occurs. It also maximises the number of eggs laid upon the preferred location upon the best host plant. For example, Noldus et al. (1985) showed that most whiteflies were found in the upper tomato leaves within 30 hours of their emergence and van Lenteren and Noldus (1990) state that the pre-oviposition period on tomato is 1.3 days.

Non random settlement selection of a host plant maintains polyphagy

As whiteflies are highly polyphagous (Mound and Halsey, 1978), it would seem reasonable to assume that in any given whitefly population a high degree of variability in host plant acceptance is present. Where a whitefly population has a host plant choice, random movement demonstrated upon leaving a leaf means that on average the chances of landing on a low ranking host plant are the same as that of landing upon a higher ranking host plant. However if pre - alighting orientation was correlated to host plant ranking, it might be expected that on average all individuals, independent of the plant from which they have emerged, would orientate towards the higher ranking plant. Whitefly would thus be highly concentrated upon higher ranking host plants and thus effectively remain restricted to these plants, even if lesser ranking hosts were available. Alternatively it is also possible that orientation could be associated with the plant from which the whitefly emerges, e.g. where an insect can learn to differentiate between host plants at a distance as is the case for the lepidopteran, Battus philenor (Papaj, 1986). Thus regardless of the ranking of a plant, the whitefly would inspite of other potential hosts that are possibly available, tend to orientate towards the host from which it originated. Such a mechanism could result in host plant specific whitefly races, such that the species would be polyphagous overall, but have populations that are specialised at a more local level.

The results of Verschoor van der Poel and van Lenteren (1978), van Sas et al (1978), Noldus et al. (1986b), and my results using whiteflies conditioned to a specific host plant, demonstrate that pre-alighting preference is random and not related to host plant quality. Acceptance is a post-alightive decision, whiteflies having an invariant rank order of preference. However this is not fixed with regards to the magnitude of the relative preference. The relative preference is affected by the host plant from which the whitefly population originates. The GLIM model (table 4) showed that there was a strong element of preference for the host plant species from which the population originated. This is subordinate to the effect of the invariate rank order of preference in relation to host plant suitability, already detailed. The relative preference exhibited for a higher ranking host decreases, as the suitability of the host plant from which the whitefly population originates decreases. This observation reflects at the population level prediction 6 of the hierarchy threshold model, which reads: 'Relative preference among hosts should decline as diet breadth increases. Multiple-choice tests in the laboratory will show decreased use of high ranking hosts'. The effect of whiteflies preferring the host plant from which they originate, being subordinate to the effect of them choosing the most suitable host plant available, is an important factor in reducing the likelihood of host plant specific whitefly races occurring.

It is favourable that a polyphagous species has a 'non-random settlement' host plant location mechanism as this maximises the chances of all available host plants being encountered, and where available, preferred hosts are utilised more than less preferred hosts. Further, this mechanism results in encounters with novel hosts. If whiteflies land upon a novel host which proves to be suitable for development, it will possibly be assimilated into the whiteflies host range.

How non random-settlement facilitates the maintenance of variability for host plant acceptance within a population

Prediction 11 of the hierarchy threshold model (Courtney et al., 1989), suggests that variability for the acceptance of lower ranking hosts will be maintained in a population existing upon a higher ranking host. This is because acceptance of a higher ranking host does not directly select against the potential to accept a lower ranking host. However, such a situation is complicated by the possibility that 'trade offs' [negative correlations between traits see Pease and Bull (1988)], might occur in host acceptance. Thus, a population adapting to a high ranking host, might lose variability to adapt to a lower ranking host. Further, it may not necessarily be so that a population adapted to a lower ranking host, shows increased acceptance of a higher ranking host (prediction 9 of the hierarchy threshold model reads: Cross-conditioning should be asymmetrical: experience of low-ranking hosts may increase acceptability of higher-ranked hosts, but not vice versa.). How 'trade offs' as a result of adaption to a host plant affect the variability in acceptance to other host plants is unknown for whitefly, except for the fact that whiteflies adapted to a high ranking host (cucumber) and a mid ranking host (gerbera) show equal performance on a poor ranking host (sweet pepper) and thus it would seem that at the population level, prediction 9 of the hierarchy threshold model is held in part (Thomas, 1992b).

Independent of these forementioned possibilities, the 'non random settlement' behaviour of the whiteflies, favours the maintenance of variability for host plant acceptance, as certain individuals will always land and remain upon lower ranking host plants. The offspring of these individuals may equally land upon a higher ranking plant as well a lower ranking plant. This results in a continual mixing of genes coding for, or in someway influencing the acceptance of different host plants within a population.

Furthermore this general mixing of variability for host plant acceptance, will tend to counteract the forming of host plant specific whitefly races.

Closing remarks

This study was done at a population level and it is therefore difficult to assess directly many of the predictions of the hierarchy threshold model which is described at the level of the individual. With respect to this model experiments need to be done to examine the choice of whitefly individuals originating from different host plants, using methods similar for example to those for studying single whiteflies by Verschoor-van der Poel and van Lenteren (1978). Studies of individual responses also need to include an assessment of how the acceptance by the settling of an individual is related to the number of eggs it lays, to test whether all individuals show behaviour in accordance with the population as a whole. Also further tests need to be done to assess if adaptation to a low ranking hosts improves adaption to a higher ranking host, which would be in accordance with prediction 9 of the hierarchy threshold model. The effect of egg load on preference needs to be assessed as well. Predictions 3,4 and 5, of the hierarchy threshold model read:

> 3 Individual female behaviour varies with current fecundity, so that a higher egg load results in a broader diet.
>
> 4 In populations of females , high-ranking hosts should always be accepted; low-ranking hosts should be accepted by those females with high current fecundity.
>
> 5 Diet breadth should increase with factors increasing eggloads: increasing inter-host period, decreasing host density etc.

Thus from these predictions, it is expected that as egg load increases, the acceptance threshold for any given host plant will decrease, because the urge to lay eggs is greater than any aversion there might be to the host plant(s) available. How true this if for whiteflies is unknown.

More generally, it is of interest to see if the changes in performance measured upon different host plants over successive whitefly generations (chapter 2), are correlated with a paired increase in the acceptance of these host plants for the whitefly populations: are selection for preference and performance correlated ?

How do these results relate to the situation in north western europe? Here the whitefly has, within the glasshouse, a limited availability of host plants at any one time. Usually a single cultivar of a single species for a vegetable crop or several cultivars of the same species for an ornamentals crop are grown. Therefore, within a given glasshouse a multiple choice of preference for available host plants hardly exists. Furthermore even where a choice does exist, the utilisation of this choice may be limited by the horizontal dispersion of the whiteflies, as individuals do not tend to move more than a few metres horizontally from their point of emergence (Noldus et al., 1986a and van Vianen et al., 1988b) and, therefore, where varieties of a crop are grown in blocks several metres wide (eg chrysanthemum), the dispersion of whiteflies between blocks will tend only to occur between whiteflies located on block perimeters. However, in certain situations over time, different crops (varieties and or species) are grown and therefore over time, a sequential order of various host plants is available. Here there is the possibility that selection of a population on a previous crop which is a relatively poor host plant, may increase its acceptance of and performance upon a following crop which is a relatively good host plant. Studies of such situations have to my knowledge not been done.

The whiteflies' notorious pest status has undoubtedly been and remains facilitated by its 'non random settlement' method of host plant acceptance and the high level of variability therein, which supports its polyphagy.

5 ELECTROPHORESIS OF A WHITEFLY POPULATION

Summary

Two simple electrophoresis methods (starch gel and polyacrylamide gel) were attempted for the glasshouse whitefly (*Trialeurodes vaporariorum* [Westwood]), to assess allopatric differentiation within this species. It was found, that for the three isoenzymes tested for, esterase, malate dehydrogenase and phosphoglucomutase, only esterase gave a staining band, which was very weak. These results were independent of the different sample preparation methods used. These results suggest, in conjunction with the limited success had by other workers with this species, that a sensitive method needs to be found and deployed, if an assessment of allopatric differentiation in this species upon the basis of isoenzyme variability is to be made.

Introduction

It is known that whiteflies (*Trialeurodes vaporariorum* [Westwood]) from different geographic origins, vary in their ability to develop upon and adapt to specific host plants especially sweet pepper e.g. Laska (1986), van Lenteren et al. (1989) and Zabudskaya (1989). I postulate that such differences could be explained by the allopatric differentiation of the populations. Certain studies e.g. Feder et al. (1990) had been able to assess such allopatric differentiations using isoenzyme analysis. Therefore a pilot study was made to assess the potential of two simple electrophoretic methods (starch and polyacrylamide gel electrophoresis) for studying isoenzyme variation in *T. vaporariorum*.

This study was directed at measuring the overall level of genetic variation in a whitefly population as indicated by isoenzyme variation, it being realised that electrophoretic data may often correlate poorly with conspecific ecological data concerning insect performance on a host plant. Lewontin (1984, 1986) regards such poor correlations, viewed from the point of differentiating populations, as simply being due to differences in the statistical tests used to analyze quantitative and allozyme data. However Via (1990) is of the opinion that electrophoresis is of little use in understanding population differentiation in relation to host plant use, applicable information only being attainable through the direct quantitative study of the attributes concerned. Experimental data do not clearly support either of these two standpoints. Sometimes, as in the case of host races / sibling species formation in *Rhagoletis* *pomonella*, incisively useful correlations are found (see review of Berlocher, 1989) and at other times no differences can be ascertained as for example with the pea aphid (Simon et. al., 1982). The study of Bergevoy and Starks (1986) demonstrated that even of a large geographic area, variation in host plant use by an insect pest may not be correlatable with isoenzyme variation. Such a result is possibly not so surprising when one considers the dispersive abilities of many aphid species (see review by Kring, 1972) and therefore such electrophoretic studies need to be carefully correlated to the flight behaviour of the species and its abundance upon its respective host plants (Loxdale, 1990). As the glasshouse whitefly does not tend to diperse over long distances, it was assumed that electrophoresis would provide reliable information upon genetic distances between populations.

Materials and Methods

All samples were collected live from a rearing upon tomato (*Lycopersicon esculentum* var. Moneymaker) and stored in a deep freeze at 253 K until used.

Initially two simple electrophoretic methods were attempted; starch gel electrophoresis (as described by Guldemond and Eggers - Schumacher, 1989) and cellulose acetate electrophoresis (as described by Easteal and Boussy, 1987). Staining was for esterase, phosphoglucomutase and malate dehydrogenase using the staining methods of Tomiuk and Wohrmann (1983). These staining methods were chosen because of their previous use on *T. vaporariorum* by Prabhaker et. al. (1987) and Wool et. al. (1989). Various methods of sample preparation prior to electrophoresis were attempted upon the adult and pupal stages. They were the homogenisation of single individuals in a few ml of the gel buffer used (Guldemond and Eggers-Schumacher, 1989) , and the grinding of individuals in a few microlitres of a weak detergent solution (Easteal and Boussy, 1987). At a later stage polyacrylamide electrophoresis was attempted using a 10% gel and using the sample preparation and staining techniques as already described.

Results

Regardless of the sample preparation method used, individual pupal specimens of *T. vaporariorum* gave a very weak staining band and this band showed no distinct resolution into fast / slow bands, where as adult samples yielded no success even upon dissecting the whiteflies so that only the thorax was used in the sample preparation. This method of preparation was suggested by C. Mollema (pers. comm.), as the thorax has a higher titre of isoenzymes relative to the head or abdomen and also a lower titre of esters (waxes and fats) than the head or abdomen. The lower titre of esters is important as they are known in general to have an antagonistic effect upon the electrophoretic seperation and staining up of isoenzymes. Staining for phosphoglucomutase and malate dehydrogenase yielded no visible bands for any of the methods used despite extensive attempts. Cellulose acetate electrophoresis gave no results for esterase, phosphoglucomutase or malate dehydrogenase regardless of the method of sample preparation and despite extensive trialling. Upon the few occasions that it was attempted, polyacrylamide electrophoresis gave no better a resolution than starch gel electrophoresis.

Discussion

To date I know of two research groups who have published work upon the electrophoretic analysis of *T. vaporariorum* populations. Both of these groups used polyacrylamide electrophoresis. Prabhaker et. al. (1987) found no staining bands for *T. vaporariorum* with non - specific esterases although staining patterns were obtained with malate dehydrogenase and phosphoglucomutase, whilst Wool et. al. (1989) reported the presence of a weak staining pattern for esterase and a single undifferentiated staining band for alpha glucophosphate dehydrogenase. The weak staining band I obseseved for esterase correlates with the work of Wool et. al. (1989).

Due to the limited success experienced with the methods used this study was not further pursued, due to the time constraints imposed by other aspects of my PhD research. However the pilot methods deployed here could most certainly be refined and improved upon. Comments received by experts in electrophoretic techniques suggest the following lines of improvement. Firstly, with regards to the methods described here, more defined staining patterns may be obtained upon altering the pH of the buffers used and also their NAD/NADP and metal ion content. Should this fail then the application of more sensitive micro-electrophoretic techniques would be required, such as those used for nematodes (eg Dalmasso and Berge, 1978).

6 GENERAL DISCUSSION

Summary

Firstly this general discussion summarises and reiterates the main conclusions and findings of my studies, and places my findings within the context of current practices and situations within the commercial glasshouse industry. Lastly, consideration is given to the possible importance of *Encarsia formosa* (parasitoid of whitefly) and whitefly sex ratio as factors that may affect host plant adaptation by the glasshouse whitefly, but were not evaluated in previous chapters.

Quality control of experimental plant and insect material

High and consistent quality of plant and insect material is crucial to the comparison, interpretation and repeatability of experiments done to assess the suitability of host plants for an insect phytophage, especially in accounting for the high level of variability that polyphagous insect phytophages such as whitefly demonstrate in their performance (chapter 2). The presence of sick plant material and the use of insect rearings infested by other pests or disease may render the results obtained uninterpretable, particularly where it is being attempted to trace the adaptation of an insect to a host plant over consecutive insect generations.

The importance of host plants which 'pre-condition' a whitefly population

The study upon the adaptation of Dutch whiteflies to a Dutch sweet pepper cultivar demonstrated how important the role of a 'pre-conditioning' plant can be to the adaptation process (chapter 3). A whitefly population originating from tomato cv Moneymaker that was reared for one generation upon *Lycopersicon hirsutum* cv glabratum, showed an increased degree of adaptation to sweet pepper, compared with the same population that had not thus been 'pre-conditioned', but was transferred directly from tomato cv Moneymaker to sweet pepper. This phenomenon of 'pre-conditioning' has also been reported for other pest species e.g. for spider mites Gould (1979), for russian wheat aphid (Beregovy et al., 1988 and Schotzko and Smith, 1991) and for peach aphid Lowe (1973). In the case of whitefly this phenomenon was not specifically correlated to general host plant suitability, as whitefly populations originating from gerbera and cucumber demonstrated no significant difference in performance upon sweet pepper, although cucumber is generally a higher quality host plant than gerbera for Dutch whitefly (van Lenteren and

Noldus, 1990). However there is a possibility that these differences could be related to specific alkaloid substances present in *L. hirsutum* cv glabratum (van Gelder and de Ponti, 1987) that in someway facilitate its adaptation to sweet pepper. Specific evidence for this hypothesis must yet be found.

With respect to plant breeding I suggest that care should be taken, so that the breeding of resistance to a pest in one host plant does not enhance the suitability of another host plant for that pest. For example, in my studies on sweet pepper, 'pre-conditioning' the whitefly on *L. hirsutum* cv glabratum enhanced their performance upon, and adaptation to sweet pepper. However, *L. hirsutum* cv glabratum has also been used to improve whitefly resistance in commercial tomato cultivars of the species *L. esculentum* (de Ponti et al., 1983). Retrospectively such a situation may have given cause to a conflict of interests had whiteflies proven to become more adapted to sweet pepper since the introduction of the aforementioned tomato cultivars.

The phenomenon of 'pre-conditioning' may also be important in the commercial glasshouse situation with respect to both cultural control methods and the crops grown. Two important control methods in glasshouses are the removal of favourable weed species for insect pests from in and around the glasshouse, and the removal of waste crop material within the glasshouse. Both of these measures effect a reduction in possible sources of pest infestation. Where such a measure is not taken, whiteflies originating from plant refuse or weeds may be pre-conditioned to adapt to the new crop planted in the glasshouse. A second problem is that the crops grown in a glasshouse may enhance or hinder the performance of whitefly populations. Where one crop species is succeeded by a different one in the same glasshouse, then no problems should ensue if material from the previous crop is effectively removed and disposed of before the new crop is introduced. However multiple cropping as practised for example in Czechoslovakia (Jarosik and Pilva, 1989) and Hungary with cucumber and sweet pepper being grown in the same glasshouse, may enhance the pest status of whitefly upon sweet pepper (see chapter 3). Where glasshouses are highly congregated e.g. in the Westland area of the Netherlands, then the possibility exists of whiteflies readily migrating from one glasshouse to another (especially through ventilators) and thus from one crop to another. The effects of such a situation may be various. Upon the basis of my studies, whiteflies moving from a gerbera to a cucumber crop would flourish upon cucumber within one whitefly generation, where as whiteflies moving from a tomato to a gerbera crop would require a few whitefly generations to elapse before they have fully adapted to gerbera. The likelihood of such problems arising can be reduced by covering air vents with insect proof gauze (eg Berlinger et al., 1991). This is now also a widely accepted practice in the Westland area of the Netherlands (Bootsma, 1990), although the quantitative impact of this practice in reducing pest migration between glasshouses is not yet evaluated. Finally, where more than one cultivar of a crop is grown in the same glasshouse, as for example with ornamentals, whitefly may adapt readily to one cultivar and in thus doing become 'pre-conditioned' to adapt to another cultivar present in the glasshouse, on which its performance would otherwise have been poor. The occurrence and significance of such scenarios in the commercial situation are unknown and merit further study.

Preference - performance relationships in the glasshouse whitefly

The investigations of host plant preference by whitefly (chapter 4), demonstrated a positive correlation between the preference female whiteflies exhibit for a host plant in a choice situation and the performance of whitefly upon those same host plants. The initial choice of whiteflies at a distance from a host plant is random. Whiteflies remain upon the host plant on which they first landed, if upon feeding it proves to be of sufficient quality. A few hours after release whiteflies demonstrate their net preference. This preference has an invariate rank order independent of the host plant from which the whiteflies tested originate. This rank order of preference is the same as the rank order of suitability as given by van Lenteren and Noldus (1990) and is cucumber > gerbera > sweet pepper. The searching behaviour of the whitefly was found to closely reflect the 'non-random settlement' model of Morris and Kareiva (1991). This behaviour tends to maintain the polyphagous habit of whitefly, by ensuring that it lands and remains upon all plants available within its host range, although independent of the host plant from which the whiteflies originate, there will be a tendency to utilise the most suitable host plant available. This tendency decreases as the suitability of the host plant from which the whiteflies originated decreases. It is the result preferring the host plant from which it originates. This preference is subordinate to the preference for the most suitable host plant available. Its effect upon the relative preference a population exhibits increases as the suitability of the host plant from which a population originates decreases. The 'non random settlement' searching behaviour of whiteflies will also tend to maintain variability in the use of more marginal hosts. Further it reduces the possibility of host plant specific whitefly races, as whiteflies from any given host plant may on emergence land upon and exploit any host plant that is locally available.

That the host plant of origin of the whiteflies can influence the magnitude of preference for a host plant, underlines the pertinence of using whiteflies of different host plant origin when testing plant cultivars for their resistance against whitefly. Further, in 'no choice' tests of performance, it is important to differentiate between non-laying and laying females. Females laying no eggs, are exhibiting non-preference for the host plant and are thus responding primarily to its antixenosic properties. Females laying eggs are exhibiting a preference for the host plant and the number of eggs laid reflect its antibiosic properties. This distinction is not often made in studies aimed at measuring oviposition preference for a host plant, where the mean number of eggs laid per group of females restricted to an area of a plant part is measured independent of whether all females observed oviposit or not (e.g. Dorsman and van de Vrie, 1987, Zoebisch and Schuster, 1987, Saxena, 1990). Also studies aimed at measuring antibiosis properties of a host plant do not make this distinction when assessing female fecundity (e.g. Knutson and Gilstrap, 1990, Trichilo and Leigh, 1985, Mansour and Karchi, 1990, Zabudskaya, 1990 and van Rensburg and Malan, 1990). In the studies presented in chapters 2 and 3 the distinction was made and it was found that the number of non-laying females increased, as the suitability of the plants to which the females were exposed to decreased. Such a consideration can be used to interpret differences between laboratory and greenhouse tests of varietal resistance (Romanow, et al., 1991). In the greenhouse antixenosic factors are not excluded, females being free to alight upon a plant or not, where as in laboratory experiments females are constrained within leaf cages and antixenosic affects are suppressed if non-preference is not accounted for.

The data obtained about 'trade-offs' occurring when a population adapts from one host plant to another, indicated that no 'trade-offs' were observed when a whitefly population originating from gerbera adapted to cucumber. However this was not a detailed investigation and was conducted on just one population. 'Trade-offs' can be expected where a population from a highly suitable host plant e.g. cucumber, is transferred to a much less suitable host plant e.g. tomato, and upon becoming adapted to this host plant the population is reverted back to its original host plant. This suggestion is based upon the findings of Fry (1990), who found that a line of spider mite established from tomato upon lima bean (a poorer host plant than tomato), showed a lesser performance than the tomato line, upon being reverted back to this host plant.

Host plant suitability and the durability of plant resistance

There is no one single method which is the most suitable for assessing host plant adaptation by an insect pest and thus ascertaining the durability of resistance of plant cultivars. If, as in my investigations, life history parameters are monitored to assess changes in insect performance, then more than one parameter should be used. However, as outlined in chapter 2, no one parameter could be identified to most characteristically reflect changes in population fitness over successive whitefly generations, especially when the accuracy by which the parameters are measured is considered. Few studies except for that of Gould (1988) upon *Heliothis* spp., have been done to assess the probable durability of the resistance of new plant cultivars. However a lack of such information on durability may in future prove costly with respect to the deployment of genetically engineered crops. There are already reports of resistance against crops engineered with *Bacillus thuringiensis* which were released during the last few years (Gibbons, 1991 and Anderson, 1992).

Many tests of host plant suitability and resistance do not consider variation between generations in pest performance. However, it was clear from the study of the adaptation of whiteflies originating from gerbera to cucumber, that the performance of a whitefly population upon different plant cultivars to which it is already adapted, may vary from one generation to the next. These differences per generation between cultivars were not more than 20 % of the overall variation from all cultivars combined, but it was still enough to alter the relative rank order of suitability of the cultivars over successive whitefly generations. This has implications for the testing of different plant lines for resistance against an insect pest. It suggests that for a polyphagous pest species:

1 insect rearings should be initiated upon each plant line using the same original insect population

2 the lines compared over several generations of the insect pest to assess each lines suitability upon the basis of the pests average performance over several generations. Such an approach would greatly improve the reliability of resistance tests, especially where differences between cultivars are slight.

Genotype-phenotype aspects of host plant adaptation in the glasshouse whitefly

From the pilot electrophoresis study (chapter 5), it was clear that *Trialeurodes vaporariorum* was not readily amenable to this technique, as was also confirmed by other studies (Prabhaker et al., 1987 and Wool et al., 1989). However, the further development of this approach is necessary to help confirm whether genetically different strains of whitefly exist, e.g. are Dutch and Hungarian whiteflies genetically distinct populations ? The confirmation of genetically distinct strains of whiteflies is important in relation to phytosanitory regulations. Within the European Community from 1 January 1993 phytosanitory controls at the borders of EC member states must disappear. This introduces the possibility of pests being transferred from one member state to another without restriction. For example, were a genetically distinct whitefly population to be introduced to an area where it was not previously found, then if this bred with the local whitefly population, it may result in genetic variation for the adaptation to local crops.

This study has, for the reasons explained in chapter 2, not investigated the performance of whiteflies upon different host plants with sib analysis methods (Via, 1990) but has provided an experimental basis for such investigations. By incorporating sib analyses into the experimental methodology already developed to assess whitefly preference and performance, the components of genetic and environmental variability upon different host plants could be assessed. Such an approach would be a useful extension of my investigations as it would give insights into the potential importance of dominant genetic characters, the role of phenotype plasticity and the sort of selective forces in operation e.g. disruptive, stabilising or directional.

Do natural enemies influence host plant adaptation ?

In the introduction to this thesis (chapter 1) I highlighted the need for an evolutionary ecological approach to integrated control measures where host plant resistance is combined with the use of a natural enemy of the pest. This study has shed no light as to whether or not the presence of a natural enemy will affect the rate at which a whitefly population will adapt to a host plant. Despite the work of van Emden (van Emden, 1986), which suggested that the presence of a natural enemy can effectively increase the durability of a cultivars resistance, little is known of the selective mechanisms operating between a pest and a natural enemy upon a resistant cultivar. If integrated control systems are to rely more upon partial plant resistance and natural enemies, and less upon the use of pesticides, then we need to fundamentally understand the underlying mechanisms that determine the interactions between control components.

It has been established that:

1 plant architecture can influence the searching efficiency of a natural enemy (e.g. de Ponti and van Lenteren, 1991)
2 plants under attack by a pest may release semiochemicals that attract natural enemies (eg Dicke and Sabelis, 1988 and Nadel and van Alphen, 1987)
3 prey in sequestrating certain plant compounds may became unsuitable for their predators (eg review of Duffey, 1980)
4 hosts may vary in quality for their parasitoids dependency upon which plant they utilise (Greenblatt and Barbosa, 1981).

These are all manners in which the plant directly or through the pest may hinder the natural enemy.

Less is, however, known about the mechanisms by which a natural enemy may affect the adaptation of a pest to a host plant, thus regulating the durability of the resistance of the host plant concerned. For example, the natural enemy may select a specific life history stage of the pest, thereby, increasing or decreasing the selection pressure upon the pest to adapt to the host plant. This is the sort of scenario that Gould et al. (1991) examine. They considered monogenic models of pest adaptation to a resistant host plant and the fitness of the three possible genotypes within a population: homozygous resistant, heterozygous resistant and homozygous susceptible. Their models indicated that the affect of a natural enemy upon the rate of adaptation exhibited by a pest was variable. The precise outcome was influenced by the following factors:

1 life history stage which the natural enemy attacks
2 relative frequency of each genotype present in the pest population in any given pest generation
3 searching efficiency of the natural enemy and the preference it may exhibit with respect to prey size (quality).

Therefore, in any given tritrophic interaction which includes a of partially resistant host plant, the effect of the natural enemy upon the rate of adaptation to the host plant by the pest, may be negligible, positive or negative in character. Gould et al. (1991) concluded that in general, the selection for adaptation to a resistant plant type was lower where a partially resistant plant was combined with a natural enemy, than where a plant with solely strong resistance towards the pest concerned was used.

For the system *Encarsia formosa* - whitefly - host plant much is known about the basic ecological interactions, which provides a fundamental basis for the biological control of whitefly by *Encarsia*. There is now a need for this knowledge to be taken a step further to assess the possible influence of *Encarsia formosa* upon the adaptation to host plants by whitefly. If this is to be investigated using genetic models of fitness as detailed by Gould et al. (1991) then sib analyses of whitefly preference and performance must first be conducted. After that, it may be possible to build simulation models to analyze this problem. understood, as under such conditions *Encarsia formosa* is widely used for whitefly control.

The effect of whitefly sex ratio

In their review of 1990, van Lenteren and Noldus, suggest that the sex ratio of *T. vaporariorum* is 1:1. The data collected and tested by van Roermond and van Lenteren (1992), generally confirm this statement. There is however a notable exception which was the study of Boiteau and Singh (1988), upon potato. Here the sex ratio was found to be circa 70% females and 30 % males. The study by Hare and Kennedy (1986) of *Leptinotarsa decemlineata* upon *Solanum carolinese*, demonstrated that populations from separate localities reared upon *S. tubersoum* had different sex ratios upon *S. carolinese*. In the light of this study, it would be interesting to investigate whether the sex ratio of whiteflies from different localities or host plants differed upon being transferred to a second host plant, and if in adapting to this host plant over several generations, the sex ratio of the population was affected. Such a study might also indicate whether the observation by Boiteau or Singh (1988) was highly exceptional or not for the glasshouse whitefly. Clearly, a change in the sex ratio of a population will affect its fitness with respect to its intrinsic rate of increase. Where the host plant is of such a poor suitability that female fecundity is low and the sex ratio is male biased, then this may result in the population becoming extinct before it maximises its adaptation to the host plant. Thus the sex ratio of a population as mediated through the host plant may thus be an important limiting factor in relation to the host plant adaptation process.

Where next ?

On the basis of my studies, I suggest that future investigations should concentrate upon sib analyses of whitefly performance on different host plants and whether whitefly sex ratio is affected as a result of a population adapting to a host plant. Such fundamental studies may provide a basis for investigating the affect of *E. formosa* upon the durability of whitefly resistance cultivars which may help to reduce the need for pesticide application in integrated control programs.

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CURRICULUM VITAE

David Crawshaw Thomas was born in Reigate, Surrey England on 22 June 1967. He completed his secondary school education at Aylesbury Grammar School obtaining his 'O' levels in 1982 and 1983 and his 'A' levels in 1985. Thereafter he attended Imperial College at the University of London, reading for a Bachelor of Science in Applied Biology. This was a sandwich course study, entailing several industrial placement projects. In 1986 three months were spent working for the Forestry Commission investigating methods to improve the preservation of tree logs. In 1986/1987 six months were spent with Imperial Biotechnology Limited, London as a microbial analyst helping to develop a cheese ripening enzyme. In 1987 three months were spent again with the Forestry Commission conducting electrophoretic studies upon Scolytid Beetle populations. In 1988 six months were spent working for the Agricultural Development and Advisory Service (ADAS) working for Mr. L. Wardlow, assisting him in his role as Regional Entomologist for protected crops. The final year of these studies was in part financed by a bursary from Shell UK Limited. Having graduated in June 1989 with an Upper Second Class (Honours) three months were spent working for Shell as a laboratory assistant in the Fungicides Department of the Sittingbourne Research Centre. This PhD project was begun in October 1989 and is financed through a NATO scholarship from the Science and Engineering Research Council, Swindon, England.