Parasitoids as Biological Control Agents of Thrips Pests

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Contents

Chapter 1

Evaluation of hymenopterous parasitoids as biological control agents of thrips pest in protected crops: introduction[1]

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Abstract
In this introduction a general overview of the current status is presented of hymenopterous parasitoids attacking thrips, their prospects as biological control agents. First, thrips pests which currently play a key role in protected cultivation (fruit vegetables and ornamentals) in Europe are discussed: *Frankliniella occidentalis* (Pergande) and *Thrips tabaci* Lindeman,. We also include data on two other thrips species which we used in our experiments, *Frankliniella schultzei* Trybom and *Frankliniella intonsa* (Trybom). Information is given on their distribution, biology, economical impact and ways for control. This is followed by a short description of the most important groups of natural enemies that are currently evaluated or applied as biological control agents of thrips (predatory mites, pirate bugs, entomopathogenic pathogens and entomophilic nematodes), their potentials and their flaws. This will be viewed upon as a state of the art at the onset of our project and the recent developments in retrospect. Finally, I present the aim of my research project and the outline of this thesis.

INTRODUCTION

Thrips pests in protected crops
Of the more than 5600 recognised species of thrips (order Thysanoptera) a few hundred are recorded attacking cultivated plants. A number of species have become key pests in a wide range of agricultural and horticultural crops. During the past decades, the losses of agricultural and horticultural produce caused by thrips increased considerably, resulting in losses of millions of € (Lewis, 1997). Damage may be the result of direct feeding on leaves, flowers or fruits, transmission of viruses, as well as product contamination (Mound & Teulon, 1995). During the last decades thrips have become pests in many cultivated crops throughout Europe and elsewhere in the world (Lewis, 1973, 1997; Ananthakrishnan, 1984; Mound & Marullo, 1996; Lacasa & Lloréns, 1996, 1998). With a continuously expanding world trade in fresh horticultural produce, changes in production and marketing systems, thrips remain a constant threat to crop pest management systems. Despite post harvest and quarantine procedures, thrips species are spreading worldwide very quickly. They have become the number one key pests in many greenhouse and field crops, especially vegetables and ornamentals (Tommasini & Maini, 1995; Palmer, 1992; EPPO, 1988).

Until the early 1980s, *Thrips tabaci* Lindeman was the most prevalent thrips pest in protected cultivation in Europe (Tommasini & Maini, 1995), but it caused problems only

[1] Part of this chapter has been published in a different form in Lewis, T. (ed.), Thrips as Crop Pests, CAB International, Wallingford, UK, pp. 355-397.

occasionally. Since its accidental introduction in 1983, the western flower thrips (*Frankliniella occidentalis* (Pergande)) has become the number one key pest in European greenhouses and, under Mediterranean conditions, also caused problems in field crops and orchards. *Thrips palmi* Karny started its expansion in about the same period in the Far East and the Pacific (Loomans & Vierbergen, 1997) and is currently an important pest throughout large parts of tropical and subtropical vegetable and flower producing areas. The continuous exchange of horticultural products all over the world makes this quarantine pest a serious threat to Europe as well. Interceptions from vegetables and cut flowers imported from the Caribbean, South America and Asia have increased in numbers over recent years. Apart from greenhouse crops in temperate areas, it is an important potential problem for the horticultural industry in the Mediterranean Region. While focussing on quarantine pests, another thrips species of nearctic origin managed to sneak in and establish itself on the European continent, *Echinothrips americanus* Morgan. It was introduced into Europe in 1993 and although known from a wide range of herbs and woody shrubs, it was at first exclusively found on bedding plants, in particular Araceae (e.g. *Syngonium*). Since 1995, however, several outbreaks occurred on sweet pepper (*Capsicum annuum*) in particular towards the end of the growing season and is now hampering IPM in this crop (Vierbergen, 1998).

Various reviews on *F. occidentalis* have been published during the past years, once this pest entered a country (EPPO/OEPP, 1988; Brødsgaard, 1989; Del Bene & Gargani, 1989; Ebener *et al.*, 1989; Mantel, 1989; Pèlikan, 1989 (for Europe), Waterhouse & Norris, 1989 (for the Pacific) and Monteiro *et al.*, 1995 (for South America)), as a kind of pest alert paper'. More recently, updates have been published (*F. occidentalis*: CABI/EPPO1998; Hsu & Quarles, 1995; Cloyd *et al.*, 1998; Van Driesche *et al.*, 1998;*T. tabaci*: Suchalkin, 1983; both: Waterhouse & Norris, 1989; Tommasini & Maini, 1995) on the current state of knowledge on taxonomy, distribution, recognition, biology, plant virus vector capabilities, food plants, damage, economic importance and control of the thrips, Also through Internet one can consult various databases (Crop Protection Compendium, 2nd edition 2002), newsletters (e.g. WFT Newsletter: Miller & Moran, Australia; Sting: WPRS/IOBC, Europe; IOBC/NRS-Newsletter,Van Driesche, USA) and newsgroups ('ThripsNet') for news, developments, problems, discussion and research topics.

In this chapter I summarise available information on the thrips pests which currently play a key role in protected cultivation in Europe, with particular emphasis on *F. occidentalis* and *Thrips tabaci*. I also include two other species that I studied: *Frankliniella schultzei* (Trybom) and *Frankliniella intonsa* (Trybom), followed by additional information on thrips biology, ecology and ways of control. Then the state of the art is discussed of the most important groups of natural enemies that are currently evaluated and/or applied as biological control agents: predatory mites, pirate bugs, entomogenic pathogens and entomophilic nematodes. Specific emphasis is put on the current status of hymenopterous parasitoids attacking thrips, their prospects and the outline of my thesis work. It will be viewed as a state of the art at the onset of our project and, in retrospect, the most recent developments.

Thrips Pests Species

Frankliniella occidentalis (Pergande 1895)

Frankliniella occidentalis (Pergande) or 'Western Flower Thrips' originates from the western part of the United States, west of the Rocky Mountains (Bryan & Smith, 1956), where it occurs from sea level to sub-alpine altitudes. It was recorded as a pest for the first time in 1881 in California on apricot and was subsequently described by Pergande in 1895. Later records originate from Canada (Alberta, British Columbia: Treherne, 1923), Oregon, Washington, Idaho, Montana, Wyoming, Colorado, Utah, Nevada, Arizona (Bailey, 1933), Iowa (Moulton & Andre, 1935), New Mexico (Eyer & Medler, 1941), Texas

Figure 1: Geographical distribution and spread of *Frankliniella occidentalis* (Pergande), ● = widespread, ○ = present or localised (Crop Protection Compendium, 2002)

(Riherd, 1942, North Dakota and Alaska (Bryan & Smith, 1956), Oklahoma (Ahring & Howell, 1968), South Carolina (USDA, 1981) and Louisiana (Graves *et al.*, 1984). From Florida it has been reported as early as 1910 (Morgan, 1913; Watson, 1918) (figure 1).

Outside continental America, it was first recorded from New Zealand in 1934 (on lupine: Zur Strassen, 1973), but it was not considered a pest. Later it was described from Hawaii (in 1955: Sakimura, 1972; see however Kurosawa, 1941), Korea (Woo, 1974) and Peru (Ortiz, 1977). In 1934 it was intercepted in Japan on chrysanthemum flowers from Hawaii (Kurosawa, 1941). In 1981 it was taken in New Zealand from an import from California (Manson, 1981), and only one year later it was found to be widespread (Mound & Walker, 1982). Presumably in 1983 it entered Europe through the Netherlands (Mantel & Van de Vrie, 1988). It was erroneously identified at first as *Frankliniella pallida* (Uzel) (see Dicke & Groeneveld, 1986) and managed to establish in greenhouses. In the years thereafter it spread quickly across the European continent (figure 1; Tommasini & Maini, 1995). Elsewhere in the world, it managed to get a foothold in eastern Africa in the late 1980s (Nakahara, 1997), Colombia, Costa Rica (Baker, 1988), South Africa, 1989: Giliomee, 1989), Japan, 1990: Hayase, 1991) and in West-Australia, 1993: Malipatil *et al.*, 1993) in the early 1990s. More recently it has entered Brasil, 1994: Monteiro *et al*., 1995), Argentina, 1993: DeSantis, 1995) and Chile, 1995: Gonzalez, 1996).

Thrips tabaci Lindeman

Before the introduction of *F. occidentalis*, *T. tabaci* was a thrips pest of the highest economic significance in Europe and elsewhere (see Ghabn, 1948; Waterhouse & Norris, 1989) for a review). The “onion thrips” (or sometimes also called “tobacco thrips” or “cotton thrips”) is a widespread pest throughout the world, but is probably originating from the central palaearctic region (Lindeman, 1889), more specifically the Middle East and Black Sea area. It was introduced from Europe in many parts of the world. It was first noticed in the USA in 1872, where its spread was very slowly until 1907, when it appeared simultaneously all over the USA (Chittenden, 1919), from Canada to Mexico, in the West Indies and the Bermudas. *T. tabaci* is extremely polyphagous, feeding on wide range of host plant species (Waterhouse & Norris, 1989; Doederlein & Sites, 1993). It is considered a major pest of open field crops like onions, leek and garlic (Harris *et al.*, 1963; Lall & Singh, 1968; Vierbergen, 1990; Franco *et al.*, 1999), cabbage (North & Shelton, 1986; Shelton, 1995), cotton (Ghabn, 1948; USDA, 1962), tobacco (Fedorov, 1930), cereals and fodder crops. Since the 1950s its importance in greenhouses

increased (Morison, 1957; Smith & Webb, 1976) on vegetable crops like cucumber (Binns *et al.*, 1982) and sweet pepper (Ramakers, 1980) and ornamentals like chrysanthemums (Shevchenko & Popov, 1989). Since *F. occidentalis* became the dominant species in most greenhouse grown crops, the impact of *T. tabaci* has sharply decreased. *T. tabaci* is, however, the predominant thrips pest in open field crops and natural vegetation in temperate areas and in the Mediterranean area, which mainly invades greenhouse crops during the summer period onwards, when mass flights occur (Kahrer, 1993; Shelton, 1995).

Frankliniella intonsa (Trybom), *Frankliniella schultzei* Trybom

Frankliniella schultzei Trybom ("cotton bud thrips") is pantropical in distribution. Like *F. occidentalis* it is a very polyphagous species, including monocotyledons and dicotyledons, but commonly found in flowers. *F. schultzei* varies largely in morphology, 17 described species are currently placed in synonymy with it (Mound & Marullo, 1996) and different colour forms are known: a dark from which is widespread on the southern hemisphere (South America, Africa and Australia) and a pale form (also considered as a distinct species, *Frankliniella sulphurea* Schmutz, by some authors: (Bhatti, 1990) which is more common on the northern hemisphere (Africa, Asia) (Nakahara, 1997), but an intermediate form exists as well. There is a clear difference in tospovirus transmission efficiency between the pale and black colour form (Wijkamp, 1995, Peters *et al.*, 1996). Colour forms also differ in their mode of reproduction: besides arrhenotokous (Palmer *et al.*, 1989) populations, thelytokous populations are known from both forms, originating from Africa (pale) and Brasil (black). *F. schultzei* is a common pest on field crops like cotton, tobacco, tomato, groundnut and flower crops (Pinent & Carvalho, 1998; Vierbergen & Mantel, 1991). It is regularly found on imported flower products (Hayase, 1991; Vierbergen, 1995). In The Netherlands it has established in cultures of Cactaceae in greenhouses (Vierbergen & Mantel, 1991; originating from Brasil) and on hyacinth bulbs in propagation rooms (Mantel, 1968).

Frankliniella intonsa Trybom is from a palaearctic origin, where it is widespread from Japan to Portugal, from Finland to India. It has been introduced into the neartic region some 30 years ago (USDA, 1973; Nakahara, 1997). It is a very common flower dwelling species, recorded from various plant species (Miyazaki & Kudo, 1988). Although it is predominantly considered a pollen feeder, it occasionally has been reported as a pest in Asia (Japan: Murai, 1988; Taiwan: Chen & Chan, 1987; Wang, 1990) on garden peas (Kakizaki, 1996; Fang, 1996), adzuki beans (Hachiya, 1990), tomatoes (Murai, 1988) and asparagus (Tong, 1976). On the other hand, *F. intonsa* has rarely been intercepted from import consignments (Vierbergen, 1995). In Europe, it is sometimes considered a pest of nectarines (Kourmadas *et al.*, 1982) and field crops like strawberries (UK: Buxton & Easterbrook, 1988; Italy: Gremo *et al.*, 1997). *F. intonsa* is known to enter greenhouses in summer (Vierbergen, 1988; Sauer, 1997), together with other indigenous thrips pests like *T. tabaci* and *Thrips fuscipennis* Haliday, but damage reports are yet scarce.

Thrips Biology

Like most members within the family Thripidae (order Thysanoptera, suborder Terebrantia), species within the genera *Frankliniella* and *Thrips* have a characteristic life-cycle that consists of six stages (Moritz, 1997): an egg, two active larval stages, an inactive and non-feeding propupal and pupal stage and an adult stage (female and male). Development intermediates hemimetabolism and holometabolism (Moritz, 1995). Eggs are deposited in host plant tissue, both larval stages and adults are active feeding on host plant tissue, second stage larvae search for shelter to pupate, mostly in the soil, under leaf litter or between debris (Binns *et al.*, 1982; de Kogel, 1997). All species are haploid (male) – diploid (female) (Moritz, 1997). Most species are arrhenotokous, i.c. exhibit a facultative parthenogenesis: unfertilised females produce male offspring, whereas

fertilised females produce female offspring from fertilised eggs and male offspring from unfertilised eggs. However, adult sex ratio patterns in most species like *F. occidentalis* (Higgins & Myers, 1992; Terry & Kelly, 1993) and *T. palmi* (Kawai, 1990) are often female-biased, which can be caused by several processes. In part it may result from a differential sex allocation pattern (Hamilton, 1967), but mostly its is determined by differential dispersal and distribution patters of sexes towards host plant quality and a shorter longevity of adult males (Terry & Kelly, 1993) and thus adult density (Higgins and Myers, 1992; Kawai, 1990). In other species, like *T. tabaci* and *F. schultzei*, thelytokous populations occur: females are diploid and are produced by obligate parthenogenesis by unfertilised females.

T. tabaci is parthenogenic over much of its geographical range, since sex ratio patterns are strongly female biased in most field populations. In particular those found on onion, leek and garlic are predominantly thelytokous (Vierbergen, 1990, Ester & Vierbergen, 1997; Franco *et al.*, 1999). Although sex ratio patterns vary in time and place (Kendall & Capinera, 1990; Torres-Vila *et al.*, 1994), males are rather rare in most parts of the world (Hawaii on *Emilia*: Sakimura, 1932; Sudan on cotton: MacGill, 1927) or completely absent (Sakimura,1937; Zawirska, 1976 all on onion). On the other hand, males are very common on tobacco (Lindeman, 1889; Zawirska, 1976), while Torres-Vila *et al.*, 1994) found 40-50% males on onion in late season, coinciding with a high relative amount (80%) larvae in the population. When reared in the laboratory on leek, some populations of *T. tabaci* exhibit complete thelytoky, others, like those collected form tobacco are arrhenotokous. What the exact mechanism behind these sex- ratio patterns, remains yet to be studied.

Developmental times and life history traits, like pre-oviposition period, fecundity, longevity and reproductive potential in *Frankliniella* and *Thrips,* are largely governed by temperature, host plant species (Tommasini & Maini, 1995), host plant cultivars (Jarošik & Lapchin, 1998) and to some extent by photoperiod (*F. occidentalis:* Brødsgaard, 1991). Life history traits of flower living species like *F. occidentalis, F. schultzei* and *F. intonsa* are particularly favoured by the availability of plant pollen (Trichilo & Leigh, 1988; van Rijn *et al.*, 1995), while leaf feeding species such as *T. tabaci* or *T. palmi* take far less profit from pollen and temperature for *F. occidentalis* (Van Rijn *et al.*, 1995; Gaum *et al.*, 1994; Lowry *et al.*, 1992; Brødsgaard, 1994; Gerin *et al.*, 1994; Katayama, 1997; Lublinkhof & Foster, 1977; DeGheele *et al.*, 1997; Soria & Mollema, 1995; Trichilo & Leigh, 1988; Mollema *et al.*, 1990; de Kogel, 1997; Jarošik & Lapchin, 1998) and *T. tabaci*: (Harris *et al.*, 1936; Waterhouse & Morris, 1989; Suchalkin, 1983; Shevchenko & Popov, 1989; Lall & Singh, 1968)

Although *F. occidentalis* is primarily considered a phytophagous species, feeding on vegetative tissues, flower tissues, pollen and extra-floral nectar sources, it is basically an opportunistic feeder, exhibiting predacious and cannibalistic behaviour at times as well (Lewis, 1997). It has been reported as an early season predator of spider mite eggs in cotton (Gonzalez *et al.*, 1982; Trichilo & Leigh, 1986) and of *Ephestia kuehniella* eggs in the laboratory (Hulshof & Vänninen, 1999). This feature is not uncommon in phytophagous thrips: also *Scirtothrips citri* (Moulton) (Mollet & Sevacherian, 1985), *F. schultzei* (Milne & Walter, 1996; Wilson *et al.*, 1996), *T. tabaci* (Lewis, 1973; Mound & Teulon, 1995: Wilson *et al.*, 1996) and *T. imaginis* Bagnall (Wilson *et al.*, 1996) have been recorded as facultative predators of spider mite eggs.

Thrips Ecology

Knowledge on the ecology of thrips pests is relatively poor. Except for species like *T. tabaci* and *F. intonsa* that occur naturally outdoors in temperate areas, most thrips pests originate from subtropical (*F. occidentalis; E. americanus*) or tropical (*T. palmi, F. schutlzei*) areas, that can only survive in temperate areas in protected environments such as greenhouses or internal plantscapes. In its native area of distribution, *F. occidentalis* is

able to overwinter outdoors in California (Bryan & Smith, 1956), Texas (Chambers & Sites, 1989), Georgia (Chamberlin *et al.*, 1992), North Carolina (Cho *et al.*, 1995) and Pennsylvania (Felland *et al.*, 1993; 1995), but also in Alberta, British Columbia (Madsen & Jack, 1966), Saskatchewan (Burgess & Weegar, 1988) and as far north as Alaska (Bryan & Smith, 1956). It is unable, however, to overwinter in harsh conditions as are prevailing in Southern Ontario (Broadbent & Hunt, 1991). In central and northern Europe, *F. occidentalis* can occur and reproduce outdoors during warm summer periods (Denmark: Brødsgaard, 1993; Netherlands: Vierbergen, 1995; Czechia: Sedivy, 1994; Hungary: Jenser, 1990), but it is not able to survive adverse winter conditions. In the Mediterranean Area, however, *F. occidentalis* is present outdoors all year (Chyzik *et al.*, 1995; Lacasa & Lloréns, 1996; Del Bene & Gargani, 1989). Although *F. occidentalis* can survive short periods of low temperature, its level of cold tolerance apparently is not sufficient enough to survive in severe winter conditions (Brødsgaard, 1993; McDonald *et al.*, 1997).

Various components in the lifestyle of species like *F. occidentalis, T. tabaci* and *T. palmi,* give them opportunity to colonise new habitats. First, these species have important features of an intrinsic opportunistic life-style, which can make them become a pest once they have arrived in a new habitat, such as a high reproductive capacity, parthenogenic mode of reproduction, multivoltinism, vagility, pesticide resistance, a wide host plant and habitat range (Mound & Teulon, 1995). Second, their preference for young host plant tissue, together with their hidden lifestyle (inside plant tissue and soil), which protects them during short periods of travel in horticultural products like vegetables and flowers and bedding plants, allows them to cover long distances without problem. Besides that, *F. occidentalis*, *T. tabaci, T. palmi* and also *F. schultzei*, are extremely variable species. Intraspecific variation has been found between populations from various parts of the world in a variety of traits:

- In morphology: most species have a large number of described species names which are currently synonym with its valid scientific name (*F. occidentalis*: 23; *F. schultzei*: 17; *T. tabaci*: 2). A specific characteristic is the large variation in colour of the adult female (*F. occidentalis*: Bryan & Smith, 1956; *T. tabaci*: Bournier, 1983; Klein & Gafni, 1995; *F. schultzei*: Nakahara, 1997). although different forms of *F. occidentalis* are found together all year, the dark form is more abundant in winter and early spring (Bailey, 1938); colour differentiation in thrips can be both genetically based as well as being a phenotypic expression of differential exposure to temperature or season (Lewis, 1997).
- In an increased tolerance or resistance to various insecticides: *F. occidentalis* (Immaraju *et al.*, 1992; Martin & Workman, 1994; Brødsgaard, 1994; MacDonald, 1995; Zhao *et al.*, 1995; Broadbent & Pree, 1997; Jensen, 1998), *T. palmi* (Nozawa *et al.*, 1994; Murai personal communication, 1998) and *T. tabaci* (Deryabin, 1979; 1993; Rossiter & Giesemann, 1976; Zil'-bermints *et al.*, 1979):
- In virus transmission efficiency (*F. occidentalis* : Van de Wetering, 1999; *T. tabaci* and *F. schultzei*: Wijkamp, 1995);
- In performance on different host plant species (*T. tabaci*: Zawirska, 1976) or on different cultivars of the same host plant (cucumber, chrysanthemum) with different levels of resistance, expressed in differential levels of damage and reproduction (*F. occidentalis*: de Kogel, 1997) and in sex ratio patterns (onion, tobacco: *T. tabaci,* Zawirska, 1976);
- In restriction patterns as expressed by RAPD-PCR techniques in *F. occidentalis* (Gillings *et al.*, 1996) and *T. tabaci*; (Klein & Gafni, 1995) populations of *F. occidentalis* originating from Europe and Australia, did not show any differences (Kraus *et al*., 1999). *T. tabaci* populations on the other hand, show a much larger variation (Jenser *et al*., 2001), e.g. those originating from Egypt (bean) and the Netherlands (leek) respectively could be separated easily (Kraus *et al*., 1999).

This intraspecific variation is partly genetically based, partly it is a phenotypic expression, suggesting a large genotypic plasticity and great adaptive potential. Given this large variation within one single thrips species, its phenotypic plasticity and adaptability, this could largely explain the complexity and difficulty ánd complicate finding adequate ways of control thrips pests. Besides a large intraspecific variation between populations, large variations in reproduction seem to exist between iso-female lines within the same population (de Kogel, 1997).

Economical impact

In the mid 1920s, *F. occidentalis* was already considered a pest of economic significance with in particular early season outbreaks in open field crops like alfalfa, bean, cotton, potato, safflower, squash, strawberry and tobacco (Bailey, 1933, 1938). It was also recorded from table grapes and from orchards (apple, apricot, nectarine, orange, peach), in southern California where it was particular prevailing during the blossom stage. In ornamental greenhouses it occurred only occasionally as a pest (Compton, 1930; Pritchard, 1949: roses, carnations). Mid 1970s economic significant outbreaks occurred in Hawaii, particularly on lettuce and chrysanthemums (Waterhouse & Norris, 1989). In the late 1970s it spread towards the east of continental America (figure 1): in 1980 a new state record was made for South Carolina (USDA, 1981) and Georgia (Beshear, 1983). In 1983 it was reported from Ontario-Canada (Allen & Broadbent, 1986). In these new areas it was largely observed in greenhouses. During its expansion period it also was recorded as a key greenhouse pest in Georgia (Beshear, 1983), Alberta, British Columbia (Steiner & Elliott, 1983) and Ontario (Allen & Broadbent, 1986) in Canada (see figure 1).

Nowadays, *F. occidentalis* has a huge economic impact and has become a key pest in a large range of agricultural and floricultural production areas in the world. It has a very extensive host range (Yudin *et al.*, 1987; CABI/EPPO, 1998), including field crops, orchards, greenhouse crops and weeds. There is also an indirect economic effect: when introduced into a new area, western flower thrips has been and still is also a major economic driving force of greenhouse and field crop IPM research during the past 15 years worldwide (figure 2).

In addition to causing direct damage to plants through feeding on parenchym cells, *Frankliniella* and*Thrips* species are also primary vectors of various tospoviruses, such as tomato spotted wilt (TSWV: *F. occidentalis, F. schultzei, F. intonsa, T. tabaci*), tomato chlorotic spot (TCSV: *F. occidentalis, F. schultzei, F. intonsa*), groundnut ringspot (GRSV: *F. occidentalis, F. schultzei*), impatiens necrotic spot (INSV: *F. occidentalis*), groundnut bud-necrosis (GBNV: *T. palmi, F. schultzei*) and iris yellow spot (IYSV: *T. tabaci*) virus (Wijkamp, 1995; van de Wetering, 1999). Some species, like *F. occidentalis* and *F. schultzei* (dark form: Klose *et al.*, 1996), also transmit viruses (tobacco streak ilar, TSV) with pollen or cause secondary infections by pathogenic fungi or bacteria (Lewis, 1997).

Measures to control thrips pests

Development of an IPM system for thrips pest management in greenhouses, generally is built on four corner stones: cultural and mechanical measures, host plant resistance, chemical control and biological control. In addition, monitoring (including sticky traps and direct counts) to follow population development, is an important component to determine economic injury levels for thrips damage (Shipp *et al.*, 1992, 1998, 1999; Schmidt & Frey, 1995), for a right timing and subsequent choice of control measures (Van Driesche *et al.*, 1998). It also is an essential part of cost-effective expert-systems or decision-support systems for IPM of greenhouse crops (Shipp *et al.*, 1996, 1999).

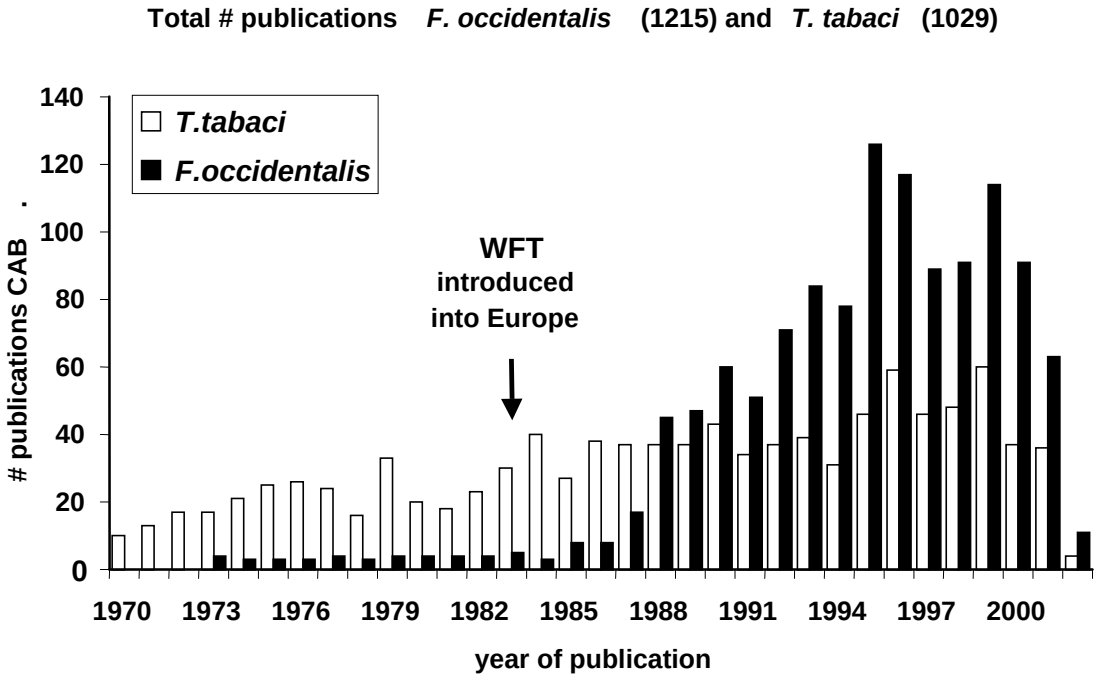

Figure 2. Number of publications on "*Frankliniella occidentalis*" and "*Thrips tabaci*" over time (CAB database, situation 1969 – October, 2002), prior to 1969: 160 records *F. occidentalis* (Mantel, 1988)).

A large variety of measures can be taken to keep thrips pests out as long and as much as possible or to slow down population build up. Prevention is the first step, including the use of clean propagation material in a clean greenhouse, a right timing of the planting season, choosing a right location for the plots and weed control. Additionally cultural measures, like irrigation (flooding of cotton fields (Bournier, 1994) or overhead irrigation in greenhouses and field crops), mulching, the use of mixed cropping systems (Theunissen & Schelling, 1998) or exclusion systems (windbreaks and barriers in open field; screening cloth or ultraviolet absorbing vinyl film). The use of resistant cultivars can become a useful tool in IPM programmes in crops like cucumber, chrysanthemum, tomato and sweet pepper on the short term, and are about to be integrated (de Kogel, 1997).

Chemical control is the most frequently used method to suppress and control thrips pest populations. Thrips pests are difficult to control chemically (Lewis, 1997), owing to the hidden life style and because during a large part of the immature development, stages are not exposed to insecticide contact: eggs are embedded in the leaf, pupal stages are protected in the soil, dirt or debris. Furthermore, most chemicals have a short-term effectiveness and frequent spraying (twice a week) is required for an effective control.

In the early part of this century, not much could be done to prevent a building up of *F. occidentalis* or *T. tabaci* populations. Sulfur, nicotine, derris and Paris green were originally used as insecticides to control thrips (Richardson, 1934), but these only reduced numbers. Chemical control of thrips pests really started with the application of tartar emetic in combined use with brown sugar (Richardson, 1934; Ewart & Watkins, 1944). Meanwhile there is an extensive amount of literature on the chemical control of *T. tabaci* and *F. occidentalis* (see Lewis, 1997 for an overview). From the early 1940s onwards, many growers in California, Arizona, New Mexico and Texas routinely applied organic compounds (first non-systemic and later also systemic) at planting, to prevent early season damage in cotton (Eyer & Medler, 1941; Tuttle & Wene, 1959; Race, 1961, 1965), bean, strawberry (Wilcox & Howland, 1954), vegetable crops (Harding & Wolfenbarger, 1963; Shorey *et al.*, 1962; Shorey & Hall, 1962, 1963), onion (Wilcox *et al.*, 1949; Harding, 1961) and a variety of other crops. In the early 1980s e.g. Dintenfass *et al.*,, 1987) observed an exponential population resurgence of *F. occidentalis* attacking onion in

Texas, after insecticide (parathion, oxydemetonmethyl) applications. Furthermore, strains of *F. occidentalis* have rapidly developed resistance against organophosphates and chlorinated hydrocarbons (Brødsgaard, 1994). Populations of *F. occidentalis* in Great Britain (Helyer & Brobyn, 1992), Europe, Africa (Brødsgaard, 1994), America (Immaraju *et al.*, 1992; Zhao *et al.*, 1994) and Australia (Herron *et al.*, 1996) are highly resistance to various chemicals. Highly effective insecticides in trials in one part of the world, can be quite ineffective in others (Seaton *et al.*, 1997). Nevertheless, every year, new evermore promising compounds come onto the market, including biorational chemicals, such as film-forming products, horticultural oils, insecticidal soaps (Allen *et al.*, 1993), natural macrocyclic lactone products like for instance Spinosad (Eger *et al.*, 1998) and, likely, in the nearby future, Genetically Modified Organims. A novel development of disease and insect control, including thrips, is the utilisation of aqueous formulations of particle (kaolin) films (Glenn *et al.*, 1999) for tree fruit production systems.

Among the insect pests, thrips (Thysanoptera: Thripidae) are responsible for most of the pesticide use (twice a week, up to 35 sprays per growing season: *T. tabaci* on salad onions, *F. occidentalis* (Lewis, 1997) and hence the residue problem on vegetable crops. The latter has gained special importance, since new regulations for maximum residue limits and safety intervals have been activated by the European Union in 1995, with partial enforcement since 1997. The reduction of pesticide applications and a change of plant protection methods that minimise the risk of surpassing these residue levels are the only way to maintain the export volume. Exporters that will not comply to these strict regulations will soon be driven out of the market. However, the greenhouse industry is growing in size and economic importance. Pesticide resistance, an increasing concern and awareness of the potential risks for human health and the environment, residue problems and problems with phytotoxicity has resulted in a decreased availability of insecticides. Because of that ánd because biological control is offering an economic, sustainable and safe alternative for chemical pest control, the greenhouse industry is gradually moving away from pure chemical control of insects to an integrated crop management system worldwide. Development of adequate biological control methods for thrips pests, often the bottleneck in greenhouse IPM systems, is the challenge.

NATURAL ENEMIES OF THRIPS

A large spectrum of natural enemies is known to attack thrips (table 1). They basically fall apart in two groups: macrobials (predators: Riudavets, 1995; Sabelis & van Rijn, 1997, parasitoids: Loomans *et al.*, 1997) and microbials (entomopathogens: fungi (Butt & Brownbridge, 1997) and nematodes (Loomans *et al.*, 1997)). During the past two decades, most attention has been paid to augmentative releases of generalist predators like phytoseiid mites (*Amblyseius* species) and pirate bugs (*Orius* species) (Riudavets, 1995; Sabelis & van Rijn, 1997). They are commercially available and are currently used as biological control agents in a variety of crops (Riudavets, 1995; Sabelis & van Rijn, 1997; Van Driesche *et al.*, 1998; van Lenteren & Loomans, 1998; table 1).

In 1988, when *F. occidentalis* had well established in Dutch greenhouses, most attention was focussed on a rapid development of a biological control method for this new key pest (Ramakers *et al.*, 1989). Although it was known that they fed on thrips prey, it was only since a decade or two that the potential role of phytoseiid mites and pirate bugs as biological control agents of thrips pests in greenhouses was emphasised (*T. tabaci*: Ramakers, 1978; *F. occidentalis*: Salas-Aquilar, 1977; Stoltz & Stern, 1978; Letourneau & Altieri, 1983). Predatory mites, like *Amblyseius barkeri* (= *mckenzei* Schuster et Pritchard) and *Amblyseius cucumeris* Oudemans, were the first option for commercial application on a wide scale. They were commercially available since 1985 (de Klerk & Ramakers, 1986), were applied successfully as biological control agents against *T. tabaci* in sweet pepper

Table 1. Overview of natural enemies currently evaluated as biocontrol agents of thrips pests (after van Lenteren & Loomans, 1998; van Driesche *et al.*, 1998)

	Prey / Host	Generalist / Specialist	Cropping system	Mass production?
Predators				
Heteroptera (pirate bugs)				
Orius spp.	Fo Tt Tp	generalist	gh, field	possible, expensive
Anthocoris nemorum	Fo	generalist	gh	possible, expensive
Geocorus spp.	Fo	generalist	field	not yet developed
Nabis spp.	Fo Tt	generalist	field	not yet developed
Dicyphus spp.	Fo Tt	generalist	gh, field	not yet developed
Macrolophus spp.	Fo	generalist	gh	possible, reasonable
Thysanoptera (predatory thrips)				
Aeolothrips spp.	Fo Tt	generalist	field	not yet developed
Franklinothrips spp.	Tp Hh Pd	generalist	gh	possible, expensive
Acari (predatory mites)				
Amblyseius/				
Neoseiulus spp.	Fo Tt Tp	generalist	gh	possible, cheap
Hypoaspis spp.	Fo Tt	generalist	gh, field	possible, reasonable
Various predators				
Neuroptera, Diptera	Fo Tt Tp	generalist	gh, field	some available
Parasitoids				
Ceranisus spp.	Fo Tt Tp	specialist	gh, field	difficult
Thripobius semiluteus	Hh	specialist	gh, field	possible, expensive
Pathogens (nematodes, fungi)				
Steinernema spp.	Fo, Tp	generalist	gh	possible, cheap
Heterorhabditis spp.	Fo	generalist	gh	possible, cheap
Thripinema spp.	Fo	unknown	gh, field	not yet developed
Verticillium lecanii	Fo Tt Tp	generalist	gh	possible, cheap
Beauveria bassiana	Fo Tt Tp	generalist	gh	possible, cheap
Metarhizium anisopliae	Fo Tt	generalist	gh, field	not yet developed
Paecilomyces fumerosus	Fo Tt Tp	generalist	gh	not yet developed

*Fo = *Frankliniella occidentalis*, Tt = *Thrips tabaci*, Tp = *Thrips palmi*, Hh = *Heliothrips haemorrhoidalis*, Pd = *Parthenothrips dracaenae*; gh = greenhouse.

(de Klerk & Ramakers, 1986; Ramakers, 1988), but control cucumbers often was insufficient (Ramakers, 1980; Ramakers & van Lieburg, 1982; Hansen, 1988; Gillespie, 1989; Brødsgaard & Stensgaard Hansen, 1992). Later, other species such as *Amblyseius degenerans* Berlese (Ramakers & Voet, 1995) and *A. limonicus* (Garman & McGregor) (van Houten *et al.*, 1995; van Houten, 1996) proved to be more effective predators of *F. occidentalis*, but they are difficult to mass-produce.

Orius species (*insidiosus, tristicolor*) (Heteroptera: Anthocoridae) in particular, were since long known as generalist predators, preying on a wide range of prey species such as spider mites, lepidopteran eggs, aphids and whiteflies (McCaffrey & Horsburg, 1986), with a certain preference for thrips, both adults and larvae (Isenhour &Yergan, 1981). They were known as common thrips predators, which are found on a wide range of field crops (cotton, soybean, alfalfa, potatoes, corn, peppers), orchards as well as on ornamentals (Herring, 1966) in temperate and mediterranean areas in North America and Europe. Observations indicate that they have a capacity of invading field crops rapidly. Various native anthocorid species were already known to enter greenhouses spontaneously during the summer period in temperate areas, controlling infestations of *T. tabaci* (Ramakers, 1978) or *F. occidentalis* (Tellier & Steiner, 1990) or controlling *F. occidentalis* infestations in addition to released exotic species (Altena & Ravensberg,

1990; Chambers *et al.*, 1993). In the Mediterranean area, a wide range of native species spontaneously enters greenhouses, in particular *Orius laevigatus* (Fieber) (Tavella *et al.*, 1991; Riudavets & Castañé, 1994) and are most common in non-pesticide treated crops.

At the onset of this research in 1991, experimental releases of phytoseid mites were unsatisfactory in most crops and studies on the use of pirate bugs (anthocorids), were still in its initial phase. *Orius insidiosus* Say, had just been imported from a laboratory culture in Eastern USA in 1989 (Fransen *et al.*, 1993). It was mass-produced and released on an experimental scale in greenhouse sweet pepper crops (van de Meiracker & Ramakers, 1991) and proved to be very successful. Evaluation of various species originating mainly from the Mediterranean, like *O. minutus, O. majusculus* and *O. albidipennis* (Reuter) and *O. laevigatus,* ultimately resulted in the wide use of the latter 2 species (Tommasini & Nicoli, 1995, 1996), which do not enter a reproductive diapause at short-day length (van den Meiracker, 1994; Tommasini & Nicoli, 1995, 1996).

Until now, control of western flower thrips has been most successful, in those crops were alternative food sources (pollen) and microhabitats (flowers) are available after initial decline of the thrips population, such as sweet pepper (van den Meiracker & Ramakers, 1991; Chambers *et al.*, 1993). Control successes in other crops, such as cucumber, melon, aubergine, strawberry and ornamentals largely depend on the availability of alternative food sources, such as natural occurring pollen or extra-floral nectar sources (van Rijn *&* Tanigoshi, 1999). In many other ornamentals, such as rose, *F. occidentalis* control has not been successful yet (Fransen *et al.*, 1993; DeCourcy-Williams, 2001). Another bottleneck is early season thrips control. Although *F. occidentalis* is less active in winter outdoors in the Mediterranean area and indoors in greenhouses, population build-up starts already in the early growing season. Because in most *Orius* and *Amblyseius* species, a short photoperiod induces reproductive diapause (van den Meiracker, 1994; Tommasini & Nicoli, 1995, 1996; Kohno, 1997), recent efforts are put into the search of new strains of these predators for early season releases (Van Houten *et al.*, 1995). Tommasini & Nicoli, 1995, 1996) for instance demonstrated that populations of *O. laevigatus* from Northern Italy and from Sicily differed in their ability to reproduce during short-day length, whereas Sicilian strain showed no diapause.

Because *F. occidentalis* control results were often still erratic and not reliable in a number of crops, biocontrol research was prompted in two directions. First, a search for more effective biological control agents was needed, either guilds, species or strains of predators. This search particularly focussed on non-diapause strain selection (table 1) and the use of indigenous natural enemies (Nicoli & Burgio, 1997). Second, a search for more effective ways of releasing biological control agents, in order to improve control of thrips in non-pollen crops: adjusting numbers or by supplying additional food sources such as pollen (Ramakers & Voet, 1996; van Rijn *et al.*, 1999) or by introducing mixes of different predatory species (Ramakers, 1995). Within integrated pest management programmes much attention is currently focussed on improving the establishment and efficiency of polyphagous predators with a low innate dispersal capacity. This goal can be reached by supplying alternative food sources like plant pollen or *Ephestia* eggs, by increasing the amount and number of introductions in time and space. In a so-called ‘push-pull’ strategy (Bennison *et al.*, 1999), *F. occidentalis* is attracted to areas where supplementary biological control agents could be applied for improved, cost-effective control. Commercial availability, costs of mass-rearing, are additional factors affecting these biocontrol options as well. The potential of predatory thrips and entomopathogens as specific biocontrol agents of thrips are still under investigation, as well as more generalist predators, which are applied for the control of other pests primarily, such as mirid bugs and chrysopids. The impact of others, like coccinellids and predatory bugs are still largely unknown.

Interactions with hymenopterous parasitoids

For quite some time there has been renewed interest in the use of hymenopterous parasitoids as potential biological control agents of thrips pests. Classical biological control of thrips, by inoculative releases of parasitoids, has been tried in the past without great success. Efforts to incorporate thrips parasitoids into greenhouse integrated pest management (IPM) programmes by inoculative releases or inundation to control thrips pests are of a more recent date. Augmentative and inundative releases of generalist predators like *Amblyseius* and *Orius* (Riudavets, 1995; Tommasini, 2003; this chapter) have gained most attention in thrips pest control. Since control of thrips pests like *Thrips palmi* Karny and *Frankliniella occidentalis* (Pergande) by predators, however, is only partly successful in some crops, the option of using parasitoids is worth consideration (Loomans *et al.*, 1995).

Larval parasitoids

Hymenopterous parasitoids of thrips all belong to the superfamily Chalcidoidea. Most are solitary endoparasitoids of eggs (Trichogrammatidae, Mymaridae) or larvae (Eulophidae). In this section, thrips parasitoid species will be discussed and characterised by their taxonomy and distribution, their ecology (host range, host plants), behaviour (host selection, searching) and biology (development, life history). This information is used to evaluate the potential role of thrips parasitoids for biocontrol, related to the type of programme and the type of thrips pest involved. Details on how to culture thrips are dealt with in Chapter 2. For a comprehensive review on thrips parasitoids, we refer to Loomans *&* van Lenteren, 1995), on which this section is based, with new material added.

Taxonomy

Except for a single species in the genus *Thripastichus* (Tetrastichinae) and *Pediobius* (Entedontinae), all larval parasitoids can be found in four closely related genera: *Ceranisus*, *Goetheana*, *Thripobius* and *Entedonastichus* (Entedontinae) (Boucek, 1976). They vary largely in morphology, behaviour and biology and currently the placement of species is under review (Trjapitsyn *&* Headrick, 1995).

They all are minute (0.5 to 1.1 mm), solitary endoparasitoids of thrips larvae, although sometimes the prepupae and/or pupae may be attacked. Currently, 27 species are described, parasitizing over 70 species of Thysanoptera (Loomans *&* van Lenteren, 1995, also for synonyms of genera and species), many of which are known as pests. In some records mentioning *Ceranisus* sp. (e.g. Greene *&* Parrella, 1993; Siddapaji *&* Reddy, 1974; Saxena, 1971; Hirose, 1989), specimens have been named, in others (e.g. Chiu, 1984) they await identification. General keys to eulophids, including thrips parasitizing genera, are provided by, for example Graham (1959, 1987), Boucek (1988) and Schauff (1991), and to trichogrammatids by Doutt *&* Viggiani (1968). A description and keys to some species of this group are presented by Graham (1959, 1963), Boucek and Askew (1968), Erdös (1971) and Trjapitsyn & Headrick (1995), but no key is available yet to all species of the world.

A few species in the genera *Psilogaster* and *Orasema* (Eucharitidae) are reported as ectoparasites of thrips larvae (Clausen, 1940; Beshear, 1974; Johnson, 1988). Sphecid species (Sphaecoidea) in the genera *Spilomena*, *Ammoplanus* and *Xysma* (Muesebeck *et al.* 1951, Krombein, 1958) and *Microstigmus* (Matthews, 1970) have been reported as preying on thrips larvae and *Aphanogmus fumipennis* (Thomson) (Ceraphronidae) was reared from *Thrips tabaci* (Dessart *&* Bournier, 1971), but they will not be further discussed here.

Distribution of species

Species within the genus *Ceranisus* are either cosmopolitan (*C. menes*: from tropical, subtropical and temperate regions), palaearctic (*C. lepidotus, pacuvius, planitianus*:

European), nearctic (*C. americensis, loomansi, russelli, nubilipennis*), neotropical (*C. nigrifemora*), oriental (*C. bicoloratus, femoratus, javae, maculatus, vinctus*) or Australasian (*C. margiscutum*) in origin, the last eight species have been recorded incidentally (references in Loomans *&* van Lenteren, 1995). *Thripobius* species have been recorded from tropical and subtropical areas of Africa, Asia, South America and Australia. Whereas *T. hirticornis* only occurs in Africa (Ghana, Tanzania, Uganda, Zimbabwe, Kenya), *T. semiluteus* has been reported from Africa (Sao Tomé: Boucek, 1976; South Africa: Steyn *et al.*, 1993), Asia (India: Boucek, 1976), Japan (collection BMNH)), Australia (Boucek, 1988) and South America (Brasil: LaSalle *&* McMurtry, 1989). Between 1986 and 1998 *T. semiluteus* was introduced from Australia (McMurtry *et al.*, 1991) and Brasil (LaSalle *&* McMurtry, 1989) into California and from there into Hawaii (Early, personal communication, 1990), Israel (Wysocki, personal communication, 1991), Italy (Mineo *et al*., 1999) and New Zealand (Froud *et al*., 1996)

Goetheana shakespearei Girault is Australasian, Afrotropical, oriental, neotropical and palaearctic, recorded from Australia (Girault, 1920; Goodwin *&* Steiner, 1995), Indonesia (van Heurn, 1923), India (Narayanan *et al.*, 1960) and Japan (Takagi, 1988: *Goetheana* sp.), Ghana (Ferrière, 1931), South Africa (Annecke, 1962), Benin (Tamò, personal communication), Venezuela (Annecke, 1962) and the Bahamas (Bennett *&* Baranowski, 1982). *G. shakespearei* has also been found in Spain (Viggiani *&* Nieves-Aldrey, 1993) and Bulgaria (*Goetheana* sp., Pelov personal communication). *Goetheana incerta* Annecke has been recorded from South Africa (Annecke, 1962) only. Recent introductions into California, USA for the control of *Scirtothrips persaea* Nakahara have so far been unsuccessful (Hoddle *et al.*, 2001).

Species belonging to the genus *Entedonastichus* are palaearctic (*E. albicoxus, E. gaussi, E. carbonarius*), nearctic (*E. kaulbarsi*) or Australasian (*E. dei, E. mirus*) in distribution. Most records are from Central Europe: *E. gaussi* from Germany (Ferrière, 1958) and the Ukraine (Dyadechko, 1964, 1967), *E. carbonarius* from Hungary (Erdös, 1971), South Slovakia (Boucek *&* Askew, 1968) and *E. albicoxis* from Hungary (Szelényi, 1982). Specimens belonging to *Entodonastichus* have been found in Sweden (Hedqvist, pers. coll.), Bulgaria (Pelov, pers. coll.) and Russia (Trjapitsyn, personal communication), but these are not yet identified to the species level. Three species are known from Australia: *E. dei*, *E. mirus* (also in New Zealand) and *E. carbonarius* (Boucek, 1988; Goodwin *&* Steiner, 1996) and a single brachypterous species (*E. kaulbarsi*) from Canada (collection BMNH) and Florida (Yoshimoto, 1981).

Thripastichus gentilei (Del Guercio) is cosmopolitan. Species, previously recorded as *Tetrastichus* under various synonyms (Domenichini, 1966; Graham, 1987; Boucek, 1988) have been collected from the Mediterranean (Del Guercio 1911; Bournier, 1967), the Caribbean and Florida (Waterston, 1923; Simmonds, 1933; Dozier, 1937) and India (Narayanan *et al.*, 1960; Ananthakrishnan *&* Swaminathan, 1977) on the northern hemisphere and from Brasil on the southern hemisphere (Bennett, 1965). *Pediobius thysanopterous* Burks was reared from material originating from Israel and Egypt (Burks, 1971). Tawfik (1967) recorded a *Pediobius* sp. from Egypt. Other records of a *Pediobius* associated with thrips (Risbec, 1951, 1958) might refer to yet another species (Burks, 1971), but its identity and host relation needs to be confirmed.

Host species and host plants

Most thrips parasitoids are host specific to a single subfamily, a few genera or even a few species. Between species there is considerable variation in host range. That of *C. menes* is very wide: it has been recorded from over 20 species, Thripinae and Panchaetothripinae (Loomans *&* van Lenteren 1995), multivoltine as well as univoltine species. *C. menes* inhabits a wide range of host plants in different biotopes (see survey of Loomans *&* van Lenteren, 1995; Goodwin *&* Steiner, 1996; Lacasa *et al.*, 1996). it has been found along roadsides and natural ecosystems (Chapter 2), in agricultural

ecosystems like gardens (Bühl, 1937; Hirose *et al.*, 1992, 1993), cultivated fields, weeds, fallow land as well as trees and forests. Occasionally it has been found among thrips-infested crops in greenhouses (Loomans, 1991; Rubin *&* Kuslitzky, 1992). Though present on leaves of onion (van Heurn, 1923; Sakimura, 1937ab; Saxena, 1971; Carl, 1971), aubergine (Hirose *et al.*, 1992, 1993), castor (Daniel *et al.*, 1983) and waxapple (Chang, 1991), *C. menes* mostly has been collected mostly from flowering plants, representing more than 20 different families. *Ceranisus russelli* also has a relatively wide host range: in addition to its major host *Caliothrips fasciatus* (Russell, 1911, 1912a; Bailey, 1933), infesting bean fields and wild plants surrounding them, it is also recorded as parasitizing *Thrips tabaci, Frankliniella tritici* (Russell, 1912b) and *Thrips simplex* (McKenzie, 1935). Other species have a more restricted host range, such as *C. americensis* on *F. occidentalis* (Seamans, 1923) and *T. tabaci* (Chapter 3), *C. lepidotus* on *Limothrips denticornis* and *F. occidentalis* (Lacasa *et al.*, 1996), *C. vinctus* on *Megalurothrips usitatus* (Fullaway *&* Dobroscky, 1934). Yet others specialise on a few thrips species with a univoltine life cycle: *C. pacuvius* (and *C. menes*) to *Kakothrips pisivorus* and *Odonthothrips* species on *Fabaceae* (Teulon *et al.*, 1996; Thuróczy *&* Jenser, 1996) and a *Ceranisus* sp. from Turkey on *Taeniothrips inconsequens* (Teulon, coll. 1994).

All host records for *Thripobius hirticornis* as well as *T. semiluteus* fall into the subfamily Panchaetothripinae (Thripidae). The former is only known to parasitise *Retithrips syriacus*. For *T. semiluteus*, *Heliothrips haemorrhoidalis* is often reported as a host (Boucek, 1976, 1988; McMurtry *et al.*, 1991; Steyn *et al.*, 1993). Also closely related species like *Panchaetothrips indicus*, *Brachyurothrips anomalus* (Boucek, 1976), *Selenothrips rubrocinctus* (Early, personal communication) are mentioned as hosts. In the laboratory it also parasitises *Hercinothrips femoralis* (Early, personal communication), but thripine species like *F. occidentalis* are not accepted as hosts (Loomans, 1991). *Thripobius hirticornis* and *T. semiluteus* have been collected on evergreen shrubs and trees belonging to different families (*T. semiluteus*: cardamom, croton, hibiscus, liquid amber, Valencia oranges, macadamia, avocado; *T. hirticornis*: coffee, rose) (Loomans *&* van Lenteren, 1995). A *Ceranisus* sp. is known from *Rhipiphorothrips cruentatus* in Taiwan (Chiu, 1984) and also *C. maculatus* is known from this host in India (Rahman *&* Bhardwaj, 1937).

Host species of *Goetheana shakespearei* all belong to the thripine and panchaetothripine subfamilies (Thripidae). Host plants are related to these records: *Selenothrips rubrocinctus* (on cacao, cashew, mango, tropical almond, *Acalypha wilkesiana*), *Heliothrips haemorrhoidalis* (croton, avocado, orange), *Caliothrips insularis*, *C. indicus* (groundnut, *Achyranthes aspera*), *Hercinothrips femoralis* (amaryllis, passionfruit, bougainvillaea) and *Dinurothrips hookeri* (laboratory). Its first record however was from *T. tabaci* (onion: van Heurn, 1923). It has been reared from it in the laboratory (Bartlett, 1939; Callan, 1943), but field records are scarce and parasitisation levels are low. Adamson (1936) and Bartlett (1939) also reared *G. shakespearei* on two other unidentified species of thrips in Trinidad, Bennett *et al.*, 1993) from *Echinothrips caribeanus* on *Clitoria* sp. in Guadeloupe, and Takagi (1988) reported it from *Pseudodendrothrips mori* on mulberry in Japan. *Frankliniella parvula* and *F. intonsa* (as *F. formosa*), have been mentioned as hosts (Ananthakrishnan, 1984), but Billes (1941) reported that the first was not attacked by *G. shakespearei*, the latter probably has been erroneously mentioned as such. *Goetheana incerta* is only known to parasitise *Scirtothrips aurantii* (Grout *&* Stephen, 1995).

From *Entedonastichus,* hosts are only known for *E. gaussi*: all are plaeothripids living on leaves and bark (*Liothrips setinodis*) (Dyadechko, 1964, 1967), or on or under bark (*Crypothrips nigripes*, *Acanthothrips nodicornis*, *Phloeothrips coriaceus* and *Hoplandrothrips pillichianus*) (Dyadechko, 1964) of conifers and broad-leaved trees, on species which are often occur in groups in mixed stands. In some years *E. gaussi* is assumed to have great importance in surpressing thrips. In 1957 in the Ukraine, *E. gaussi*

parasitised 34 per cent of the total *P. coriaceus* population and 87.6 per cent of the *L. setinodis* population (Dyadechko, 1964, 1967). *Entedonastichus* species have been collected from grassy areas (*E. carbonarius, E. albicoxis, E. dei, E. kaulbarsi*) and forests (*E. gaussi, E. mirus*) or from a combination of both. Boucek (1988) mentioned collections of *E. dei* from rose, *Discaria* and *Juncus*. The closely related *Ceranisus nubilipennis* and *C. bicoloratus* have been reared from tubuliferan species as well: the first from *Cryptothrips rectangularis* and *Megalothrips spinosus* from willow galls in a swamp in Massachussets USA (Williams, 1916). Murai (personal communication) reared the latter species from *Liothrips wasabiae,* infesting leaves and roots of wasabe (*Cruciferae*) in a forest in Shimane – Japan in August 1990.

Except for a single record on *Rhipiphorothrips cruentatus* (Panchaetothripinae) (Narayanan *et al.*, 1960), thrips host records of *Thripastichus gentilei* fall within the genus *Liothrips (floridensis, laureli, mikaniae, oleae, urichi, varicornis)*, *Gynaikothrips ficorum*, *Hoplothrips pedicularius*, and a number of other species from India, all Phlaeothripidae. *Liothrips* species are leaf feeders, all other hosts inhabit leaf galls of various trees and shrubs (Raman *&* Ananthakrishnan, 1984). *Thripastichus gentilei* also parasitises the phlaeothripid predator *Androthrips flavipes* (Ananthakrishnan *&* Swaminathan, 1977; Varadarasan *&* Ananthakrishnan, 1981), one of the controlling factors of gall inhabiting thrips in India, and *Liothrips mikaniae*, a potential biocontrol agent of weeds (Cock, 1982).

Host selection

The actual host range of a parasitoid depends on the probability of a host being found (ecological host range), host defense reactions (behavioural interactions) and host suitability (physiological host range). How thrips parasitoids locate their hosts is not clear. Whereas panchaetothripine host species generally complete their life cycle in the open on mature leaves and shoots, thripine host species prefer young plant parts, leaf folds, buds and flowers. *Ceranisus menes* searches in these places (Saxena, 1971), but parasitisation is much lower when hosts are concealed than in the open and searching efficiency of *C. menes* and *C. russelli* declines on hairy leaves (Russell, 1912b; Sakimura, 1937a,b). Semiochemicals seem to be involved in host searching by *C. menes*, wasps searching longer in areas where host larvae have fed (Bazzocchi *&* Santi, 1994; Chapter 6). *Thripastichus gentilei* searching for hosts slowly enters galleries made by scolytids, occupied by *Liothrips oleae* larvae or seeks them on branches, leaves and fruits (Del Guercio, 1911). The accessibility of thrips galls plays a role in its parasitisation efficiency: in galls of *Schedothrips orientalis*, parasitisation reached 20 per cent, but in other species it was restricted to individuals at the base of the galls, or sometimes there was no parasitisation at all (Ananthakrishnan *&* Swaminathan, 1977; Varadarasan *&* Ananthakrishnan, 1981; Raman *&* Ananthakrishnan, 1984). *Frankliniella occidentalis* produces an alarm pheromone (see Chapter 6) that acts as a kairomone for polyphagous predators (*Amblyseius, Orius*) (Teerling *et al.*, 1993a,b). Whether these substances are used by parasitoid species to locate their hosts is yet unknown.

Host examination and acceptance behaviour is similar for various host-parasitoid combinations (Russell, 1912b; Williams, 1916; Bailey, 1933; Sakimura, 1937a; Saxena, 1971; Carl, 1971; Hirose, 1989; Loomans *&* van Lenteren, 1995). Once a host is encountered and examined with the antennae, the ovipositor is thrust forward between the legs and inserted into the host's thorax or abdomen. Most parasitoids stay in this position, but *C. menes* immediately turns 180^0, lifting the vigorously moving larvae up in the air (Carl, 1971; Murai, 1988; Loomans, 1991; Galazzi *&* Bazzocchi, 1993; Chapter 3). With large larvae, wasps often stay standing tail-to-tail to their host. *Goetheana shakespearei* attacks the host larva by inserting its ovipositor standing laterally to the anterior part of the abdomen (Daniel, 1986; Hessein *&* McMurtry, 1989), *T. semiluteus* to the posterior part.

Once the ovipositor is inserted, a first stage larva becomes paralysed or immobilised (Daniel, 1986; Loomans, 1991) and a single egg is deposited. Oviposition times vary from

20 to 60 s (range 3-240) for *C. menes* parasitizing *Frankliniella occidentalis*, *Thrips palmi* (Hirose, 1989), *T. tabaci* (Sakimura, 1937a; Carl, 1971), *Zaniothrips ricini* and *Retithrips syriacus* (Daniel, 1986). For *C. russelli* attacking *Calitothrips,* oviposition time ranged from 15 to 240 s (Bailey, 1933), but 20 to 50 s according to Russell (1912b). *Ceranisus americensis* takes less time to parasitise *F. occidentalis* (15 s) than *T. tabaci* larvae (45s) of the same age (Chapter 3). For *Goetheana shakespearei* parasitizing *Heliothrips*, oviposition takes 20 to 48 s (Hessein *&* McMurtry, 1989), but for *T. semiluteus* it is only 5 to 12 s. In *C. nubilipennis* oviposition takes 10 to 15 min, sometimes 30. When host feeding occurs, no egg is laid, stinging and feeding follow each other repeatedly, up to 12 min is spent handling the host before the host is killed. *Ceranisus menes* is able to discriminate between unparasitised and parasitised hosts (Carl, 1971; Hirose, 1989), after antennal examination and probing.

Within its host range, a preference may occur for certain thrips species. In some cases parasitoids do not seem to prefer any particular size or age (*C. menes: Kakothrips pisivorus* (Bühl, 1937); *Frankliniella intonsa* (Sakimaura, 1937a); *Thrips tabaci* (Carl, 1971); *C. russelli*: *Caliothrips fasciatus* (Russell, 1912b); *C. nubilipennis* (Williams, 1916)). Other records state a certain preference, even within the same host-parasitoid combination: parasitoids prefer large (*Thrips tabaci,* Saxena, 1971; *Caliothrips fasciatus*, Bailey, 1933) or medium-sized larvae (*Zaniothrips ricini* and *Retithrips syriacus,* Daniel *et al.* 1983, 1986; Daniel 1986).

Goetheana shakespearei and *T. semiluteus* attack both larval stages of panchaetothripine hosts, but small and medium-sized larvae are required for successful parasitisation. The female mostly rejects late second stage larvae, propupae and pupae (Daniel, 1986), in which *T. semiluteus* (McMurtry *et al.*, 1991; Newberger *&* McMurtry, 1992) and *G. shakespearei* (Dohanian, 1937; Hessein *&* McMurtry, 1989) fail to complete development. In thripine species, like *Pseudodendrothrips mori, G. shakespearei* lays its eggs in first and second instar larvae (Takagi, 1988). Others like *Frankliniella*, which are more active, probably manage to escape from attacks by *G. shakespearei* (Billes, 1941). Female *T. gentilei* lay their eggs preferably inside young larvae and never attacks second stage larvae, propupae or pupae (*Gynaikothrips ficorum:* Bournier, 1967). In *Liothrips oleae*, newly hatched and old larvae are not attacked (Del Guercio, 1911). In *Liothrips laureli*, the female lays her eggs inside both larval stages (Mason, 1922).

Behavioural defense reactions (walking away, violent abdominal movements, shaking off the attacker) by old and large thrips larvae, can prevent parasitisation in many species (Bailey, 1933; Saxena, 1971; Carl, 1971), especially in host species whose larvae are more active and easily disturbed like *T. tabaci*, *F. tritici* (Russell, 1912b), *Megalurothrips usitatus* (Fullaway *&* Dobroscki, 1934) or *M. sjostedti* (M. Tamò *&* K. Diop, personal communication). If insertion occurs, the larva drags the wasp along (Williams, 1916), trying to escape. Sakimura (1937a) noted oviposition failures on *Haplothrips subtilissimus* due to violent defense measures. *C. menes* attacked *Haplothrips chinensis* (Murai, 1990) but could not develop. Larvae can also defend themselves by excreting anal droplets. Larvae of a number of Panchaetothripinae (*Retithrips*, *Caliothrips*, *Selenothrips*, *Heliothrips*, *Rhipiphorothrips*) constantly keep their abdomen in an uplifted position bearing a droplet of intestinal liquid, enclosed by the whorl of anal bristles (Rivnay, 1935, 1939; Entwistle, 1972; Chiu, 1984) and in other species the abdomen is partly covered with liquid excrements. *Ceranisus russelli*, observed in the open on a croton leaf, attempting to oviposit in larvae of *Heliothrips haemorrhoidalis*, was frequently caught by the sticky excrement of its host, and only with great difficulty succeeded in freeing itself (Russell, 1912b).

Developmental biology

Thrips parasitoids are all koinobionts, allowing the host to grow beyond the stage attacked. Parasitised larvae move about freely, feed normally and cannot be distinguished

externally from unparasitised ones. Parasitism becomes evident at propupation of the host (*Ceranisus*: Fullaway *&* Dobroscky, 1934; Kutter, 1936; Bühl, 1937; Sakimura, 1937a; Rahman *&* Bhardwaj, 1937; Daniel, 1986; Murai, 1988; Galazzi *&* Bazzocchi, 1993; Greene *&* Parrella, 1993; *Goetheana*: Dohanian, 1937; Takagi, 1988; *Thripobius*: McMurtry *et al.*, 1991). The absence of propupal wing buds, a slightly swollen body, a central spot in the propupa which can vary according to the host-parasitoid combination and varies from creamish white, yellow, orange, crimson to deep red (Chapter 2). The pupa is almost white (*C. menes, C. americensis, T. gentilei*) to deep red (*C. maculatus*) when newly formed, becoming dark brown to black in all cases.

Pupation takes place outside the larval skin (Chapter 2). The site of pupation is related to that of its host, usually the soil (Thripinae), sometimes it remains on the surface where the parasitised thrips larva has been feeding (Panchaetothripinae: Rahman *&* Bhardwaj, 1937; Newberger *&* McMurtry, 1992; Chiu, 1984), sticking to the leaf surface hanging head downwards from the skin of the host (Entwistle, 1972; Daniel, 1986). In *Thripastichus* and *Pediobius*, the black-brown pupa stays inside the host larva integument, sticking on the leaf (*Ripiphorothrips cruentatus*: Sharma *et al.*, 1965) or hidden under bark or underside of dead leaves (*Liothrips oleae*: Melis, 1935). In *Gynaikothrips ficorum* some *T. gentilei* individuals emerge and pupate within the curled leaf (Bennett, 1965). *Thripastichus* larvae exhibit slight up and down movements within the host. Shortly before adult emergence the parasitoid rotates 180^0 within the host's body, facing its hind end (Del Guercio, 1931; Melis, 1935; Bournier, 1967; Ananthakrishnan *&* Swaminathan, 1977). All species mentioned above are solitary, but in *Ceranisus nubilipennis* and *C. bicoloratus* multiple parasitism seems to be the rule: two to three or even more pupae can emerge from the same host, males as well as females (Williams, 1916; Ishii, 1933).

Life history

Life history parameters (development rate, immature mortality, sex ratio, longevity, oviposition period, fecundity) vary with temperature, the host-parasitoid combination and geographical origin of the parasitoid. Intraspecific differences in qualitative and quantitative aspects of host physiology and nutrition clearly affect development in *C. menes*. In multivoltine hosts, developmental time varies with host age (Sakimura 1937a), sex of the larva on which the egg is laid (Murai, 1988) and the host species attacked (Murai *&* Loomans, 1995). In general males emerge shortly before females (*C. menes*: Sakimura, 1937a; Murai, 1990; Castineiras *et al.*, 1996; *C. pacuvius*: Kutter, 1936). Developmental differences occur between strains of *C. menes* according to their geographical origin (Castineiras *et al.*, 1996). Overall developmental time can vary to a large extent (Murai, 1988; Galazzi *et al.*, 1992) up to 4 months or more, in unisexual strains. Murai (1990) did so in a bisexual strain, whereas others did not (Sakimura, 1937a; Castineiras *et al.*, 1996). Daniel (1986) notes an extreme short life cycle of 10.8 days parasitizing *Zaniothrips ricini* and 16.3 days on *Retithrips syriacus*. Pupal duration of the parent had no relation to that of its offspring (Murai, 1988). Parasitizing a univoltine host like *Kakothrips pisivorus*, *C. menes* development is largely governed by host physiology, producing only one generation a year (Bühl, 1937).

Developmental times of host and parasitoid can be similar: *C. russelli* and *Caliothrips fasciatus* (Russell, 1912b; Bailey, 1933) and *C. vinctus* and *Megalurothrips usitatus* (Fullaway *&* Dobroscky, 1934). Mostly, host species like those belonging to the genera *Thrips* and *Frankliniella* develop much faster than *C. menes* and *C. americensis* (Loomans *&* van Lenteren, 1995), development times of the parasitoid are approximately 1.5 to 2 times longer than that of the host, leading to asynchronous generations. For *G. shakespearei* the whole life cycle takes about 17 to 21 days at temperatures above 24^0C, but is much longer at lower temperatures. This is much longer or about equal to some of its hosts, *Caliothrips indicus* (Ananthakrishnan, 1984) and *Selenothrips rubrocinctus*

(Entwistle, 1972), but somewhat faster than *Heliothrips haemorrhoidalis* (Rivnay, 1935; Hessein *&* McMurtry, 1989). Compared with *H. haemorrhoidalis*, *T. semiluteus* develops much faster (McMurtry *et al.*, 1991): at 23^{0}C the life cycle takes 35.6 (34 to 39) days for the host and 23.6 (22 to 25) days for the parasitoid. Also *T. gentilei* develops much faster than most of its hosts: emergence of *T. gentilei* adults from the host occurs on day 8 to 10 of pupation of *Schedothrips* (Ananthakrishnan *&* Swaminathan, 1977), and from *Liothrips laureli* after a week (Mason, 1922). In India, approximately 12 to 14 days were required to complete the life cycle on *R. cruentatus* (Sharma *et al.*, 1965), while in Europe its life cycle took about 20 days on *Liothrips oleae* or *Gynaikothrips ficorum*, (Melis, 1935; Bournier, 1967). On the other hand *L. laureli* (Mason, 1922), *G. ficorum* (Rivnay, 1947) and *L. mikaniae* (Cock, 1982) take 30 days or more to complete development.

Temperature strongly mediates developmental time and seasonal synchronisation. Although able to survive cold and hot weather extremes, field temperature requirements for parasitoids are between 20 and 30^{0}C. In univoltine hosts like *Kakothrips pisivorus*, *C. menes* and *C. pacuvius* have one generation a year and overwinter as pupae, whereas the host overwinters as full-grown second stage larvae (Kutter, 1936; Bühl, 1937). In multivoltine host species, parasitoids have more generations a year (four in *C. menes:* Sakimura, 1937b; five to eight in *C. russelli:* Russell 1912b; five in *T. gentilei*: Melis, 1935). At 20^{0}C or lower, life cycles of *C. menes* can be very long (Murai, 1990; Castineiras *et al.*, 1996). At 17.8^{0}C, *G. shakespearei* did not pupate (Hessein *&* McMurtry, 1989) and at 30^{0}C, high mortality occurred. In *C. menes*, this can vary with the geographical origin of the parasitoid. Castineiras *et al.* (1996) calculated a developmental threshold of 8^{0}C (egg-adult) for Japanese and Thai females of *C. menes* and a thermal constant of 500 degree-days. For Thai males the minimum threshold was 13.7^{0}C and the thermal constant of 333 degree-days. With the advance of cold temperatures Sakimura (1937a) noticed an increase of the number of specimens that did not emerge ('hibernated'). At low temperatures *C. menes* pupae probably are not in diapause, but in a quiescent state: pupae readily started hatching when transferred to higher temperatures (Murai, 1988). *Ceranisus maculatus* hibernates as pupae on the host plants and the host (*R. cruentatus*) as pupae in the soil (Rahman *&* Bhardwaj, 1937). *Thripastichus gentilei* hibernates, as a larva or pupa in diapause induced by its host *Liothrips oleae*, which itself passes winter in adult diapause (Del Guercio, 1911; Melis, 1935), but when parasitizing *Gynaikothrips ficorum* in a greenhouse at temperatures of 20 to 25^{0}C, diapause did not occur (Bournier, 1967).

Ceranisus menes (Murai, 1988) can start to oviposit from the day of emergence onwards, but Sakimura (1937a) recorded a pre-oviposition period of 1 day in summer and 2 days in autumn. Daniel (1986), however, noted a 2 to 3 day period for *C. menes* and Rahman *&* Bhardwaj (1937) 3 to 5 days for *C. maculatus*. According to Sakimura (1937a), several oocytes mature within 24 h after emergence and full grown oocytes vary from 29 to 48 per female with an average of 38.6 for *C. menes*. Maturation of eggs continues over the female's lifetime, but in all cases numbers decrease with age. At its peak, *C. menes* can lay 20 to 30 eggs per day (Murai *&* Loomans, 1995), but this varies with temperature and host species. Parasitizing *Zaniothrips ricini* and *Retithrips syriacus*, Daniel (1986) recorded a maximum of 46±2.6 eggs per day. Total fecundity (and net reproduction R_o) is also significantly affected by temperature, and variable per host-parasitoid combination (*C. menes - F.intonsa*: Murai *&* Loomans, 1995; *C. maculatus - R. cruentatus* : Rahman *&* Bhardway, 1937; *C. russelli - C. fasciatus*: Russell, 1912b). *Goetheana shakespearei* can produce 24.2 (Bartlett, 1939), 25.5 (Dohanian, 1937) or up to 70 offspring per female (Adamson, 1936) parasitizing *Selenothrips rubrocinctus*. Progeny yield per female was highly variable in *Heliothrips haemorrhoidalis,* with 40 to 60 offspring recorded by McMurtry *&* Johnson (1963), but in the laboratory, reproduction was lower: 25.3 offspring per female for 3 days on avocado leaves, but only 10.1 (7 to 13 at 22.2^{0}C) and 3.43, 1.4 to 5.7 at 29.4^{0}C) on Valencia oranges, suggesting a host plant effect (Hessein *&*

McMurtry, 1989). In India, when parasitizing *Caliothrips indicus* in the laboratory, a single female of *G. shakespearei* laid an average of 78 ± 3.1 eggs per day, with a range of 53 to 105 parasitised offspring per day on *Arachis hypogea* (Daniel, 1986).

Adult longevity is relatively short: females live for 3 to 10 (*C. russelli*) and to 10 to 20 (*C. menes*) days at 20 to 25^{0}C (Murai, 1990; Murai *&* Loomans, 1995). In *G. shakespearei* it was only 3 to 5 days (Daniel, 1986; Hessein *&* McMurtry, 1989). Total lifespan of *T. gentilei* was 2 to 3 days in the laboratory (Ananthakrishnan *&* Swaminathan, 1977) and up to 10 days in field cages (Melis, 1935), which is much shorter than most of its hosts. Longevity of females increases when fed with sugar or honey solution (Dohanian, 1937; Sakimura, 1937a; Antsiferova *&* Timraleev, 1974; Hessein *&* McMurtry, 1989), but it is considerably reduced at high temperatures.

Parasitoid species reproduce parthenogenetically, and are thelytokous (*C. lepidotus, C. vinctus, C. americensis, C. russelli; T. semiluteus*), arrhenotokous (*C. maculatus, C. pacuvius, C. loomansi, C. nigrifemora, C. planitianus; T. hirticornis; G. shakespearei, G. incerta*) or both (*C. menes, T. gentilei*). In other species the type of reproduction is unknown (*C. margiscutum, C. femoratus*: both described from a few females). *Ceranisus menes* collected and cultured in Europe, North and South America and the Near East (Chapter 2) only produce females. In several Asian countries (Ishii, 1933; Saxena, 1971; Tachikawa, 1986) and Australia (collection BMNH), sexual populations predominate in field collected material, but non-sexual populations are present as well. In culture, females mostly dominate (sex ratio 3:2, Japan: Sakimura, 1937a; India: Daniel, 1986; Indonesia: van Heurn, 1923), or ratios are equal, 1:1, India: Carl, 1971; Thailand: Hirose, 1989; Japan: Murai, 1990), but in occasional laboratory records males predominate, 1:2, Thailand: Castineiras *et al.*, 1996). Murai *&* Loomans (1995) noticed a gradual change in sex ratio in the laboratory to thelytokous parthenogenesis. In *T. gentilei*, males only occur in Europe and India, the sex-ratio is nearly 1:1. Sex ratio's for *G. shakespearei* may vary from 2:1 (Daniel, 1986) to 6.5:1 (Hessein *&* McMurtry, 1989), but more females occurred at 30^{0}C (4.8:1) than at 22^{0}C (2.8:1). Temperature did not affect sex ratio (Castineiras *et al.*, 1996) in *C. menes*. Population growth parameters, the intrinsic rate of increase (r_m) and net reproduction rate (R_0), varied largely with temperature and host species (*C. menes:* Murai, 1990; Murai *&* Loomans, 1995). This mainly due to differences in adult longevity, and are usually lower than or equal to that of their hosts (Murai, 1990; van Rijn *et al.*, 1995).

Egg Parasitoids

Parasitoids attacking thrips eggs, except for *Polynema indica* (Mymaridae), all belong to the genus *Megaphragma* (Trichogrammatidae). Egg parasitoids have been recorded only from terebrantian hosts, i.c. species belonging to the family Thripidae, which lay their eggs *inside* the plant tissue. No parasitoids are known to parasitise eggs of terebrantian and tubuliferan species, which lay their eggs *on* the substrate. Keys to some of these are presented by Subba Rao (1969) and Lin (1992), but no key is available to all species.

Taxonomy

The genus *Megaphragma* is characterised by a small, flattened body size, linear long-fronged wings and an extremely large phragma. Since *Paramegaphragma* Lin was synonymised to *Megaphragma* (Delvare, 1993), 13 species are unified under this genus. Several other specimens have been collected in various parts of the world, but have only been described to the genus level. *Polynema indica* measures 0.94 mm (Daniel, 1986). *Megaphragma* species belong to the smallest of all insect parasitoids, most of the collected species measure 0.20-0.35 mm, *M. caribea* however measures only 0.17 mm (Delvare, 1993), and *M. mymaripenne* 0.17 to 0.20 mm (Dozier, 1932; Doutt *&* Viggiani, 1968). *Megaphragma priesneri* is the largest at 0.50 mm (Kryger, 1932). The size can partly be explained by the size of the eggs of the thrips host from which they have

developed, such as *Leucothrips* (Dozier, 1932) and *Retithrips* (about 0.30 mm: Rivnay, 1939). The circular exit holes, characteristic for the emergence of the parasitoids (avocado: Ebeling, 1959; McMurtry, 1961; eggplant: Hirose, 1989; tea: Takanashi *et al.*, 1996), are minute: 0.08 to 0.09 mm in diameter (Pemberton, 1931) and are found mostly on the underside of leaves. Because of their small size, the collection and research of this group has been greatly hampered.

Distribution

Megaphragma species are tropical and subtropical, distributed roughly between 45° N and 45° S. A *Megaphragma* sp. was first collected in 1920 in Hawaii by Pemberton (1931) and described as *Megaphragma mymaripenne* by Timberlake (1924). Later this species has been recorded from other parts of the nearctic (Dozier, 1932; Hessein *&* McMurtry, 1988), neotropics (DeSantis, 1965; Delvare, 1993), palaearctic (Viggiani & Bernardo, 1997) and the Afrotropical area (Polaszek, personal communication). Other species are only known from certain regios.

Host range and host plants

Megaphragma species have been collected in a wide range of habitats, from cultivated evergreen crops like tea (Kenya, Taiwan, Japan), coffee (Zaire), guava (Guadeloupe, Galapagos Islands), citrus, mulberry, tea (Japan) and avocado (California), from annuals like eggplant (Thailand) and cowpea (Benin), as well as from wild plants belonging to *Leguminosae* (Benin), *Liliacae* (India), *Myrtaceae* and *Caprifoliaceae* (Italy), infested with a wide range of host species. Others have been collected in yellow pans (Lin, 1992), malaise traps (Noyes & Valentine, 1989), sticky traps (Takagi, 1988), emergence cages (Tamò, 1991) or by sweeping vegetation (Yousuf & Shafee, 1987). *Polynema indica* has only been found in India (Narayanan *&* Subba Rao, 1961).

Hosts belong to the Panchaetothripinae as well as Thripinae. *Megaphragma mymaripenne* is reported on *Heliothrips haemorrhoidalis* in California, Hawaii, Guadeloupe and Chile, and on *Selenothrips rubrocinctus* in Guadeloupe, but also on thripine *Leucothrips* sp. (Dozier, 1932) and *M. sjostedti* (Tamò *et al.*, 1993). Other species are only reported on a single host species: *M. ghesquièrei* on *Panchaetothrips noxius* infesting coffee (Ghesquière, 1939) and *M. priesneri* was found within colonies of *Retithrips syriacus* on vine leaves (Kryger, 1932; Rivnay, 1939). In Japan, *Megaphragma* spp. developed from eggs of *Scirtothrips dorsalis* (Takanashi *et al.*, 1996) and *Pseudodendrothrips mori* (Takagi, 1988) and in Thailand, Hirose (1989) and Hirose *et al.* (1993) collected a *Megaphragma* sp. from aubergines infested with *T. palmi. Megaphragma longiciliatum* attacked the eggs of *Frankliniella lilivora* on *Polyantes tuberosa* in India (Subba Rao, 1969) and Narayanan (1971) reared a single individual from several eggs of *T. tabaci* exposed to it in the laboratory. *Poluynema indica* occurred in relative large quantities on groundnut (*Arachis hypogea*) as well as an annual weed (*Achyranthes aspera*) present in the crop field, both infested with *Caliothrips indicus* (Panchaetothripinae) (Daniel, 1986).

Host selection

When searching for hosts *M. mymaripenne* locate the softer parts of an egg blister with their antennae. During oviposition the female puts her weight on the hind legs and the wings, curving her abdomen forward and inserting her ovipositor into the side or sometimes middle of the egg blister. The same egg blister can be stung more than once. After ovipositing in several egg blisters, which can range from 30 to 120 min, with intervals of drinking and cleaning, the adult female walked or flew to another part of the leaf, where she resumed searching. Oviposition takes 0.5 to 7.5 min, but no parasitoids emerge when oviposition time is less than 2.5 min. Eggs that were completely covered with thrips faecal material are also stung, but this takes longer (Hessein *&* McMurtry, 1988). *Polynema*

indica locates the embedded hosts egg by probing the surface of thrips-infested plants. It moves around the host egg area for 30 to 45 s, assessing the suitability of the egg for oviposition, then inserts its ovipositor to lay a single egg into it. Once parasitised, the eggs were not attacked again (Daniel, 1986).

Differences in egg laying strategy by panchaetothripine and thripine host species may affect the searching efficiency of the parasitoid. Semiochemicals are likely involved in host searching by *M. mymaripenne*: excrements (sealing fluid, faeces) of the host *(Heliothrips)* seem to elicit probing and oviposition responses by the female, though egg blisters without faecal material are sometimes also stung (Hessein *&* McMurtry, 1988).

Life history

Most species are arrhenotokous. In *P. indica* and *M. longiciliatum* only the female is known*,* in *M. mymaripenne* (Hessein *&* McMurtry, 1988) and *Megaphragma* spp*.* (Takanashi *et al.*, 1996) parthenogenetic thelytoky occurred in the laboratory, males were very rare in the field. Developmental time from egg to adult at 22 to 23^{0}C and 10 to 42 per cent relative humidity, ranged from 36 to 46 days, with an average of 41.4 days for *M. mymaripenne* attacking *Heliothrips haemorrhoidalis. Heliothrips* has a shorter developmental time: under similar conditions it ranged from 24 to 58 days, average 31 days (Hessein *&* McMurtry, 1988). Total developmental time of a single adult that emerged from one of the eggs of *T. tabaci* exposed to *M. longiciliatum* was 20 days (Narayanan, 1971) and Takanashi *et al.* (1996) found a similar period for *Scirtothrips doralis*. Longevity of adult parasitoids ranges between 1 and 2 days, their egg laying capacity is unknown. Adult *H. haemorrhoidalis* live 40.6 days on average, ranging from 24 to 36 days, laying 1 to 2 eggs per day, or an average of 38.3 per female (Hessein *&* McMurtry, 1988), producing 5 to 6 generations in a year in California (Ebeling, 1959).

The life cycle of *P. indica* is similar to that of its host, *Caliothrips indicus* (Ananthakrishnan, 1984): within 12 to 15 days a single adult emerged from each parasitised host by making a hole in the egg blister; the sex-ratio was constant 3f:2m; 18 ± 3.2 adults emerged from the egg mass of single *C. indicus*, 12 to 17 per cent of which was parasitised on the weed and 9 per cent on the crop itself (Daniel, 1986).

Field incidences and natural control

Rates of parasitism found in the field sometimes exceed 50 per cent (*G. shakespearei*: Cotterell, 1927; Daniel, 1986; Takagi, 1988; ; *M. mymaripenne*: Hessein *&* McMurtry, 1988; *C. menes*: Bühl, 1937; Sakimura 1937b; Hirose, 1989; *C. pacuvius*: Kütter, 1936; unknown parasitoid: Hukkinen, 1936), but this is in itself not always a good indicator of parasitoid impact (Van Driesche, 1983) and natural control.

In multivoltine hosts, *C. menes* shows a gradual seasonal increase in numbers (Sakimura, 1937b; Hirose *et al.*, 1992, 1993), reaching a maximum following a peak of pest outbreaks. In onion, the rate of parasitism went up to 80 per cent in summer, and almost 100 per cent at some sites in autumn (Sakimura, 1937b). Parasitoid occurrence was well synchronised with the *T. tabaci* population, but only during the latter half of the season they were kept in check. Sakimura's sampling data shows a clear positive density-dependent relationship, but the percentage parasitism was not specified per age-classes sampled and it is not clear if this increase in parasitism with host density was due to an numerical response (aggregative or reproductive) or to a functional response (Lewis, 1973). In Taiwan, *Ceranisus* sp. attacking *R. cruentatus* in wax apple fields (Chiu, 1984) showed a clear negative density-dependent relationship and although parasitism was as high as 52 per cent during summer, it was not able to control thrips population outbreaks.

Parasitism by *C. menes* of *Thrips palmi* larvae, infesting leaves of aubergines in home and commercial gardens in Japan and Thailand, was very localised and ranged from 0 to 75 per cent (Hirose *et al.*, 1992) and 0 to 60 per cent, respectively (Hirose *et al.*, 1993). A high percentage (40 to 60 per cent) parasitism was frequently observed in unsprayed,

small-scale home gardens, while the level was significantly lower in pesticide-treated gardens (Hirose, 1990). On *Ricinus communis* in India, *C. menes* preferred *Zaniothrips ricini* (48 per cent) and *Craspedothrips minor* (50 per cent) over the simultaneously occurring *Retithrips syriacus* (20 per cent). When the first species were absent, it switched over to *R. syriacus* and sustained itself but did not increase (Daniel *et al.*, 1983, 1986; Daniel, 1986). Parasitism levels of *Caliothrips fasciatus* by *C. russelli* ranged as high as 70 per cent in southern California (Russell, 1912b), but only 5 per cent parasitism was found in central California years later (Bailey, 1933, 1937). In field collections of *Thrips tabaci,* parasitisation ranged from 15 to 60 per cent, with an average of 33.5 per cent (Russell, 1912). Parasitism rates of *T. tabaci* quoted for *C. menes* from other regions were low (Indonesia: van Heurn, 1923; Franssen *&* van Heurn, 1932; Japan: Sakimura, 1937b; Europe: Carl, 1971) and varied between 0 and 10 per cent (India: Narayanan, 1971) and 12 to 18 per cent (India: Saxena, 1971, 1981). *C. menes* is common on flowers of various wild plants, with parasitism levels up to 8 to 25 per cent. In cultivated crops it has been found only occasionally in low numbers (Europe: Carl, 1971; Loomans, 1991; Galazzi *et al.*, 1992) or is absent (California: Heinz *et al.*, 1996).

In univoltine hosts, like *Kakothrips pisivorus* (on pea, *C. pacuvius*: Kutter, 1936; *C. menes:* Bühl, 1937) and *Chirothrips hamatus* (on *Alopecurus,* species unknown: Hukkinen, 1936), parasitoid occurrence is well synchronised with the host population, in others like *Taeniothrips inconsequens* (unknown: Carl *et al.*, 1989) this needs to be ascertained. Rates of parasitism varied with locality (*C. pacuvius*: 0 to 68 per cent and even 92 per cent (Kutter, 1936, 1937); unknown: 0 to 58.2 per cent (Hukkinen, 1936). The number of parasitoids found was related to the infestation level by *K. pisivorus* the year before (Kutter, 1937), and fluctuated over the years, but the impact on the thrips population is not clear. In Russia up to 17 per cent of the *Kakothrips* larvae were parasitised by *C. menes* (Antsiferova *&* Timraleev, 1974), in others higher numbers were found (Vuillet, 1914; Bühl, 1937: 35.1 per cent). Although parasitoids were present in pea fields during one month and reached 40 per cent parasitism at its peak, *C. menes* did not contribute significantly to thrips control. Sampling home gardens in Northern Germany and Switzerland, Teulon *et al.* (1996) found no signs of parasitism.

Natural incidence of *G. shakespearei* is largely affected by climate, numbers being very low in spring and summer (Bennett, 1970), reaching a peak in the dry season in Ghana (Entwistle, 1972) and Benin (Tamò, personal communication) but during wet weather in the Caribbean (Entwistle, 1972). In India, Daniel (1986) recorded parasitism rates up to 92 per cent during winter months by *G. shakespearei* in groundnut fields on the weed *Achyranthes aspera*, infested by *C. indicus*, resulting in a gradual decline of the thrips population in the latter. Compared to the weed the incidence on the crop was low, and mainly governed by host availability. On cacao infested by *Selenothrips rubrocinctus* in Ghana (Cotterell, 1927), up to 70 to 80 per cent was parasitised, leading to its ultimate control. In Benin (Tamò, personal communication) *G. shakespearei* controls *S. rubrocinctus* infestations on mango and keeps populations of *Hercinothrips femoralis* in check on bougainvillaea and passionfruit. Attacking *Pseudodendrothrips mori* on mulberry trees in Japan, Takagi (1988) registered parasitisation levels up to 59 per cent in one orchard, but only 19.5 per cent in another.

In the field, *Megaphragma* spp. are sometimes abundant. Parasitisation reached 51 per cent in avocado orchards in California (McMurtry, 1961), and 20 to 53 per cent on wild *Leguminosae* in south Benin (Tamò *et al.*, 1993). However, the parasitisation level is highly variable, varying between and within localities (Hessein *&* McMurtry, 1988; Tamò, 1991), with season (Hessein *&* McMurtry, 1988; Takagi, 1988; Takanashi *et al.*, 1996), with the host plant (Tamò, 1991; Tamò *et al.*, 1993), cultural practices (Takanashi *et al.*, 1996) and the application of chemicals (Takagi, 1988). In spite of the sometimes high parasitisation levels, Hessein *&* McMurtry (1988) and Tamò (1991) consider it doubtful that *Megaphragma*, by itself, regulates thrips pests. Its relative short longevity of about 2

days and the long developmental time compared to that of its host might limit its ability to suppress increasing pest populations. The incidence of *P. indica* was only seasonal; although the host was present on the weed almost all year, parasitisation was only moderate in winter. The presence of *P. indica* coincided with that of *G. shakespearei*, attacking the larvae of *Caliothrips indicus*. Both populations followed a similar trend. However, the impact of *G. shakespearei* was considered much larger (92 per cent) than that of the egg parasitoid (Daniel, 1986). Recent results on the control of Megalurothrips in cowpea in fact are the only example of a classical thrips biocontrol programme, were introduction of a parasitoid, *Ceranisus femoratus*, was successful (Neuenschwander & Markham, 2001).

Thripastichus gentilei was the most important natural control agent of *Liothrips oleae* in the Mediterranean (Del Guercio, 1911, 1931; Melis, 1935). In Italy, it has five generations a year, whereas the host has three. At the end of the season, it parasitised 60 to 70 per cent (Del Guercio, 1931), 75 per cent (Melis, 1935) or 90 per cent of the larvae (Del Guercio, 1911), controlling the thrips population almost completely (Paoli, 1931). Nowadays this species is not considered as a pest anymore and *T. gentilei* is rare. Sharma *et al.* (1965) regarded *T. gentilei* as an important natural control agent of *Mallothrips indicus* in the area of New Delhi, parasitizing up to 73.6 per cent. In Trinidad, levels of 40 per cent have been found on *Liothrips mikaniae*, control agent of the strangler vine, *Mikania micrantha*, but it was rare on *L. urichi* infesting *Clidemia hirta* (Simmonds, 1933). On *Gynaikothrips ficorum*, 75 per cent parasitisation was found (Bournier, 1967) in a greenhouse in France. It was introduced from Brasil into Bermuda as a potential biological control agent of *G. ficorum* on *Ficus* spp., but it failed to establish (Bennett, 1965). On *Ficus nitida* in Egypt, *Pediobius* sp. was present most of the year, except when temperatures were above 29^0C and relative humidity below 45 per cent, and reached its peak in winter at 14.0^0C and 78 per cent relative humidity, three months after its host, *G. ficorum* (Tawfik, 1967). In Israel (Rivnay, 1947), an obvious fall in the number of thrips in autumn coincided with an increase in numbers of the parasitoid.

Biological control of thrips pests by insect parasitoids

Generally, four types of biological control are distinguished where macrobials are considered (van Lenteren, 1990), recently adapted by Eilenberg *et al.* (2001;):

1. *Classical biological control:* a single or a limited number of intentional introductions of an exotic, usually co-evolved, biological control agent for permanent establishment and long-term pest control; mostly applied for open areas, forests and orchards.
2. *Inoculation biological control*: every growing season natural enemies are released intentionally one or more times and whose progeny keep the pest population at low densities during the season, but not permanently. developed and applied successfully during the past 30 years in greenhouse cultivated crops, in particular vegetables.
3. *Inundation biological control*: natural enemies are released multiple times in large numbers, like a bio-insecticide. Immediate control is aimed at, not a long-lasting interaction with the pest insect. This method is mostly used in open field crops for the control of univoltine pests used, or in greenhouse cultivated crops when damage threshold levels are extremely low (for instance cut flowers). During recent years, however, this method has become a common strategy in greenhouse grown vegetables as well.
4. *Conservation biological control*: modification of the environment or existing practices to protect and enhance specific natural enemies or other organisms to reduce the effect of pests. This strategy has become a spearhead of recent outdoor biological control research programmes: how we can use biodiversity as a source of natural enemies, either native or permanently established, and tailor them to specific agricultural needs. Although natural enemies regularly invade greenhouse crops in

summer, greenhouse biocontrol of thrips pests in a temperate climate cannot rely solely on this method.

In the past, biological control of thrips pests in open field crops and in plantations, has been accomplished according to the classical method. In these biological control programmes, the selection and release of biological control agents has often been driven empirically (by “trial and error” experiments), because the attributes that govern their efficiency were often poorly understood. Parasitoids were released in an inoculative way, restoring old and establishing new combinations (Carl, 1982) of pest and parasitoid species, 1930s, *T. tabaci* in Hawaii; 1930s, *S. rubrocinctus*, *T. tabaci* in the Caribbean; 1970s *T. tabaci* in Europe; 1960s and 1980s, *H. haemorrhoidalis* in California), without great success. Efforts (Sakimura, 1932) to introduce *C. russelli* into Hawaii from California for the control of *T. tabaci* proved unsuccessful (Bailey, 1937) and later attempts with *C. vinctus* also failed (Clausen, 1978). *Ceranisus menes,* introduced from Japan (Sakimura, 1937c), established itself and was subsequently occasionally recovered (Swezey, 1936, 1937, 1950; Yoshimoto, 1965; Hirose, 1990), but no accounts have been published regarding increase and spread, or on its influence in reducing populations of *T. tabaci* (Clausen, 1978). Its effect on *Thrips palmi* and *Frankliniella occidentalis*, which have recently been introduced into Hawaii, is probably low. Attempts to introduce *C. menes* from India into Barbados (Narayanan, 1971; Alam, 1974) for the control of *T. tabaci* failed due to shipping problems and introductions (from Thailand and Japan) into Florida to control *T. palmi* (Castineiras *et al.*, 1996), were also unsuccessful.

Several attempts have also been made to control thrips pests with *G. shakespearei* in a classical way. Shipments were sent from Ghana to Trinidad (Adamson, 1936) and from there to various islands in the Caribbean for the control of *Seleonothrips rubrocinctus,* Puerto Rico (Dohanian, 1937), Jamaica, Bermuda and Granada (Callan, 1943) and into continental USA, Canada and Hawaii (Callan, 1943; McMurtry *&* Johnson, 1963; Bennett *et al.*, 1993) for the control of various species of thrips. In a semi-open greenhouse in Trinidad nearly 100 per cent was parasitised, controlling *Selenothrips* populations, but counts in very restricted areas of a few cacao trees gave parasitism rates of only 20 to 30 per cent (Callan, 1943). It successfully established in Trinidad, Jamaica (Cock, 1985) and Puerto Rico (Clausen, 1978), but it did not become established elsewhere, either in the field (Caribbean: Bennett, 1970; California: McMurtry *et al.*, 1991) or in a greenhouse (Florida: Bennett *et al.*, 1993). Although not deliberately introduced, it was reported recently from Guadeloupe and Florida (Bennett *et al.*, 1993). Where it has established, the incidence usually is very low (Cock, 1985) or highly seasonal, such as during high infestations of *S. rubrocinctus* on mango, cashew and tropical almond (Bennett, 1970; Bennett *&* Alam, 1974). No regulatory effects were found on thrips populations (Callan, 1943; Bennett *et al.*, 1993) and economically it is of little importance. Two examples of insect parasitoids that have been successfully applied for thrips control are *Thripobius semiluteus* for greenhouse thrips control in New Zealand and California (Froud *et al.*, 1996; McMurtry *et al.*, 1991) and the introduction of *Ceranisus femoratus* into West Africa for control of the cowpea thrips (Neuenschwander & Markham, 2001)

For other thrips pests that occur in greenhouses, classical biological control has never been considered a serious option: for example *F. occidentalis*, seasonally important in outdoor crops in the Mediterranean and Central Europe, is mainly a key pest in greenhouses. Application by seasonal inoculative or inundative releases, or by conservation, are considered more useful strategies for control. Attempts to release thrips parasitoids to control thrips pests by seasonal inoculation or inundation in temperate greenhouse ecosystems, a common strategy with predators, have been very rare.

Evaluation of natural enemies

With the increase in fundamental knowledge of a species attributes, successes and failures of biological control programmes can be better understood. Pre-introduction

evaluation criteria and methods have been developed for selecting the “ideal” biological control agent (van Lenteren, 1986; Hokkanen, 1989; Mackauer *et al.*, 1990) within the specific type of control programmes: for classical biological control programmes (Hokkanen & Pimentel, 1984; Waage, 1990; Waage & Mills, 1992), for introduced or native pests (Pimentel, 1963; Carl, 1982) or for conservation of native natural enemies (Luck, 1992; Luck *et al.*, 1988). Although applicable for a number of thrips-parasitoid combinations and thrips pest situations, these programmes will not be elaborated here further. Developing primarily a biological control method in greenhouse systems, the procedure is followed as described below, which is based on its proven value in the past either for seasonal inoculative (van Roermund, 1995) or inundative (Pak & van Lenteren, 1988) biological control. For a qualitative selection of candidate thrips parasitoids for application in greenhouse systems, criteria and characteristics have been formulated by e.g. van Lenteren (1986), van Lenteren & Woets (1988), Minkenberg (1990) and van Roermund (1995):

1. Seasonal synchronisation with the host;
2. Internal synchronisation with the host (development on the host);
3. Climatic adaptation (develop, reproduce and disperse under greenhouse conditions);
4. No negative effects (no attack of beneficial organisms);
5. Good culture method (ability to mass-produce);
6. Host specificity (host range including the pest organism);
7. Great reproductive potential (population growth rate to cause substantial mortality);
8. Good density responsiveness.

These pre-release selection criteria are primarily used to sort out hyperparasitoids and those natural enemies that have little or no potential for biological control. Quantitative pre-release selection criteria, such as host kill rate, a great reproductive potential and host searching capacity (a good density responsiveness), can be used in addition to qualitative criteria to rank and predict the potential of different natural enemies and their efficiency in an applied situation (see e.g. van Roermund, 1995 and Drost *et al.*, 1998 for developing evaluation criteria for parasitoids of whitefly pests). Second best natural enemies, i.c. natural enemies that cannot do the job by themselves, and that need some additional help, can be perfect biocontrol agents though. A low innate dispersal ability, for instance, can be compensated to some extent by the number of parasitoids to be released, by timing the place and number of these releases in a crop and / or supplying additional prey or alternative hosts (bankerplant system, pollen supply). A prerequisite for this kind of application is that natural enemies can be mass-reared easily at low costs. In recent years evaluation of nontarget effects of exotic natural enemies introduced for the biological control of pests has become an additional selection criterion. Post release studies are necessary for evaluating any nontarget effects in the area of release.

OUTLINE OF THIS THESIS

At the start of the present research project, no adequate method for biological control of thrips was available. Earlier research largely focussed on the mass-release of predatory mites of thrips, but that had not yet resulted in a satisfactory control solution. Studies with predatory bugs (anthocorids) were still in an experimental phase. In addition, chemical control of thrips proved to be difficult in a number of crops, either because certain chemicals are not allowed in food crops, or because thrips has become resistant to the chemicals. As indicated above, little or no experiments had been done on the potential of thrips parasitoids for the control of *F. occidentalis*. The general situation with regard to control of thrips pests at the start of the project created the need to collect, evaluate, and field test natural enemies for the biological control of these noxious organisms. My research was part of a collaborative programme, financially supported by the EC Commission's Second Framework Programme for research, the so-called CAMAR programme: Competitiveness of Agriculture and Management of Agricultural Resources, a research and technological development programme covering competitiveness of

agriculture, and management of agricultural resources. Our partners in the project in Italy (Istituto di Entomologia 'Guido Grandi', Università degli Studi di Bologna, Bologna) and Spain (Institut de Recerca I Tecnologia Agroalimentàries, Centre de Cabrils, Entomologia Aplicada, Cabrils) focussed on predacious bugs, c.q. the natural occurrence of anthocorids and mirids and the mass-production and experimental releases of anthocorids, respectively, whereas I concentrated myself on thrips parasitoids.

At the start of the project, most information on thrips parasitoids was known from other thrips species. Little was known about the direct relationship with *F. occidentalis*. Based on the general information presented above, potential useful parasitoid species were selected and areas of distribution chosen that could be explored. A sampling programme was started for the collection of parasitoids attacking thrips, based on their general occurrence, potential negative effects and association in the field with the target pest, *F. occidentalis*, or closely related thrips hosts.(Chapter 2). As result of that, various strains of two parasitoid species were collected from various parts in the world: *Ceranisus menes* (Walker) and *Ceranisus americensis* (Girault). In the next chapter (Chapter 3) a method is described and evaluated for rearing thrips and parasitoids and bioassay techniques presented, necessary for further evaluation experiments.

Because selection of a "best" parasitoid is the most critical phase in any biological control programme, a better understanding of some fundamental interactions - such as detailed observation of the host specificity, host searching capacity and population growth parameters relative to that of the pest host - was considered necessary. In a seasonal inoculative procedure, a "best" parasitoid should have a high host-location capacity: it should be able to locate and parasitise the suitable host stage at very low densities and be host specific. Various aspects of the host selection process, including the biology of the host and the parasitoid, and whether foraging and host location is mediated by signals (colour, oudour, shape, size) from the host or host plant complex or not are presented in Chapters 4, 5, 6 and 7. I respectively describe and quantify the results on the parasitoid's host specificity, developmental characteristics and the effect and importance of genetic diversity in the thrips host as well as in that of the parasitoid (Chapter 5), their host age preference and the role of host defense attributes (Chapter 4).

Another characteristic we considered important is the innate capacity to build up a *population* and how this compares to that of the pest host, indicated as the intrinsic rate of increase (r_m). This includes development time, age-related mortality of the parasitised host, longevity of ovipositing females, age-related reproductive potential and additional host kill rate through host feeding. In Chapter 6 the life-history parameters of the thrips hosts, *F. occidentalis* and other thrips species, are described and analysed, as well as the relative population growth parameters by means of life table studies performed on two colour types of *C. menes* and *C. americensis* with respect to *F. occidentalis*.

In Chapter 7, I quantify some of aspects of the searching behaviour involved in a short-range host location by the two parasitoid species, specifically the role of colour and chemicals, and the effect of thrips damage and feeding on the time allocation of the parasitoids. Host-location capacity or the innate dispersal capacity of a parasitoid, however, is an important but not the single criterion for a successful application of a parasitoid in a biocontrol programme. *Encarsia formosa*, for instance, is an example of a parasitoid that is applied very successfully in the biological control of the greenhouse whitefly in greenhouses, but it searches randomly (Van Lenteren, 1976; Van Roermund, 1995). The final evaluation and testing of the control capacity of the parasitoid species and strains, selected during the previous steps, in experimental and commercial greenhouses, is described in Chapter 8. In specific releases in experimental flower crops (rose) and in commercial vegetable crops (cucumber, sweet pepper) and bedding plants (various plant species) are highlighted. Finally, I conclude this study with a summarising discussion (Chapter 9). In this chapter I also indicate the pro's and con's and the

prospects of the use of thrips parasitoids for the control of thrips pests in temperate greenhouses in general and *F. occidentalis* in specific.

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Chapter 2

Exploration for hymenopterous parasitoids of thrips

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Abstract
As part of a project to evaluate parasitoid species as biological control agents against western flower thrips, *Frankliniella occidentalis* (Pergande), a survey was made in its native (United States) and newly invaded areas of distribution (Europe). In addition, parasitoids were collected form closely related *Frankliniella* and *Thrips* species, either by active search or by correspondence. Two parasitoid species, the eulophids *Ceranisus menes* (Walker) and *Ceranisus americensis* (Girault) were collected as female adults and parasitised hosts from wild vegetation and cultured crops, infested with *F. occidentalis* and related species at several locations in Europe and elsewhere. They were subsequently processed, shipped and reared in the laboratory, together with their thrips hosts. Methods for collecting, processing and shipment of both thrips and parasitoids are described and preliminary rearing results are presented.

Introduction
Since its first introduction in 1983, western flower thrips, *Frankliniella occidentalis* (Pergande), has rapidly spread throughout Europe and currently is a key pest in many greenhouse crops. Its great economical impact, because of direct damage to flowers and fruits, made fast actions necessary. These first concentrated themselves on chemical applications, but because these severely hampered IPM programmes already in use, major efforts were put into improvement and development of biological control methods. Research has largely focussed on predators and, more recently, on pathogens. Although this has resulted in a satisfactory solution for some crops, thrips pests cannot be controlled in a number of other crops. No previous attempts have been made using hymenopterous parasitoids as biological control agents of *F. occidentalis*. A literature review showed that, at the start of the project, no parasitoids were known to attack and develop on *F. occidentalis* specifically. Only one, *Ceranisus americensis* (Girault), had previously been found in association with *F. occidentalis* infesting alfalfa in Alberta-Canada in 1922 (Seamans, 1923). No proof was available of its ability to attack and develop on western flower thrips and it had never been reported since. On the other hand, a number of parasitoid species had been recorded from closely related thrips pest species within the genera *Frankliniella* (e.g. *Frankliniella intonsa* Trybom, *Frankliniella schultzei* Trybom) and *Thrips* (*Thrips tabaci* Lindeman, *Thrips palmi* Karny) all belonging to the same subfamily (Thripidae: Thripinae) (Loomans & van Lenteren, 1990, 1995; Chapter 1). Literature reviews also showed that thrips parasitoids are specific to species within the same (sub)family of Thysanoptera and that no negative side-effects, such as parasitising beneficials (like predatory thrips) or hyperparasitism, had been found. Based on host records and geographic distribution records, my interest was at first directed at species belonging to the genus *Ceranisus* (Walker) (Hymenoptera: Eulophidae), solitary larval parasitoids of thrips species that are closely related to *F. occidentalis.* In this paper , I present the result of my exploration for parasitoids of *F. occidentalis* and describe and discuss methods for their collection, processing and shipment.

Exploration for parasitoids of Frankliniella occidentalis

Selection of exploration areas

Research on parasitoids of *F. occidentalis* had to start almost from scratch. Since only few parasitoid species of thrips had been reared in the laboratory until 1990, sampling *Frankliniella* populations in the field would be an important means to collect potential candidates. Previous experience in selecting the best natural enemy for a particular pest, showed that all options should be open and combinations of exotic and indigenous pests and natural enemies are worthwhile trying (van Lenteren, 2000). Therefore I followed a threefold approach:

1. *Exploration in its native home (USA)*: A major part of the search was concentrated on sampling *F. occidentalis* populations in its original area of distribution (Southwest USA, Northwest Mexico). A central theory of classical biological control says that the best prospect for finding natural enemies of a particular pest will be found at the pest's evolutionary centre-of-origin (DeBach, 1964; Rosen & DeBach, 1992; Bellows & Legner, 1993). Many explorations for natural enemies (Van Driesche & Bellows, 1996; González *et al.*, 1993, 1994) have followed this approach with great success. West of the Rocky Mountains, i.c. California, Arizona and Mexico, *F. occidentalis* is infesting outdoor agro-ecosystems (field crops and orchards: Bryan & Smith, 1956; Pearsall & Myers, 2000) as well as natural habitats (Bailey, 1938, 1957; Goeden & Ricker, 1968, 1974ab, 1976abc, 1986abc, 1987ab, 1989; Yudin *et al.*, 1986,1988; Pearsall & Myers, 2000) and this area has a high diversity of species in the genus *Frankliniella* (Sakimura & O' Neil, 1979; Mound & Marullo, 1996). In this way also climatic conditions of the regions of origin were matched with those of the "target" areas in Europe: greenhouses in the temperate and Mediterranean area and field crops in the Mediterranean area.

2. *Exploration in newly invaded areas (Europe)*: On the other hand, neo-classical biological control theory (Hokkanen & Pimentel, 1984, 1989), indicates that new combinations of a pest and a natural enemy (Carl, 1982) are likely to result in successful biological control results. Therefore, besides regular sampling of *Frankliniella* populations in The Netherlands, other newly invaded areas were explored as well. The Mediterranean area seemed the most appropriate region to search for thrip parasitoids, because:

- this region probably is most similar to the ecological conditions of glasshouses in northwest Europe and the original area of distribution of the western flower thrips, California; in this region *F. occidentalis* rapidly has become a major pest, in protected as well as outdoor crops (Spain 1986 – Lacasa, 1990; Portugal 1989 – Mateus & Mexía, 1995; France 1986 - Bournier & Bournier, 1987; Italy 1988 – Arzone *et al.*, 1989);
- most recent records on field observations of parasitoids attacking thrips originated from the Mediterranean Area (France: CAB, 1971; Dessart & Bournier 1971; Italy: Domenichini, personal communication, 1990; Greece: Gijswijt, personal communication, 1990. Twelve parasitoid species, attacking thrips species, have been described from Europe, five of them from this region. It was thought that the chance of finding parasitoids would be greatest at the end of the season, when *F. occidentalis* and crops were still present and there would have been a parasitoid population build-up during the summer.

3. *Exploration for related host species worldwide:* Besides that I also included populations of closely related *Frankliniella* and *Thrips* species, distributed world wide, preferably from areas with climatic conditions similar to European glasshouse conditions. Collection of this parasitoid material was done either through correspondence with colleague researchers or by active search in the field. Infested field crops and flowering wild vegetation were searched for adult parasitoids and sampled for thrips larvae.

Site selection within the collection areas

Frankliniella occidentalis is known for its very wide host range and hidden life-style: eggs are laid inside host plant tissue, larvae and adults are feeding on leaf and flower tissues and pollen. Adults and larvae are often found inside flowers ('western flower thrips'). Similar niche preferences are known for *F. schultzei* ('cotton bud thrips') and *F. intonsa* ('flower thrips'). There is a large amount of literature available on collecting and culturing

either thrips or parasitoids. Little or no information, however, was available on the combination of both groups. The review of literature provided important information on known parasitoids of thrips, the European thrips species and their host plants, and methods to collect, monitor and rear parasitoids (Loomans & van Lenteren, 1995; Chapter 1). Specialists working on thrips, parasitoids or both, taxonomists as well as researchers of biocontrol were requested for information on the occurrence and collection of parasitoids and thrips in the South of Europe and Western USA. Collection was performed by sampling *F. occidentalis* populations in its original area of distribution (USA) and newly invaded areas (South of Europe), and on closely related species like *T. tabaci*, distributed worldwide, preferably in areas with climatic conditions similar to Northwest European glasshouses. Collection of parasitoid material was done either through correspondence with colleague researchers or by active search. Infested field crops and flowering wild vegetation were searched for adult parasitoids and sampled for thrips larvae.

In selecting habitats, I directed my search to agro-ecosystems, infested with *F. occidentalis* which thrips parasitoids might invade, as well as natural ecosystems. During my collection trip in the South of Europe, in 1990, I concentrated my search to the major vegetable growing areas: Provence (France), Maresme, Valencia and Murcia region (Spain) and Emilia Romagna, Po Valley and Tuscany (Italy). In this latter region, I made additional collections in 1991. In these regions several crops, vegetables (tomato, cucumber, pepper, bean, lettuce and strawberry) as well as ornamentals (carnation, chrysanthemum and others), field crops as well as protected crops, were searched and sampled for thrips parasitoids. Special attention was paid to crops that were controlled biologically or grown organically, and thus not intensively treated with pesticides, as well as to abandoned crop-sites, field-edges and glasshouse surroundings. Crops searched were cucumber, sweet pepper, egg-plant, piment, strawberry and French bean (vegetables), gladiolus, carnation, chrysanthemum and rose (ornamentals), alfalfa, onion and leek. During travelling in between these areas wild vegetation, especially flowers, was searched in natural, undisturbed sites, including roadsides, sides of ditches, ruderal places, parking lots and pastures (grassland). In the USA (California, Arizona) and Mexico (Mexicali area), a more or less similar programme was followed, but there I largely focussed my search on natural ecosystems (roadsides, ruderal sites, desert shrubs) and agro-ecosystems (field crops, orchards, gardens). Colleagues working on biocontrol and familiar with the local occurrence of thrips infestations and language helped me out.

In the Netherlands, thrips infested field crops (pea, onion, leek, cabbage) and wild vegetation were sampled regularly from late spring till early fall from 1990 till 1996. Occasionally, protected crops were sampled as well. Areas, sites and habitats searched for thrips parasitoids in The Netherlands:

1. Natural vegetation along roadsides, field-edges, dikes and ditches: Ede-Utrecht (N224), Wageningen-Utrecht (N225), Ewijk-Hedel (N322), Ravenstein-Sevenum (N277), Lierop-Veghel (N266)-Ravenstein (N265), Arnhem-Zutphen (N48)-Borne (N346), Nijmegen-Arcen (N271), Deventer-Hoogeveen (N48), Goeree-Overflakkee, Westland, Berkel & Rodenrijs, Noord-Limburg, Betuwe (Waaldijk), Peelland (N270), Slagharen-Hardenberg, Veluwezoom, Zuid-Limburg;
2. Cultivated crops in greenhouses, open fields and gardens, or as undergrowth in orchards, meadows and pastures.

Collection: equipment & methods

For field collections of live thrips and parasitoids I used general devices and followed advises described earlier by Sakimura (1937), Lewis (1973), Bournier (1983) for Thysanoptera and Noyes (1982, 1989) and Steyskal *et al*. (1986) for Hymenoptera (see also Schauff, 1999) and general handbooks such as Huffaker & Messinger (1976) and DeBach (1964). Equipment included sweep-nets, beating trays (black and white), white blotting paper sheets (60 x 40 cm), various aspirators (constructed from a 60 cm piece of plastic tubing, a piece of gauze material (80 mesh) and disposable transparent pipette tip,

9.3 ∅mm, the outer edge of which fits tightly into the inner edge of an Eppendorf tube®, ∅ 9.34mm), various marten hair brushes (size 10 and 15, 00 and 000), large and small plastic vials, reaction tubes (Eppendorf®) and boxes to store these (Boehringer Mannheim 800058, 50 units each), food (honey, pollen, water, bean pods), field-rearing units (jars, plastic rings, Sealon-film: see below), preservation material (either alcohol 70% or AGA (ethanol: acetic acid: glycerol: water), syphons and various additional laboratory tools (various pairs of tweezers, droppers, preservation needles, scalpels, scissors, hand-lenses, min.-max. thermometer, pencils, etc.). While travelling I stored most of this equipment in a special easy-to-carry kit, originally designed for storing fisherman's tools (Albatros®). Methods for collection, processing, and small-scale rearing of both thrips and beneficials are described as well by Steiner *et al.* (1996) and Steiner & Goodwin (1996).

The method of collection varied with the situation and no special sampling plan was followed. I basically followed 3 methods of collection and trapping:

1. Sampling field crops, pastures and roadside vegetation, in general those stands consisting out of a single plant species by using a sweep-net (for collection of live and reference material), for instance alfalfa fields, clover undergrowth (USA, Mexico), *Polygonum* bushes (France, Italy). Plots were sampled by making at least 50 sweeps per plot; if no adult parasitoids or thrips larvae were found, the sampling was stopped. When thrips larvae were present, I sampled first and second larval instars. These larvae were transferred into aerated glass tubes (± 50 larvae/tube with additional food, usually a host plant flower or leaf) until further processing.
2. Sampling individual plants, by beating in particular the flowering heads or growing points, over a white, occasionally black tray or paper sheet (for collection of live and reference material); Sampling individual plants for thrips larvae by collecting thrips infested leaves; these were stored in a plastic or paper bag until processing, usually later on the same day (for the collection of live thrips larvae);
3. Monitoring seasonal occurrence of a parasitoid population (phenology) by using sticky traps.

The presence of thrips and parasitoids on the sampling site was verified by tapping flowers, beating vegetation above a white surface (tray or blotting paper). The majority of samples were preserved as a reference source for future collections. However, wherever possible, live beneficials were collected and reared in the laboratory for assessment as effective controlling agents for thrips.

Storage and processing

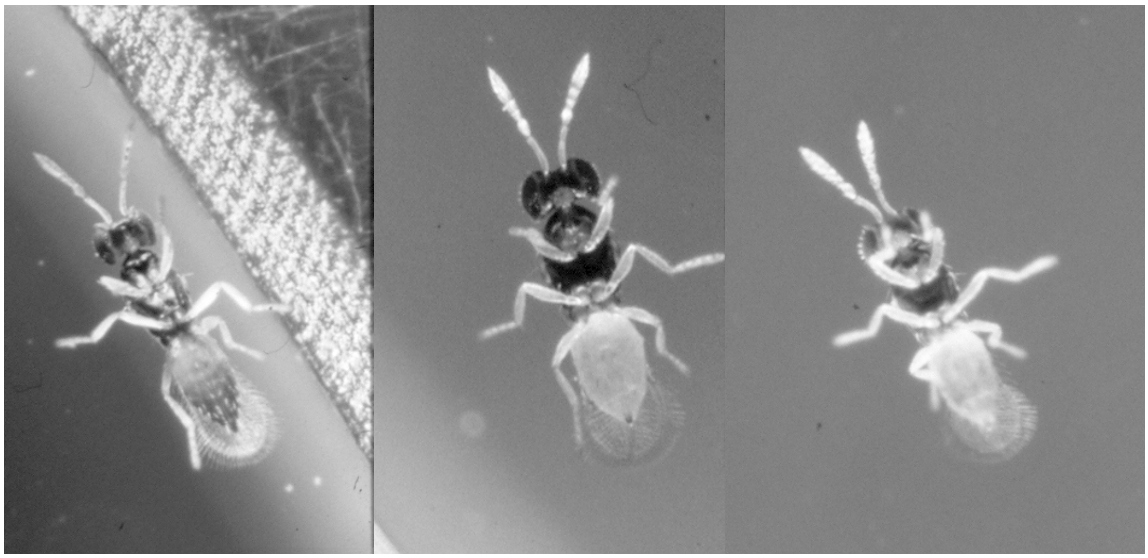
Parasitoids and thrips specimens were collected and processed on the spot, using an aspirator, putting live adult parasitoids and thrips in an Eppendorf tube with a droplet of honey and some reference thrips adults on alcohol in an Eppendorf tube. Occasionally, whole plants were individually put into a bag and taken into the laboratory for further processing of the material, separating parasitoids and thrips adults and larvae as mentioned above or putting them in an emergence box (ventilated, dark enclosure, with an Erlenmeyer or plastic vial on top or side. Adult parasitoids found were aspirated and put into vials supplied with honey and stored in cooling boxes. Live plant material was stored in bags respectively until processing. In warm and hot climate conditions, like prevailing in southern Europe and the United States, keeping the material cool is a prerequisite for preserving live material. A refrigerator, working on the battery of the car or a cooling box with cooling elements, could solve this problem during part of the day (about 12-15^{0}C). Later that day parasitoids were offered young thrips larvae, using the rearing methods described below. Rearing was done partly in the trunk of the car (20-35 °C), partly in laboratories and hotel rooms on the way. Samples of larvae collected were transferred into rearing tubes. No dissections of larvae were made. At every sampled spot, adult thrips were collected and put on alcohol 70 % or AGA for identification. Adult parasitoids were stored live at 15°C until usage and larvae were reared until pupation and subsequently shipped to Wageningen.

Travel-rearing units
While being on the road, I reared part of the collected adult parasitoids and thrips larvae on freshly hatched thrips larvae. The materials and methodology used basically followed that of the laboratory rearing set-ups described in Chapter3. I used both the artificial method on pollen and honey-water and the bean-pod method for rearing thrips (*F. occidentalis* while travelling in the USA and Europe; *F. intonsa* while travelling in the south of Europe). The pollen-water units were stored in closed plastic boxes, bean jars in open boxes, both as much shockproof as possible, in the back of the car, while travelling or in the hotel room. Some rearing units were placed in a climate room, office or laboratory at a base camp (Cavaillon-France, Riverside-California). Adult thrips cultures (oviposition units) could be maintained rather well, producing even-aged cohorts of larvae. Culturing the emerged and parasitised larvae to maturity, however, proved to be rather difficult, because of a lack of fresh food and light (back of the car), but largely because of condensation inside the jars and rings, due to (slight) changes in temperature.

Field-cultures
Field collected adult parasitoids readily attacked first stage larvae of *F. occidentalis* when brought into contact with them. While travelling, however, rearing was mostly unsuccessful, due to hot climate conditions. Therefore in almost all cases, adults collected during the trip were shipped to the Laboratory of Entomology for further processing (USA-material) and those collected at the end of the trip were stored at 12 ^{0}C and personally taken to my laboratory. Maintaining a thrips culture at a base station (Cavaillon, France; Riverside, USA) resulted in some additional offspring, but conditions and maintenance intervals were inappropriate. Artificial rearing of sampled larvae on pollen and honey-solution was more successful (table 3). However the system used (see Chapter 3) was quite vulnerable under travelling conditions and a number of rearing efforts failed because of that. Parasitoids and thrips both reared from a single batch of sampled larvae (table 3) can give an indication of the possible relationship between *C. menes* and the thrips species found.

Shipment
Thrips parasitoids were processed and shipped either as adult females (in a ventilated plastic vial, provided with a droplet of honey, as parasitised larvae in transparent vials with pollen and honey-water between stretched film (see below), or as parasitoid pupae. In the latter case, pupae were collected from the cultures, placed on moist filter-paper, covered with a second piece of moist filter-paper, folded and placed into a closed plastic tube (1cm∅, 10cm tall) or Petri dish. Live thrips were shipped either as eggs (in host plant tissue, mostly bean pods) or as larvae or adults. Prior to being shipped the moving and feeding phases of thrips were provided with a (piece of) bean pod, wrapped in tissue (to avoid or absorb condensation in case of strong temperature changes on the road and placed in a ventilated tube (single bean pod) or vial (multiple bean pods). Bean pods were cut at such a length that they were firmly fixed inside the vial or tube and could not move. All material was shipped by courier service on top of some ice bars, separated by layers of paper.

Results
The results of the explorations are presented in tables 1- 5. Only those sites are mentioned were parasitoids, as adults or larvae, were found. Individuals collected during field surveys in Europe were all females and all parasitoids belonged to a single species, *Ceranisus menes* (Walker) (Hymenoptera: Eulophidae). Females of different origins differed, however, in colouring of the abdomen, varying from yellow (to buff = brownish yellow) to brown with a pale base (see figure 2a, b, c). Asian specimens were of the yellow-shape type (figure 2b), its colour varying in intensity of black bars on the side of the abdomen from none (distinctively yellow: a few in Indian collections) to brown with a yellow base.



a) brown colour-type **b) yellow colour-type** **c) buff-type**

Figure 2. Pictures of a a) brown colour-type specimen (Hyères – France), b) yellow – type specimen (Brignoles – France) and c) buff colour-type specimen (Holambra – Brasil) of *Ceranisus menes* (Walker). Width : length ratio of abdomen for brown = 0.67; yellow = 0.50; buff = 0.55.

In the USA two additional species were collected: *Ceranisus americensis* (Girault) and a new species, described as *Ceranisus loomansi* Trjapitsyn.

The Netherlands

From 1990-1996, over 200 sites were sampled within various natural habitats (roadsides, sides of ditches and fields, hedgerows; broom bushes near forest edges), cultivated fields (commercial fields: leek, onion, rape, potato, cabbage, pea and fieldbean; private gardens: bean, pea, onion, leek and cabbage, mostly infested with *Thrips tabaci*; in total 43 plots) and greenhouses (sweet pepper, cucumber, ornamentals: in total 11 plots). On 54 occasions (~25%) thrips parasitoids (*C. menes*) were found. My search, however, was more qualitative than quantitative and not completely random or systematic. Searches were "success-motivated": after a number of failures (~5) in finding thrips parasitoids in some sites (e.g. forest edges, greenhouses) and on some plants species (e.g. Umbelliferae) these were less intensively checked again on later occasions.

On one occasion *C. menes* was found in a crop outdoors: on July 4th a single female of was found in a private pea plot at Venzelderheide, 500 m from the Dutch-German border. In the laboratory it readily attacked first stage larvae of both *F. occidentalis* and *F. intonsa*, but rearing was not successful. On only occasion females of *C. menes* were found inside a glasshouse, amongst a mixed population of *F. occidentalis* and *Frankliniella schultzei* (Trybom) inhabiting cactus flowers in Reeuwijk: They originated from Holambra, Brasil and were accidentally imported with a quarantine shipment of cactuses. From a sample of larvae, 107 (15 %) parasitoid pupae emerged (table 3). In an additonal sample, collected in Holambra itself, contained 2 specimens of the same colour-type, found in association with *F. schultzei.*

Table 1. Collections of thrips parasitoids (*Ceranisus menes* (Walker), (Hymenoptera: Eulophidae) at different localities and host plants in The Netherlands in association with thrips species (Thysanoptera) (positive sites only; 1990-93).

Plant species	month	habitat	location (#, colourtype)
Fabaceae (Papilonaceae)			
Pisum sativum	vii.90	c.garden	Venzelderheide (1b)
Trifolium repens	vii.92	orchard	Someren (1b)
Lathyrus sp.	vii.92	garden	Wageningen (2b)
Lotus corniculatus	viii.92	roadside	Scherpenzeel (1y)
Apiaceae (Umbelliferae)			
Pastinaca sativa	viii.92	roadside	Kesteren (24y;7y), Velddriel (12y, 2b), Dreumel (4y;3y),Wamel (1y),Andelst (2y)
	viii.92	dike slope	Heerewaarden (1y)
Angelica sylvestris	*v*ii.92	road-ditch	Wageningen (1b)
Heracleum sphondylium	vi.92	road-ditch	Kesteren (1y)
Asteraceae (Compositae)			
Achillea millefolium	vii.92	fieldedge	Stramproy (1b), Boekel (2b)
	vii.92	roadside	Asten (3b), Lierop (3b), St. Anthonis (2b) Uden (2b), Mook (1b)
Matricaria recutita	vi.93	fieldedge	Renkum (10b)
	vi.91	side ditch	Wageningen (10b)
	vi.91	fieldedge	Wageningen (9b; 4b), Reek (2b)
	vi.91	abandoned	Wageningen (1b)
Senecio jacobea	vi.92	roadside	Kesteren (2y), Rhenen (2y)
Senecio vulgaris	vi.92	abandoned	Kesteren (1y), Lienden (1y)
Rubiaceae			
Galium verum	vi.92	garden	Wageningen (1y)
Cruciferae			
Sinapis arvensis	*v*ii.92	roadside	Ravenstein (4y)
Brassica sp.	vii.93	roadside	Dreumel (52y), Ravenstein (4y)
	viii.92	disturbed	Veenendaal (3y), Ede (7y)
Rosaceae			
Filipendula ulmaria	vi.92	side pond	Wageningen (1y)
		side ditch	Wageningen (7y), Veenendaal (2y)
Caprifoliaceae			
Sambucus nigra	vi.90	field-edge	Aaldonk (1b)
Ericaeae			
Erica tetralix	vi.92	garden	Wageningen (3b)
Hypericaceae			
Hypericum perforatum	viii.92	roadside	Liempde (4b), Boxmeer (2y)
Polygonaceae			
Polygonum aubertii	viii.92	fence	Wageningen (1y), Wychen (2b),
	ix.92	fence	Raalte (3y)
Oleaceae			
Ligustrum ovalifolium	vi.93	bush	Wageningen (23buff*)
	vii.93	bush	Wageningen (6buff; 3buff)
	vii.93	hedge	Wageningen (3buff), Beek-Donk(11buff).
Cactaceae			
Various species	xi.91	glasshouse	Reeuwijk (11buff); Waddinxveen (3buff)

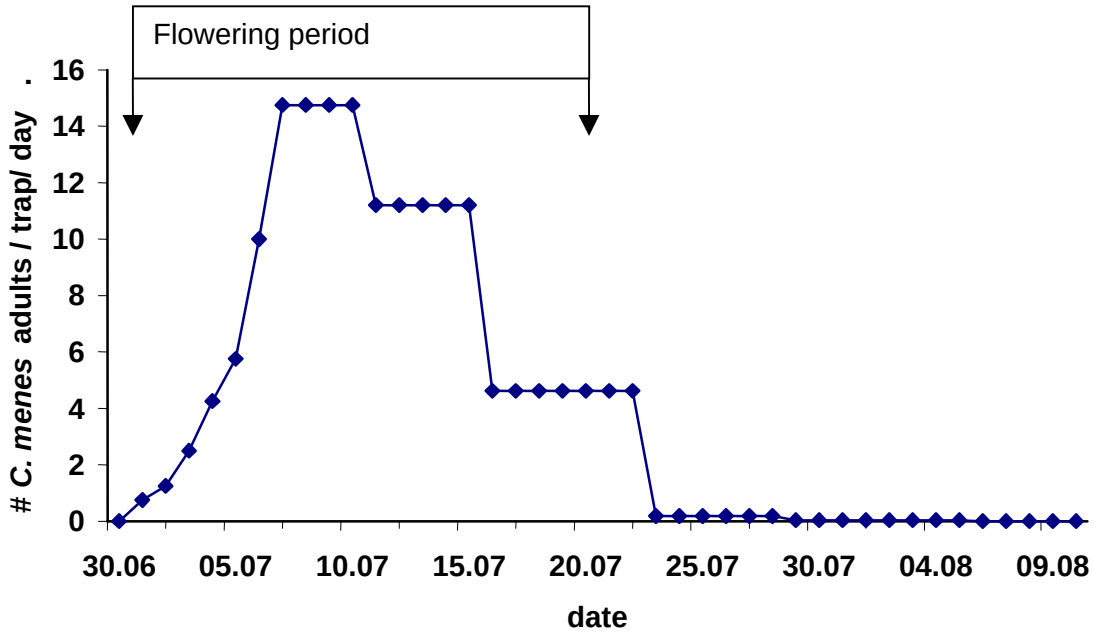


Figure 3. Monitoring the incidence of *Ceranisus menes* (Walker) adults on ligustrum, *Ligustrum ovalifolium* L., near the Laboratory of Entomology, Wageningen , The Netherlands during 1995; 4 yellow sticky traps (Horiver®) exposed for the entire bush (4 m high, 4m ∅).

Individuals of *C. menes* were found on flowering plants in general and were not limited to specific host plants. Nor was occurrence strictly correlated with the presence of thrips larvae. Two colour-types of *C. menes* were found in various habitats and host plants belonging to a wide range of families. Although some types were collected from certain host plant flower colours (brown: *Achillea*, *Matricaria*; yellow: *Pastinaca*), there does not seem a relation between colour of the host plant and the colour of the parasitoid. Regardless various samples taken from *Tanacetum vulgare* L., in roadsides and ditches, I never collected thrips parasitoids from these stands. Except for *Pastinaca sativum* L., I rarely did so either on other Apiaceae (Umbelliferae) which are very common, such as *Anthriscus sylvestris* (L.) Hoffm.; *Daucus carota* L., *Angelica sylvestris* L., *Heracleum sphondylium* L. and regardless the mostly large amounts of (adult) thrips foraging on their flower-heads and the presence of larvae. This is in sharp contrast to the relative abundant population that we found on a large bush of ligustrum (*Ligustrum ovalifolium* L.) in Wageningen. During a number of years, at the flowering period of this bush (figure 3), large numbers were caught, either on sticky traps or by hand during a 3-4 week period, its fluctuation largely coinciding with the presence of open flowers and of (adult) thrips. The number of thrips larvae, however, was relatively low and few were parasitised (table 3).

Samples containing *C. menes* were taken in association with adults and larvae of a single thrips species, either*Thrips tabaci* Lindeman, *Thrips major* Uzel, *Thrips vulgatissimus* Haliday, *Thrips fuscipennis* Haliday or *Frankliniella intonsa* (Trybom), or from a multiple species population. Larvae of *T. vulgatissimus* taken from *Rumex crispus* L. (yellow dock, Polygonaceae) collected at various sites (Deurne, Ravenstein, Renkum, St Anthonis, Wageningen) and of *T. tabaci* (Wageningen) from *Sambucus nigra* L. (common elder, Caprifoliaceae) were not parasitised in the field, but when exposed in the laboratory to *C. menes*, they were readily attacked and parasitised. No parasitoids emerged from larvae of *Limothrips denticornis* (Haliday) collected in wheat fields. Larvae (131 L1, 14 early L2), collected late May 1992, were taken into the laboratory. When exposed to female *C. menes*, they were rarely attacked, parasitisation was unsuccessful and no offspring was produced.

Table 2. Collections of thrips parasitoids (*Ceranisus menes* (Walker), (Hymenoptera: Eulophidae) at different localities and host plants in the Mediteranean Area in association with thrips species (Thysanoptera) present; n.i. = not identified (positive sites only; 1990-91).

Locality	hostplant	thrip species abdomen	date 1990/91	# parasitoid (colour)
Italy				
Pietra Ligure	*Centranthus ruber*	*Thrips brevicornis*	16.ix.90	16 b
Bologna (San Luca)	*Trifolium repens*	*Frankliniella pallida* *Frankliniella intonsa*	13.ix.90	1 b
	Hieracium sp.	*Frankliniella pallida* *Frankliniella intonsa* *Thrips hispanicus* *Thrips hukkineni* *F. occidentalis*	13.ix.90	1 b
	Dittrichia viscosa	n.i.	28.ix.91	51 y
	Solidago virgaurea	n.i.		7 b
Pietramora	-	-	02. x.91	1y, 2b
Pescia	*Dittrichia viscosa*	n.i.	25.ix.91	21y
Ponte diSerravalle	*Picris hieracioides*	n.i.	25.ix.91	1y, 1b
Borello-Ranchio	*Dittrichia viscosa*	n.i.	26.ix.91	5y, 5b
Piavola	*Polygonum aubertii*	n.i.	26.ix.91	1y
Cesena	*Polygonum aubertii*	n.i.	04. x.91	6y
Torreglia	*Leontodon* sp.	n.i.	27.ix.91	1y, 1b
France				
Beausoleil	*Centranthus ruber*	*Thrips tabaci* *Thrips brevicornis* *F. occidentalis* *Thrips (fuscipennis?)*	11.ix.90	7 b
Pernes les Font.	*Hieracium* sp.	*Thrips hukkineni* *Taeniothrips hispanicus* *F. occidentalis*	18.ix.90	4 b
Salon de Prov.	*Centranthus ruber*	*F. occidentalis* *Thrips tabaci*	29.ix.90	1 b
St. Maximin (Autoroute)	*Centranthus ruber*	*Thrips tabaci* *Thrips brevicornis*	29.ix.90	6 b
St. Maximin (Aire Barcelone)	*Centranthus ruber*	*Thrips brevicornis* *Thrips tabaci*	29.ix.90	4 y
Brignoles	*Medicago sativa*	*Thrips tabaci*	29.ix.90	2 b
Hyères [g]	*Rosa* spp.	*F. occidentalis*	17.ix.90	6 b
			28.ix.90	66 b
	Lantana camara	--	28.ix.90	1 b
Jonquières-Saint-Vincent	*Hieracium* sp.	*Thrips tabaci* *Taeniothrips pallidivestis* *Thrips hukkineni* *Taeniothrips hispanicus*	18.ix.90	2 b
Salses (Perpignan)	*Polygonum aubertii*	*Thrips major,* *Thrips tabaci*	18.ix.90	12 b, 8 y
		ibid.+ (Taeniothrips sp.)	27.ix.90	74 b, 78 y

g: collected inside glasshouses

Table 3. Number of parasitoids (*Ceranisus menes*) present in batches of thrips larvae collected from host plants at different localities, autumn 1990 - 1993. Thrips larvae were reared to maturity using an artificial method on pine pollen and honeysolution 10 %. Only batches containing parasitoids are listed.

Locality (year)	plant species	thrips number	species	parasitised # larvae	%	# adults emerged
Mediteranean (1990)						
Hyères (Fr) [g]	*Rosa* sp.	800	*F. occidentalis*	113	14 %	66
Perpignan (Fr)	*Polygonum aubertii*	40	*T. major* *T. tabaci*	10	25 %	1
St. Maximin (Fr)	*Centranthus ruber*	12	*T. tabaci* *T. brevicornis*	1	8 %	0
Bologna (Italy)	*Hieracium* sp.	90	*F. pallida* *F. intonsa*	14	15 %	6
Netherlands (1992)						
Wageningen	*Ligustrum ovalifolium*	45	*T. tabaci/T.major*	2	5 %	2
Beek en Donk	*Ligustrum ovalifolium*	87	*T. tabaci/T.major*	6	7 %	4
Renkum	*Matricaria recutita*	21	*T. tabaci*	1	5 %	1
Reeuwijk [g]	Cactaceae 1	425	*F. occidentalis* *F. schultzei*	107	15 %	83
Waddinxveen [g]	Cactaceae 2	46	*ibid.*	3	7 %	0

[g] collected inside glasshouses

Southern Europe

During late summer 1990, 125 plots (host plants, greenhouses) were sampled in 96 different sites in the Mediterranean Area. We sampled greenhouse crops (cucumber, melon, sweet pepper, pepper, aubergine, bean, tomato; chrysanthemum, gerbera, datura, rose), open field crops (leek, strawberry, tomato, aubergine, sweet pepper, pepper, bean, tomato; anjer, chrysanthemum, rose, aubergine, gladiolus) and various natural types of vegetation (road sides, abandoned sites: various flowering plants). In southern Europe greenhouse crops are grown in plastic houses. Most often these are not closed systems, but wide open at the sides, thus allowing a constant moving about of pests and natural enemies.

At several locations in the South of France adults of *C. menes* could be collected from flowers of wild vegetation, inhabited by various thrips species belonging to the genera *Frankliniella, Thrips* and *Taeniothrips* (Thripidae: Thripinae) (Table 2). In samples from 2 locations parasitised larvae were found (table 3). Collection of parasitoids of thrips was less successful in cultivated crops in France as well as Italy and Spain. On one occasion only adults of *C. menes* were collected inside a glasshouse, from a rose crop at Hyères (France), infested with *F. occidentalis.* In 93 flowers of different varieties, 66 adults were present and from an additional 800 larvae collected 113 were parasitised.

In northern Italy, it was difficult to locate thrips infested crops. No recoveries of thrips parasitoids were there made during September 1990. Collections made on several places in Northern and Central Italy in September 1991 (table 2) show, however, that *C. menes* is distributed regularly in these parts of Italy on ruderal locations. At one location, a natural reserve field near Collina San Luca (Bologna), recoveries of *C. menes* could be made (table 2 and 3) as adult ánd parasitised larvae during that year. In the same locality this parasitoid was collected before in August (Galazzi *et al.*, 1992) on natural vegetation (*Trifolium repens* L.*, Polygonum aubertii* L. Henry). In 1991, *C. menes* was collected again near Bologna and Cesena on wild plants (Galazzi *et al.*, 1992) and were shipped to Wageningen for further evaluation.

In Spain population densities of *F. occidentalis* were already at its decline during mid September 1990, after severe infestations earlier that year. In the South (Murcia and Valencia region), most of the greenhouse crops already had been harvested. *F. occidentalis* still was present but in low numbers, on crops (piment, sweet pepper) as well as wild vegetation. In spite of sampling several crops and wild vegetation no thrips parasitoids were found. *F. occidentalis* was more abundant in the north, but here also no parasitoids were found. In 1991, in Cabrils (Catalunya, Spain), colleagues sampled one hundred and thirty fields with vegetable (tomato, cucumber, pepper, bean, lettuce and strawberry) and ornamental (carnation and others) crops which were not intensively sprayed with pesticides along the Spanish Mediterranean coast. Parasitoids, identified as *C. menes*, were only found in carnation. After rearing it for one generation in the laboratory, the offspring was shipped to Wageningen. Collections made in the Mediterranean area of Europe, France and Italy (see Galazzi *et al.*, 1992) and later in Spain (Pays Vasco, Cantabria, Navarra: Goldarazena *et al.*, 1999), resulted in obtaining different colour-types of *C. menes*. In the Emilia Romagna region of Italy collections of wild plants resulted in the collection of *C. menes* too.

In addition, specimens of *C. menes* were collected in Portugal (Azores-San Miguel in 1995- collection: I. Silva; Santa Cruz-Torres Vedras in 1994) in Italy (Sicily in 1995), Belgium (Limburg in 1992), France (Les Landes in 1992; Picardia and Touraine in 1999), Hungary (in 1995) and Turkey (Antalya in 1997). Most of these were collected on roadside and ruderal vegetation, occasionally specimens were recovered from greenhouses in large amounts (on Sicily, November 1998 in a 4 week old tomato crop). All these specimens belonged to the brown colour-type, but in samples from Emilia Romagna and Hungary yellow types occurred as well. Only some of these are included in my evaluation experiments (see table 6).

Other natural enemies, although not actively searched for, such as different *Orius* species and mirid bugs, were observed on various occasions in crops and vegetation infested with thrips in Italy, France as well as Spain.

Southwest USA

Because previous surveys in Europe resulted in the collection of (various strains) of only a single native species, *C. menes*, foreign exploration was initiated to search for potentially other, more host specific parasitoid species. I therefore focussed on the original area of distribution of *F. occidentalis,* thus also matching climatic conditions of the “target” areas, greenhouses in temperate and mediterranean areas with its origin. During my initial survey in California, Arizona and Mexico (Mexicali area) parasitoids were found at various locations on flowering plants. These belonged to the families of Cruciferae (genus *Brassica* - 17 out of 33 sites) and Fabaceae (genus*Trifolium* (white clover) - 2 out of 5); genus *Melilothus* (sweet clover) – 3 out of 5 sites, genus *Medicago* (alfalfa) – 6 out of 16, genus *Lupinus* (lupine) – 4 out of 9), but not on broom, totalling a score of 32 sites out of 68 (47%). Only female parasitoids were collected: *C.menes* in the coastal area and central valley in California and in Mexico, *C. americensis* also in the interior of Arizona and in California. Two colour-types of *C.menes* were found: the brown type throughout the searched region from Mexicali to Davis, the yellow type only in the northern part of the Central Valley, near Davis.

Table 4. Collection results of adult thrips parasitoids, April - May 1993, USA/Mexico; brown, yellow indicates the colour-type of *C. menes.* All adult females, except *C. loomansi;* [s]= sweep-net collections, * = collected, preserved brought into culture.

Species	date	place	site	host plant	nr
California					
C. americensis	29 iv.	Cape San Martin	roadside	*Lupinus* sp.	1
C. americensis	02 v.	Riverside	parking	*Brassica nigra*	4
C. americensis?	05 v.	Temescal	roadside	*Brassica nigra*	3
C. americensis	13 v.	Needles	field	alfalfa	8
C. americensis	15 v.	Lake Casitas	roadside	*Juniperus* sp.	1
C. americensis	15 v.	Lake Cachuma	picnic-area	*Juniperus* sp	1
C. americensis	16 v.	Mendota	roadside	*Brassica nigra*	4*
C. americensis	17 v.	Davis	field	alfalfa	2
C. americensis	18 v.	Davis	roadside	*Brassica nigra*	3
C. menes brown	02 v.	Riverside	parking	*Brassica nigra*	2
C. menes brown	04 v.	Irvine	orchard	*Brassica nigra*	1*
C. menes brown	05 v.	la Sierra	roadside	*Brassica nigra*	1
C. menes brown	14 v.	Fillmore	roadside	*Brassica nigra*	1
C. menes brown	14 v.	Ventura Co	roadside	*Brassica nigra*	9
C. menes brown	15 v.	Castas Springs	roadside	*Brassica nigra*	2
C. menes brown	15 v.	Castas Springs	roadside	Compositae	1
C. menes brown	15 v.	Santa Barbara	roadside	*Brassica nigra*	8
C. menes brown	15 v.	Lake Cachuma	picnic-area	*Juniperus* sp	1
C. menes brown	15 v.	Los Olivos	roadside	*Brassica nigra*	12
C. menes brown	15 v.	Santa Maria	roadside	*Brassica nigra*	29*
C. menes brown	17 v.	Davis	roadside	*Brassica nigra*	3*
C. menes brown	18 v.	Woodland	glasshouse	alfalfa seedlings	1
C. menes brown	17 v.	Yolo	roadside	*Brassica nigra*	13
C. menes yellow	17 v.	Yolo	roadside	*Brassica nigra*	14*
C. menes yellow	16 v.	Lodi	fieldedge	alfalfa[s]	1*
C. menes yellow	17 v.	Davis	roadside	*Brassica* sp.	2
C. menes yellow	18 v.	Woodland	testplot	*Brassica* spp.	1
Arizona					
C. americensis	10 v.	Bonita Valley I	orchard	white clover[s]	1
C. americensis	10 v.	Bonita Valley II	orchard	white clover	1
C. americensis	10 v.	Willcox	garden	*Impatiens b.*	1*
C. americensis	13 v.	CampVerde	roadside	*Melilotus off.*	20*
C. americensis	13 v.	Sedona	roadside	*Melilotus off.*	4
C. americensis	13 v.	Sedona	waste dump	*Melilotus off.*	1
C. loomansi	13 v.	Oak Creek Canyon	forestroad	*Lupinus* sp.	400*
Mexico					
C. menes brown	06 v.	San Luis	field	alfalfa[s]	1
C. menes brown	06 v.	Benito Juárez	field	alfalfa[s]	?1
C. menes brown	07 v.	Colonia Bolsa	field	alfalfa[s]	?2
C. menes brown	07 v.	Gurrita	field	alfalfa[s]	?1
C. menes brown	07 v.	Campillo	field	alfalfa[s]	?1

Total live specimens		
C. menes yellow	Lodi, Yolo	15
C. menes brown	Irvine, Santa Maria, Davis	60
C. americensis	Willcox, Mendota, Camp Verde	43
C. loomansi	Oak Creek Canyon	400

Collections through correspondence

Ceranisus menes:
Additional live specimens of *Ceranisus menes* were received through correspondence from various places in the world. In collaboration with IITA-Benin, several hundred adults of *C. menes* and *Megalurothrips* larvae, collected from flowering leguminose plant species (*Pueraria*, *Centrosema* spp., *Tephrosia candida* (Leguminosae), originating from The Philippines (1992), Malaysia (Sarawak and mainland: 1994) and India (Haiderabad: 1995), were shipped to the laboratory and subsequently bred for 1 or more generation before translocation-shipment to Benin (Tamò *et al.*, 1997). All of these were representing sexual strains. Some of these were occasionally tested by us on *F. occidentalis* and *F. schultzei*. In 1990 and 1991 specimens of an asexual strain of *C. menes* were shipped from a laboratory culture in Shimane in Japan to Wageningen. In 1991 64 fields with a variety of field crops were sampled near Cabrils (Spain). From 5514 thrips larvae collected, parasitoids were found in very low numbers and in carnation only. Ten adults emerged and were shipped to our laboratory and subsequently identified as *C. menes* (brown colour-type).

Other parasitoid species collected:
Parasitoids from three other species were introduced into the laboratory and preliminary studies on their effectiveness against *F. occidentalis* were carried out:

- About 400 live adult individuals (females and males) of a previously unknown parasitoid species of thrips, collected from broadleaved lupine (*Lupinus latifolius* Lindl. ex J.G. Agardh (Fabaceae)). It was collected in May 1993 south of Flagstaff, where the Arizona State Highway 89A between Flagstaff and Sedona passes through Oak Creek Canyon and the Coconino National Forest (table 4). They were shipped to the laboratory and introduced into cultures of *F. occidentalis* and *F. schultzei.* It was later described as *Ceranisus loomansi* Trjapitsyn (Trjapitsyn & Headrick, 1995). Attempts to rear this species on *F. occidentalis* in the laboratory failed: although females readily attacked, oviposited and developed on larvae of both species, parasitoids remained in the pupal stage for many months and did not survive. Three female offspring emerged from a single female culture, originating from Temescal, California, but died in the process;
- *Thripobius semiluteus* (Boucek), known as a parasitoid of leaf-inhabiting thrips species belonging to the Panchaetothripinae (Thripidae) (Boucek, 1976), was received in June 1990 from a laboratory culture in Holland, originating from the USA. It readily attacked and developed on first stage larvae of *Heliothrips haemorrhoidalis* (Bouché), but showed no reaction to first and second stage larvae of *F. occidentalis* during behavioural observations and rearing on *F. occidentalis* failed. From Taiwan 58 pupae were received from a parasitoid attacking *Rhipiphorothrips cruentatus* Hood (Thripidae: Panchaetothripinae) in wax apple fields. However, only two adults emerged and died before testing. They were reported as *Ceranisus* sp. (Chiu, 1984), identification of both adults showed that they were similar to *T. semiluteus*, mentioned above;
- In 1994, several hundred specimens (males as well as females) of an egg parasitoid (*Megaphragma* spp. (Polaszek pers. comm.)) were shipped to Wageningen as parasitised eggs of *Megalurothrips sjöstedti* (Trybom) (Thripinae: Thripidae) in stems of *Dolichus lablab*, *Cajanus cajan* (pigeon pea), *Centrosema pubescens* (Leguminosae) from Benin, 1994 (see Tamó *et al.,* 1993). Preliminary tests on emerged adults were carried out on eggs of *F. occidentalis*. No response was observed, however, to thrips eggs, not when offered as infested leaves, not when eggs were offered directly. Because adults lived for 2 or 3 days, we could not fully explore its potential. A good rearing method needs to be developed before final conclusions can be made over its ability to parasitise F. occidentalis.

In table 6 the origin and localities are summarised of those species and strains of thrips parasitoids, that were tested during my laboratory experiments.

Table 5. Overview of the different habitats and number of plots surveyed in Europe and the USA (Netherlands: 1990-1996; France, Italy, Spain: September 1990; Hungary: 1995; USA-Mexico: April-May 1993). The number of plots were thrips parasitoids were found is placed between brackets (for details, see tables 1, 2 and 3).

Habitat	Cultivated crops and plants				Natural	
Country	greenhouse	open field	garden	undergrowth	(incl. fences)	Total
Europe						
Netherlands	11 (2)	17 (0)	26 (1)	5 (1)	~140 (50)	~200 (54)
Hungary	15 (0)	1 (0)	6 (0)	0 (0)	8 (2)p	30 (2)
France	11 (2)*	3 (0)	0 (0)	0 (0)	23 (9)	37 (11)
Italy	18 (0)	3 (3)	0 (0)	0 (0)	16 (2)	37 (2)
Spain	10 (0)	28 (0)	0 (0)	0 (0)	13 (0)	51 (0)
Total	*39 (4)*	*34 (3)*	*0 (2)*	*0 (1)*	*52 (64)*	*355 (69)*
USA						
California	4 (1)*	6 (2)**	7 (0)	1 (0)	49 (24)	67 (27)
Arizona	1 (0)	5 (0)**	4 (1)	5 (2)***	28 (4)	42 (7)
Mexicali	0 (0)	13 (5?)**	3 (0)	1 (0)	8 (0)	25 (5)
Total	*5 (1)*	*23 (7)*	*14 (1)*	*7 (2)*	*85 (28)*	*134 (39)*

* rose crop Hyères - France, 1990; *Brassica* spp., Woodland - California, 1993; ** = alfalfa (California, Arizona; including melon and onion, Mexico); *** = apple orchard

Discussion

Foreign explorations for parasitoids have been performed for various thrips pests in field crops: for *T. tabaci* (CAB, 1971: in the Caribbean and India); Sakimura, 1937: Japan), for *T. palmi* (Hirose *et al.* 1989, 1990, in Thailand), for *Megalurothrips sjostedti* (Tamò *et al.* 1997, in Asia and Cameroon), for *Heliothrips haemorrhoidalis* Bouché (McMurtry *et al.*, 1991; Froud *et al.*, 1997), for *Teaniothrips inconsequens* (Teulon *et al.*, 1996 in Central Europe) and more recently for *Scirtothrips perseae* (Hoddle *et al.*, 2002 in Central America). Except for a few (Sakimura, 1937; Tamò *et al.*, 1997) most efforts to control thrips pests with exotic natural enemies have been unsuccessful (see Chapter 1). A thorough and systematic exploration for natural enemies of *F. occidentalis* populations in its native home has never been performed properly. Except for a rather local survey around Davis - California (Greene & Parrella, 1993), our small-scale survey was in fact the first explorative survey throughout the area of origin of *F. occidentalis*. Later explorations in native area of distribution of *F. occidentalis* carried out in greenhouse and field grown ornamentals in November 1993 and during 1994 (Heinz *et al.*, 1996) and in 1998 (Ripa, INIA - Chile) did not result in the collection of any parasitoids.

Our exploration in the area of origin resulted in the collection of different thrips parasitoid species: *Ceranisus americensis* and two colour-types of *Ceranisus menes.* The first species was only collected there and is relatively unknown to science: it was first described from specimens collected in alfalfa in Utah-USA in 1912 (Girault, 1917) and has previously been found in association with *F. occidentalis* infesting alfalfa in Alberta-Canada in 1922 (Seamans, 1923). My collections show that it is common on flowering plants in Southwestern USA (cf. Trjapitsyn & Headrick, 1995), in the coastal region as wel as in the inland areas. *C. menes* on the contrary was collected only in the coastal areas of California and Mexicali, with a marked difference between the two colour-types: whereas the browntype was found throughout the sampled area, the yellow colour-type only occurred in central California.

Table 6. Collections of thrips parasitoids (Hymenoptera: Eulophidae) at different localities, either by active search (a) or correspondence (c)

Parasitoid	Locality	country	year	colour-type	collection	host[1]
C. menes	Europe	France	1990	yellow + brown	a	Tt/Fo*
	Europe	Italy	1990/1991	yellow + brown	ac	Tt/Fo*
	Europe	Spain	1991	brown	ac	Tt/Fo*
	Europe	Netherlands	1990-1993	yellow + brown	a	Tt*
	Asia	Japan	1990/1992	yellow	c	Fi
	Asia	Philippines	1992	yellow	c	Mu
	N.America	California	1993	yellow + brown	a	Fo*
	S.America	Brazil[2]	1991/1992	intermediate	a	Fs
C. americensis	N.America	California	1993	-	a	Fo*
	N.America	Arizona	1993	-	a	Fo*

[1] Fo = *F. occidentalis*, Fi = *F. intonsa*, Fs = *F. schultzei*, Tt = *T. tabaci,* Mu = *Megalurothrips usitatus*; * = including a range of native species on the collection sites; [2] = collected in the Netherlands on an import shipment from Brasil

C. menes is a common parasitoid of thrips, not only in the area of origin of *F. occidentalis*, but also in newly invaded areas. It is distributed almost worldwide (Loomans & van Lenteren 1990, Chapter 1). Most records originate from eastern Asian countries, where it is locally abundant (Japan, Korea, The Philippines, Taiwan, Thailand, India and Indonesia). From there it has been successfully introduced into Hawaii. Occasionally individuals have been reported from Dominican Republic, Brasil, Argentina, Australia and New Zealand. In Europe this species has been collected on several occasions. Our field surveys show that the occurrence of different parasitoid species is generally very low, irrespective of the host plant species, season and locality. Where it is common, it is largely associated with flowering host plants, the presence of thrips and the geographical location, more than to the mere presence of thrips larvae. Previous samplings mostly resulted in fairly low numbers collected (CAB, 1971: surveying *Thrips tabaci*), in others (Vuillet, 1914; Bühl, 1937: working on *Kakothrips robustus*), however, high numbers were found.

Explorations in various regions in the world show a predominance of *C. menes* as parasitoids attacking thrips. Surveys of natural enemies of *T. palmi*, carried out in Thailand (Hirose *et al.*, 1993) and Japan (Hirose *et al.*, 1992) on solanaceous and cucurbit crops, all showed a similar predominance of *C. menes*. Tamò *et al.* (1993, 1997) in his survey for parasitoids attacking *Megalurothrips* in India and Malaysia (mainland, Sarawak) also found a dominance of *C. menes* on leguminose crops, weeds and trees. Explorations in newly invaded areas, such as Australia (Steiner *et al.*, 1996; Steiner & Goodwin, 1996, 1998; Goodwin & Steiner, 1996) on *F. occidentalis* and on related thrips hosts, showed that *C. menes* was the most common parasitoid attacking thrips. Like in our survey, *C. menes* occurred in about 20% of the sampled locations.

It seems that both species, *C. menes* and *C. americensis,* mainly occur on flowering wild vegetation in natural habitats (table 5), with annual herbs, weeds, bushes (large range of families), in coastal and river landscapes (characterised by a relative high humidity and a moderate temperature) but not in a desert-like climate such as prevails in internal California and Arizona. They were also not found near forest edges and in natural reserves. In disturbed habitats (sides of roads, ditches, dikes, parking lots, etc.) and in pioneer vegetation rather than in vegetation in a further stage of succession, but not in hayfields and grassland. In natural habitats, *C. menes* appears rather common in some

host habitats and on some host plants, but rarely abundant. When it was found (earliest record in May, latest in September), it was mostly present in flowering annual herbs and weeds and in bushes on disturbed sites, in vegetation on sides of ditches, roads, near field edges, in hedgerows, fences, etc., but very rarely inside field plots and greenhouses (tables 1, 2 and 4). Previous collections of thrips parasitoids in The Netherlands were rather limited: Gijswijt (2003) collected *C. menes* from heather in Bussum in 1962 and *Ceranisus pacuvius* (Kütter) was found in the 1950s in pea plots on Goeree-Overflakkee (Fransen, 1960). My surveys, however, in commercial and private pea plots in that area in June 1990 did not result in the collection of any thrips parasitoids. Also at various other locations and habitats (not mentioned in the tables) similar surveys did not result in the collection of *C. menes*, although thrips (adults and larvae) were present. Collections made in malaise traps in natural reserves (The Netherlands: van Zuijlen *et al.*, 1996) or hayfields (Germany: Mohr *et al.*, 1992), did not reveal the presence of thrips parasitoids, where very low numbers of thrips were trapped (van Zuijlen *et al.*, 1996). No parasitoids were found near forest edges or collected from broom bushes.

Both *Ceranisus* species were rarely found in agricultural and/or horticultural production-systems such as greenhouses or field crops, regardless high infestations of *F. occidentalis*. Also Heinz *et al.* (1996), in their survey for natural enemies of *F. occidentalis* in ornamental crops, both in the greenhouse and from the field, did not reveal the presence of any thrips parasitoids. Mateus (personal collection, 1994) only trapped few specimens when monitoring for *F. occidentalis* in 14 plots of tomato, cucumber and melon using sticky traps in (plastic) greenhouses in the Algarve, Portugal. On the other hand, large numbers were trapped in autumn inside greenhouses with tomato crops in Sicily (Loomans, personal collection, 1998) and in Greece (Roditakis, personal collection, 2000). Besides possible, yet unknown, preferences of this parasitoid for certain host habitats, intensive chemical spraying practices certainly will have played a role in the low frequency of its presence in protected crops. Results published by Hirose *et al.* (1992, 1993) also showed a very low percentage of parasitisation by *C. menes* in sprayed crops in Thailand.

C. menes is know for its broad range of hosts of closely related thrips species, all belonging to the same subfamily Thripinae (Thripidae). Only Daniel (1986) has reported *Zaniothrips ricini* Bhatti and *Retithrips syriacus* Mayet (Thripidae: Panchaetothripinae) as hosts. Sampling wild vegetation inhabited by populations of *Frankliniella (intonsa, occidentalis, pallida, schultzei)*, *Thrips (tabaci, major, brevicornis etc.)* and/or *Taeniothrips*, in The Netherlands as well as in the south of Europe, showed that a number of these were parasitised by *C. menes.* Preliminary rearing results showed that *C. menes* is able to attack and develop on *F. occidentalis* and *F. schultzei* in the laboratory as well as in the glasshouse. *C. menes* was found earlier in association with *F. occidentalis* collected from rose in September 1988 in Cabrils (Spain) (Bordas, personal communication) and in the autumn of 1990 in Israel on several occasions (Kuslitzky, personal communication).

Only females were collected during sampling and in the laboratory they reproduced parthenogenetically. Although males are known of *C. americensis* (Trjapitsyn & Headrick, 1996), I only found females, which reproduced parthenogenetically once brought to the laboratory. Sampling *C. menes* in Europe and North America only has resulted in the collection of females (cf. Vuillet, 1914; Bühl, 1937). Only on one occasion, a male *C. menes* was collected from *Ligustrum* in Wageningen, July 1994. It is of interest to notice that in field collections of *C. menes* made in several Asian countries males are mostly absent as well: sampling vegetation in India and Malaysia resulted in the collection of adult *C. menes* (always females, never males), but when exposed to host larvae in the laboratory, they readily produced males as well as females (50:50). In Asian populations females mostly are predominating [(sex ratio 0.60: Sakimura, 1937 (Japan); Daniel, 1986 (India); 0.47: CAB, 1971 (India); 0.48: Hirose, 1989 (Thailand); van Heurn, 1923 (Indonesia)]. Murai (1988,

1990) recorded a gradual change in sex ratio in the laboratory: after several generations females reproduced parthenogenetically. The differences between these populations in apparent sex-ratios remain unclear.

Characteristic differences exist in colour type of the abdomen of *C. menes* females collected at several origins. *C. menes* was originally described from a yellow holotype (Walker, 1839). Later descriptions include specimens of other colour-types as well: a brown colour-type (DeSantis, 1961) and the sexual bicoloured forms with narrow transverse bands (e.g. van Heurn, 1923; Sakimura, 1937). Collection results indicate that the yellow type is distributed across the holarctic region and India, that the brown type occurs in the nearctic, neotropical and westpalaearctic region, whereas the sexual bicoulored form has been recorded from the aethiopian, autralian and oriental region up to Japan and Korea. Up till now all colour-types of *C. menes* have been considered taxonomically as one species. In many records however colouring has not been mentioned. The differences mentioned above could indicate that possibly different biotypes of *C. menes* exist.

Conclusions

From the potential group of candidate parasitoids of thrips, mentioned in literature (Chapter 1), I was able to collect and evaluate only a limited number of parasitoid species. However, I found that some are more common than previously known. *Ceranisus menes* was found to be the most common parasitoid of thrips species within the genera *Frankliniella, Thrips*, etc. It occurs worldwide and is widely distributed in Europe. In Italy, Spain, France and The Netherlands it was found regularly on natural vegetation infested by a wide variety of thrips species, belonging to the genera *Frankliniella*, *Thrips* and *Taeniothrips* (Thysanoptera: Thripidae: Thripinae), including important pest species like *Frankliniella occidentalis* and *Thrips tabaci*. It rarely invaded cultivated crops, either in glasshouses or open field. In 1993 it was first recorded from California-USA, was the first thrips parasitoid recorded to attack and develop on *F. occidentalis*. *C. americensis* is a second thrips parasitoid species which is known to attack this host, but no biological data are available.

The collection of parasitoids (*C. menes, C. americensis)*, able to attack and develop on already existing thrips pests like *F. occidentalis* and *T. tabaci*, is considered as an important step towards the biological control of these new pest species. The surveys indicate that differences might exist between different colour-types of *C. menes*, and their host preference for and performance on *F. occidentalis* and *T. tabaci* will be part of our evaluation programme. From a taxonomic point of view, this study can contribute to a proper identification and separation of various colour-types within the *C. menes* species group. The existence of morphological types (adults and also pupae can already be distinguished by their colour and size), indicate that different (sub)species might be involved.

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Chapter 3

Mass-rearing thrips and parasitoids[1]

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Abstract

Improved laboratory methods are described in detail for mass-rearing of various thrips species, such as *Frankliniella occidentalis*, *Frankliniella intonsa, Thrips palmi, Thrips tabaci* (Thysanoptera: Thripidae) and a thrips parasitoid, *Ceranisus menes* (Hymenoptera: Eulophidae), using various foods. In one method, plant pollen and honey solution are used as food sources. In a second method, germinated broad bean seeds are used. Thrips eggs, laid through a film in large numbers in water, are collected by a suction funnel onto a filter paper and incubated in a Petri dish. Large numbers of larvae that hatch are collected by using food traps (plant pollen). Thrips larvae can be reared on pollen or on germinated broad bean seeds until adult emergence without additional water and food. This method has been found useful for producing even-aged thrips at different densities (up to 500 larvae in a cage of 80 mm diameter) with relatively low mortality rates. Evaluation of this rearing method for *F. intonsa*, shows that during 2 weeks at 20 ^{0}C per 100 females more than 4000 females could be produced in the next generation. About 5 min per day is required to achieve this productivity of mass production. The method is also suitable for producing large numbers of the solitary endoparasitoid of thrips larvae, *C. menes*. Parasitisation levels varied with host species used (77.7% for *T. tabaci,* 63.5% for *F. intonsa*). Parasitoid mortality differed considerably with respect to the host species: 17% in *T. tabaci* and 34% in *F. intonsa*. Advantages and disadvantages of the described methods are discussed.

Introduction

Since the early 1980s, thrips have become important pests on vegetables and ornamental crops across the world. Because of their wide distribution and low susceptibility to a range of insecticides, species such as *Thrips palmi* Karny and *Frankliniella occidentalis* (Pergande) are currently ranked among the most serious pests in greenhouses and horticultural field crops. Thrips have been have been subject of numerous studies regarding life history, behaviour, host plant acceptance, interactions with natural enemies and virus transmission. For these purposes, various methods are used for rearing thrips at relatively low numbers. For other purposes, such as insecticide screening and mass-rearing of natural enemies, large amounts of thrips are needed of a constant quality (see Lewis, 1973; and Loomans & Murai, 1997, for an overview). However, all these methods often require a constant supply of fresh plant material. Risks of contamination with other thrips species, with natural enemies and diseases, of overlapping developmental stages of thrips, all increase with an increasing rearing scale. In addition, most previously described methods are not suitable for rearing large numbers of thrips in synchronized cohorts when using small containers. So far, very few thrips species have been reared on

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a purely synthetic diet (Loomans & Murai, 1997). Sakimura & Carter (1934) were the first to use a thin membrane ('fish skin') for rearing second instar larvae and adults of *Thrips tabaci* Lindeman, and Koch (1978) showed that individuals of some thrips species belonging to the Terebrantia (Thysanoptera) could lay eggs in water through an artificial film. Because it is difficult to collect eggs of terebrantian species from their host plants, Murai & Ishii (1982) developed a method for artificial egg procurement and development using plant pollen and a honey solution dispensed between two layers of stretched laboratory film. With this method, Murai & Ishii (1982) and Nakao (1993) cultured several thrips species, throughout their whole life cycle on just this food. Later, other researchers modified this method when rearing the New Zealand flower thrips, *Thrips obscuratus* (Crawford) (Teulon & Penman, 1986), the western flower thrips, *F. occidentalis* (Teulon, 1992) and its parasitoid *Ceranisus menes* (Walker) (Murai, 1990; Galazzi et al., 1992). However, this method was not suitable for large scale production.

Ceranisus menes is a solitary endoparasitoid of thrips larvae, in particular those of species belonging to the subfamily Thripinae (Thysanoptera: Thripidae),is found on a wide range of host plants in different biotopes across the world (Loomans, 1991; Goodwin & Steiner, 1996; Loomans et al., 1997) and, therefore, its mass rearing is of great interest. Recently, there has been renewed interest in the use of hymenopteran parasitoids as potential biological control agents of thrips pests (Loomans et al., 1997). Effective methods for mass rearing of *C. menes* form an important prerequisite to enable seasonal introductions. However, successful mass propagation of any thrips or its parasitoid on artificial substrates has never been established.

In the present study, methods for mass rearing of thrips and a thrips parasitoid are described and evaluated. These procedures enable standardization of the culture methods and synchronization of the life stages of thrips species for experimental work.

Materials and methods

Thrips and parasitoids

In order to test and evaluate our rearing method we used four species of thrips and one species of eulophid thrips parasitoid. The thrips species were: *Frankliniella intonsa* (Trybom) which were collected as adults in white clover flowers in Shimane prefecture (Honshu, Japan) in June 1990, *Thrips tabaci* were collected as adults in an onion field in Shimane prefecture (Honshu, Japan) in June 1990, and *Frankliniella occidentalis* were collected as adults in chrysanthemum flowers in Shizuoka prefecture (Honshu, Japan) in March 1994. These three species were reared on pollen using the method described by Murai & Ishii (1982) for approximately 30 successive generations. Adults of the fourth species, *Thrips palmi*, were collected as adults in an eggplant field in Okayama prefecture (Honshu, Japan) in October 1993, and was reared on kidney bean leaves for 20 successive generations. The thrips parasitoid was an asexual strain of the eulophid *Ceranisus menes*, collected as adults in tea flowers in Shimane prefecture (Honshu, Japan) in October 1991, and was subsequently reared on *F. intonsa* and *T. tabaci*.

Food sources.

Two kinds of pollen, tea pollen (*Camellia sinensis* (L.) O. Kuntze) and pine pollen (*Pinus thunbergii* Parl.), were used respectively for egg production and for rearing larvae. These pollen were collected in autumn and late spring and stored for more than three months in a freezer at -20 ^{0}C. Pollen is not suitable for mass-propagation of some species of thrips, such as *T. palmi*, and some strains of *T. tabaci*. Although these species can feed and develop on pollen, they thrive better on green plant material or a related food source. In these cases we used an alternate food source, *i.e.*, germinated broad bean seeds (*Vicia faba* L.). Broad bean seeds were allowed to germinate in running tap water for 3–4 days at room temperature. After their seed coats had been removed, they were used for rearing thrips larvae.

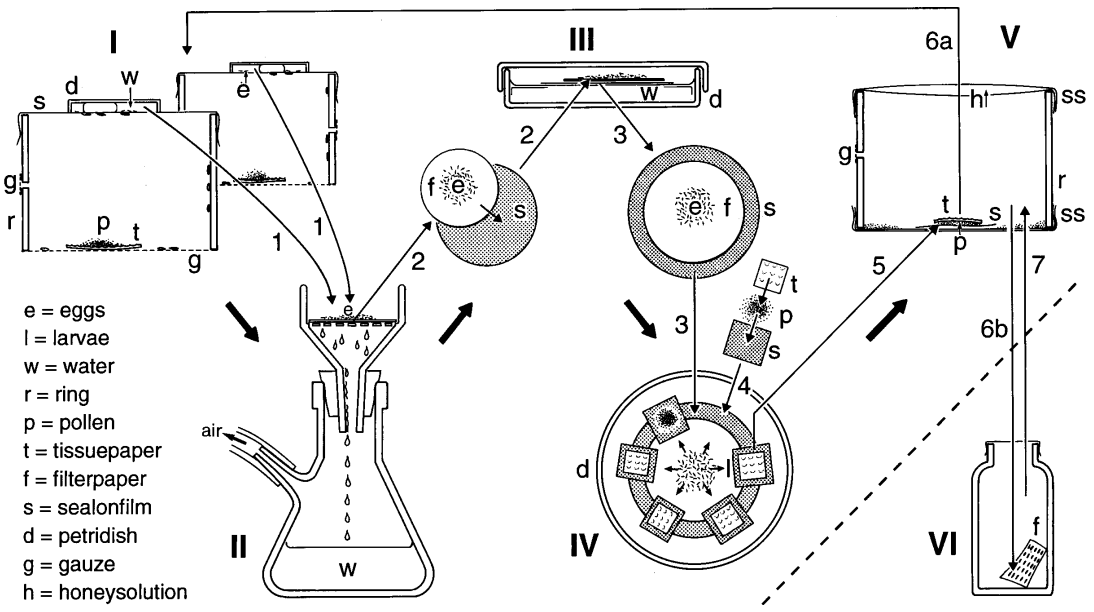

Figure 1. Procedure for mass-rearing of thrips and natural enemies using an artificial film. I. Units for oviposition, II. egg-washing, III. incubation, IV. trapping, V. rearing and VI. storage. Eggs are laid in water through stretched film (1), and are washed in a waterfilter on filterpaper (2) and subsequently incubated at high humidity conditions. Hatched larvae are trapped (3, 4) with pollen and reared (5) on pollen + 10% honey solution until maturity and then are transferred to unit I (6) for culture maintenance or stored as pupa (7). d = petri dish, e = eggs, f = filter paper, g = gauze, h = honey solution, l = larvae, p = pollen, r = ring cage, s = sealon film, t = tissue paper, w = water (Loomans & Murai, 1997; drawing Piet Kostense)

Cages.
Two types of cages are were used, depending largely on the type of food that was provided: (1) Ring cages for oviposition and rearing larvae when using pollen and honey, and (2) a box for rearing larvae on germinated broad bean seeds. The ring cage was made of a polymethacrylate cylinder (80mm diameter, 50 mm high, ring cage). In rearing units the bottom end was covered with double stretched laboratory film (Sealonfilm® , Fuji Photo Film Co., Tokyo, Japan) for Parafilm 'M' (American National Can, Chicago, IL, USA). In oviposition units, gauze (60 to 100 *µ*m) was glued to the bottom instead of the film. For mass rearing on bean cotyledons, we used a tight box (120 • 98 • 46 mm, box cage), with a hole (10 mm diameter) in the lid sealed with gauze for ventilation.

Rearing procedure.
The rearing procedure and materials used for mass production of thrips are shown in figure 1.

Oviposition and egg production.
After placing the adult females (300 to 400 per cage) and pollen (10 to single 20 mg) in the cage, the top end was covered with a single stretched film. A few ml water were placed on top of the film and covered with a small Petri dish (3.6 mm diameter). An air bubble in the water kept the lid stable on the film layer. Adult females laid eggs in water through the thin stretched film for periods of more than 20 days. Additional tea pollen was provided on a piece of tissue paper in the cage every 2 to 3 days. For some thrips species, such as *F. occidentalis* and *T. palmi*, food sources other than pollen can be used

for egg production, such as leaf powder or broad bean seeds. In the latter case, germinated broad beans without the seed coat, one bean per cage per day, were supplied for the adults. Bean seeds were replaced every single or alternate day at the time of egg collection. In this case the ring cage is covered with film over the gauze on the bottom as well, so as to prevent the beans from drying out. Although humidity in the cage was above 90% r.h., this did not affect egg production. Adult females deposited eggs in the water as well as in the beans.

Collection of eggs and hatching.
Eggs laid in water were collected on a filter paper (Toyo, No. 2, 55 mm diameter) using a water suction bottle (Figure 1,II) or an aspirator. The time when eggs could be collected varied from 1 h up to the maximum of total egg developmental period (3 to 4 days). The filter paper with eggs and a little moisture was placed in a closed Petri dish (Figure 1, III) until hatching. Just before egg hatching the Petri dish may be kept at 5 ^{0}C for one week so as to permit collection of larvae at a later date.

Collection of larvae.
Depending on the incubation temperature, the eggs hatched over a period of several days (about 3 days at 24 ^{0}C). The emerging larvae moved in the Petri dish from where they could be picked up individually with a fine brush. A quicker way to collect large numbers of larvae was to attract them to a small leaf disc (about 1 cm2) or very small amount of pollen (less than 1 mg) placed on a piece of non-stretched film in the Petri dish (Figure 1, IV). Larvae gathered on this food trap within a few hours and could be collected and counted quickly. Germinated broad bean seeds could also be placed in the Petri dish. Newly hatched larvae aggregated on the cotyledons in a few hours.

Mass rearing of thrips larvae.
1. Rearing on pollen. Newly hatched larvae were placed in a rearing cage (Figure 1, V), with 100 to 200 mg (pine) pollen (supplied only once). A thin layer of paper disc (such as kitchen paper, providing cavities) is added to the pollen, providing pupation sites. Honey (5–10% solution) was provided, enclosed between two layers of stretched film. Larvae could feed on pollen directly and on honey solution through the thin membrane. As an alternative, sugar solution or water was used. Larvae pupated in the cavities of the paper disc and developed to adults without additional food. At the time of pupation, leakage of honey solution through the film provided a high humidity in the ring cage.
2. Rearing on an alternative food source. Several germinated broad bean seeds without seed coat were provided as food for thrips larvae in a box cage. Germinated seeds (instead of leaf disc or pollen) were used for collecting hatched larvae. A sheet of kitchen paper (with small cavities) was placed at the bottom of a box for providing pupation sites, as in the pollen rearing method. Larvae were reared at densities of 20 to 40 larvae per bean and additional beans were provided if the beans had dried out at the time of pupation, thereby maintaining the humidity above 90% r.h. in the box cage. Larvae developed into pupae without additional water supply and additional bean seeds.

Thrips parasitoid rearing
Methods for rearing thrips parasitoids depend largely on the ability to rear their thrips hosts in large cohorts of even-aged larvae. *Ceranisus menes* prefers young larvae (see chapters 4 and 5), therefore female parasitoids were put into a rearing cage with newly hatched thrips larvae, at a ratio of about one female per 30 larvae per day. Parasitised and unparasitised thrips larvae pupate, after about 10 days at 25 ^{0}C, between the layers of paper placed on the bottom of the cage. When the unparasitised thrips adults had been removed (after about two weeks at 25 ^{0}C), parasitoid pupae were collected by means of

an aspirator. They were then shaken onto moist filter paper, and placed in a glass jar with 2% agar to maintain humidity above 90% r.h. (Figure 1, VI).

Evaluation tests
In order to evaluate the effectiveness of our rearing method we performed several experiments. All experiments were conducted in a climate room or incubator ((SANYO Co. MR-151)) at 20 ± 1 ^{0}C, L16:D8 and 60–70% r.h., unless stated otherwise.

Oviposition.
One hundred adult females of *F. intonsa*, *F. occidentalis* and *T. palmi* were allowed to feed on tea pollen (approx. 5 mg) in oviposition cages (80 mm diameter, 50 mm high) and to lay eggs in water at 20 ^{0}C. Germinated broad bean seeds were used for *F. occidentalis*, instead of pollen, at 25 ^{0}C. The number of eggs laid in water during 24 hours was counted under a binocular microscope. The number of eggs laid inside the cotyledons of broad beans was evaluated for hatched larvae. These experiments were replicated three times. An ANOVA test and t-test were performed to test for significant differences among thrips species and oviposition substrates, respectively.

Egg collecting efficiency.
The efficiency of egg collection by a suction funnel was tested for different egg numbers of *F. intonsa*. The number of eggs laid in water, counted before taking them up with a suction funnel for placing on filter, ranged from 100 to 558. The numbers of eggs collected on a filter paper were counted under a binocular microscope to evaluate the efficiency of egg collection. Spearman's rank test was performed to test the relationship between egg numbers laid in water and collection efficiency.

Egg hatchability.
A filter paper with eggs was placed in a Petri dish, and covered with thin membrane to maintain 100% humidity. Hatched larvae were counted daily at 20 ^{0}C and removed using an aspirator.

Collection of hatched larvae.
Three pieces of non-stretched film with approx. 500 μg tea pollen were placed in a Petri dish with 100 newly hatched larvae for 3 hours. The numbers of larvae gathered on this food trap were counted. The experiment was replicated three times for *F. intonsa* and *F. occidentalis*. A t-test was performed to test for significant differences between the two thrips species.

Rearing larvae.
The efficiency of rearing larvae of even-aged cohorts of thrips in a ring cage was tested for 2 thrips species at different densities. For *F. intonsa* larvae, pine pollen (100 mg) and honey solution (4 ml, 10%) was provided as food, which was not renewed during the developmental period. At adult emergence, adults were taken out form the cages and developmental time and mortality were determined. For *T. palmi*, being largely a leaf feeding species, the efficiency of rearing was compared for different food types and for different densities of one type of food. In the first series, three different food types were compared: sweet pepper powder and pine pollen mixture (4:1), broad bean seeds and a sweet pepper leaf. One hundred newly hatched larvae were put into a ring cage with these food sources and reared to maturity. In a second series, larvae were reared on broad bean seeds at different densities in a box cage in order to evaluate the efficiency of mass rearing of even-aged cohorts of thrips. Twenty beans per box were supplied at the time when the larvae were introduced. No additional beans were provided during the period of development. Developmental time and mortality of *F. intonsa* and *T. palmi* were observed at 20 ± 1 ^{0}C, L16:D8 and 24 ± 1 ^{0}C and L16:D8 respectively. Spearman's rank

tests were performed to test the relationship between larval density and development until adult emergence. An ANOVA test was performed to test for significant differences among food types and binomial probability 95% confidence intervals were calculated for each percent mortality for *T. palmi* (Noether, 1990). When the confidence intervals for a pair of probabilities overlapped for a given type of food, the differences were considered to be not significant.

Table 1. Numbers of eggs laid by 100 females of three thrips species in water through a thin membrane during 24 hrs at 20 ^{0}C and L16:D8

Thrips species	Number of eggs (100 females)
Frankliniella intonsa	815.3 ± 77.5 a[a]
Frankliniella occidentalis	269.7 ± 30.6 b
Thrips palmi	270.6 ± 17.5 b

[a] Means within a column followed by a different letter are significantly different from each other (P<0.05, Scheffé's multiple comparison test).

Table 3. Efficiency of egg collection, using a water funnel at different egg-densities laid by *Frankliniella intonsa* in water

Introduced egg number	Percentage of collected eggs [a]
100	63.0
376	81.1
523	82.6
558	85.5

[a] P>0.05, Spearman's rank-order correlation coefficient test.

Table 2. Comparison of different oviposition substrates on egg-production by female *Frankliniella occidentalis* at 25 ^{0}C and L16:D8

Egg numbers per 100 females *F. occidentalis*			
Alternative method			Pollen method
Beans [a]	Water	Total	Water
65.3 ± 19.3	539 ± 44.0	604.3 ± 39.8 a [b]	855.8 ± 67.6 b

[a] Eggs laid on beans were evaluated by number of hatched larvae; [b] Means within columns followed by a different letter are significantly different from each other (P<0.05, *t* -test).

Results

Egg production and collection.

The number of eggs laid by *F. intonsa*, *F. occidentalis* and *T. palmi* feeding on tea pollen through a thin membrane is shown in Table 1. The number of eggs laid per female by *F. occidentalis* and *T. palmi* was smaller than those laid by *F. intonsa*. When supplied with germinated broad beans, western flower thrips *F. occidentalis* females laid eggs inside the cotyledons as well. However, during 24 h of exposure only about 10% of the eggs (measured as hatched larvae) were laid in the root and the cotyledons, but almost 90% were laid in the water layer (Table 2). It was also found that there is a significant difference in the total egg number between pollen and broad bean seeds. Some eggs laid in water may be lost when transferred to a filter paper by a suction funnel. Table 3 shows that in case of a filter paper in a flat water suction funnel the efficiency of egg collection was greater than 80% when more than 400 eggs are introduced. There was no significant relationship between introduced egg number and collection efficiency.

Table 4. Mean number (± standard deviation) and percentage (in brackets) of egg hatching in *Frankliniella intonsa* on a filter paper at 20 ^{0}C, on 4-6 days after oviposition

Thrips species Eggs	Tested	Hatched larvae Day 4	Day 5	Day 6	Unhatched eggs
Frankliniella intonsa	120	82.0 ± 5.7 (68.3)	29.5 ± 0.7 (24.6)	0 (0)	8.5 ± 4.9 (7.1)

Table 5. Efficiency of collection of hatched larvae (± standard deviation) of two species of thrips using tea pollen as a trap at 20 ^{0}C and L16:D8

Thrips species	Mean percentage of larval collection (as hatched larvae)
Frankliniella intonsa	94.0 ± 1.0 a [a]
Frankliniella occidentalis	91.0 ± 8.9 a

[a] Means within a column followed by the same letter are not significantly different from each other (P>0.05, *t* -test).

Table 6. Mean (± standard deviation) developmental time and mortality of *Frankliniella intonsa* at different rearing densities on tea pollen and 10% honey solution at 20^{0}C and L16:D8 (P>0.05, Spearman's rank-order correlation coefficient test)

Number introduced	Developmental time larvae in days	Mortality (larva + pupa) (%)
100	10.9 ± 0.5	8.0
200	11.0 ± 0.5	14.5
400	11.1 ± 0.5	20.5
500	11.0 ± 0.5	16.4

Larval hatching and collecting.

When the filter paper is kept moist in a saturated atmosphere, eggs develop normally and hatch without problems. At 20 ^{0}C total hatch rate of *F. intonsa* was higher than 90% and about 70% of the larvae hatched on the first day (Table 4). Using food traps, by supplying a small amount of pollen on a piece of film, hatched larvae gathered on this food trap within 3 hours. The efficiency of collecting larvae was very high: more than 90% of the hatched larvae were trapped on the film with pollen (Table 5). There was no significant difference in efficiency between *F. intonsa* and *F. occidentalis*, but *T. palmi* was not tested. In this way, larvae could be collected and counted quickly, without causing any damage while handling them.

Rearing larvae

Table 6 shows that *F. intonsa* larvae developed well at all densities between 100 and 500 larvae in a ring cage. Developmental time from hatching to adult emergence was about 11 days and, except for the 400 larval density treatment, mortalities were below 20%. These results suggest that 100 mg pine pollen is enough to rear 500 thrips larvae to maturity. To evaluate mass rearing of even-aged cohorts of thrips larvae, *T. palmi* larvae were reared on germinated broad bean seeds at different densities in a box cage. At all rearing densities, *T. palmi* larvae developed well on germinated broad bean seeds (table 7). There was no significant difference in developmental period from hatching till adult

Table 7. Mean (± standard deviation) development time and mortalities of *Thrips palmi* at different rearing densities on germinated broad bean seeds in a tight box at 24 ^{0}C and L16:D8 (P>0.05, Spearman's rank-order correlation coefficient test)

Number introduced	Developmental time larvae in days	Mortality (larva + pupa) (%)
100	9.8 ± 0.6	5.0
250	9.9 ± 0.6	7.2
500	9.9 ± 0.5	5.6
750	10.0 ± 0.6	5.9
1000	9.9 ± 0.5	17.8
1200	10.0 ± 0.6	7.1
1500	9.9 ± 0.5	9.6

Table 8. Mean (± standard deviation) developmental time and mortality of *Thrips palmi* using different rearing foods in a ring cage at 24 ^{0}C and L16:D8

Food type	Tested thrips number	Mean developmental time in days (larva + pupa)	Mortality (%) (+95% C.I.)
Dried leaf powder [a] pollen	100	10.0 ± 0.7 a [b]	13.0 ± 6.6 a [c]
Broad bean seeds	100	9.8 ± 0.5 a	11.0 ± 6.1 a
Sweet pepper leaf	98	9.9 ± 0.6 a	14.3 ± 7.0 a

[a] Freeze dried sweet pepper leaf powder, pine pollen and 10% honey solution.
[b] Means within a column followed by the same letter are not significantly different from each other (P > 0.05, Scheffé's multiple comparison test).
[c] Percentages within a column followed by the same letter are not significantly different from each other (P<0.05, Binomial Probability 95% Confidence Interval Test (Noether, 1990).

emergence among rearing densities. There was also no significant relationship between rearing density and mortality rate. At all densities, except for the 1000 larvae, mortality rates were less than 10%(Table 7). Larvae of *T. palmi* developed well in a ring cage on leaf powder and broad bean as well as on pepper leaf. There were no significant differences in developmental duration from hatching to adult eclosion and mortalities among insects reared on different food types (Table 8).

Parasitoid rearing.
First instar thrips larvae, when exposed to *Ceranisus menes* in the ring cage, were successfully attacked. Parasitisation levels reached 77.7% whereas 5.4% remained unparasitised in the case of *T. tabaci*. For *F. intonsa* the figures are 63.5% and 3.0% respectively. Parasitoid mortality differed considerably with respect to the host species, about 17% in *T. tabaci* and 34% in *F. intonsa* (Table 9). Although some of the mortality was caused by host feeding by the parasitoid, we do not know whether there are differences in host feeding levels or superparasitism between both hosts.

Table 9. Mean number (± standard deviation) and percentage (in brackets) of parasitisation of two species thrips larvae, subjected to attack by *Ceranisus menes* for 3 days and reared in ring cages for 12 days

Thrips species	Thrips larvae introduced	parasitised	unparasitised	dead-unknown
Thrips tabaci	300	233.3 ± 19.1a [a] (77.7)	16.3 ± 9.1 a[a] (5.4)	50.3 ± 16.3 a (16.9)
Frankliniella intonsa	300	190.5 ± 26.2b (63.5)	9.0 ± 1.4 b (3.0)	100.5 ± 24.8 b (33.5)

[a] Means within the same column followed by a different letter are significantly different from each other ($P<0.05$, Scheffé's multiple comparison test).

Discussion

Most thrips species lay eggs embedded in tissue of the host plant, which makes the collection of large numbers of eggs difficult. Egg production per female of *F. occidentalis* and *T. palmi* using our method was similar or higher than that found by Kawai (1985), Robb (1989) and Katayama (1997) who used various leaf substrates. When using our method, many species can be induced to lay eggs in water through a thin laboratory film and their eggs can be collected in large amounts relatively easy. Earlier versions were successfully used to rear several thrips species such as *F. intonsa*, *T. tabaci*, *Thrips hawaiiensis* (Morgan), *Thrips coloratus* Schmutz, *Thrips nigropilosus* Uzel, *Anaphothrips obscurus* (Müller), *Microcephalothrips abdominalis* (Crawford), *Scirtothrips dorsalis* Hood (Murai, 1988), *F. occidentalis* (Teulon, 1992) and *T. obscuratus* (Teulon & Penman, 1986). Also predatory thrips species, such as *Aeolothrips intermedius* Bagnall and *Franklinothrips vespiformis* (Crawford), are able to lay their eggs in water through a stretched film, although those from the latter species cannot be removed from the film (A.J.M. Loomans, unpublished). However, a few thrips species, such as *Thrips setosus* Moulton and *Heliothrips haemorrhoidalis* (Bouché) are unable to lay eggs in this way (T. Murai, unpublished). Therefore, more study is needed to improve this rearing method for a wider range of thrips species. Pollen influences egg production in flower thrips (Andrewartha, 1935; Murai & Ishii, 1982; Kirk, 1985; Teulon & Penman, 1991). Many types of pollen could be used for thrips rearing, but only a few could be collected in large enough numbers to maintain stock cultures or to perform mass propagation. Pollen from plants such as pine and maize, but also *Mesembryanthemum* spp. or *Typha* spp., could be collected in large quantities. Pollen stored at -20 ^{0}C for more than 2 years could still be used for rearing thrips. Instead of pine pollen, crushed and dried bee-pollen could also be used for rearing larvae *F. occidentalis* (T. Murai, unpublished) and dry fruit and leaf powder for rearing larvae and adults of *T. palmi* (Koyama & Matsui, 1992). However, these food substances easily moisten and mould under saturated conditions. When thrips larvae are reared on these food sources, an oviposition cage with gauze at the bottom should be used to prevent high moisture levels.

In evaluating the new rearing protocol, the efficacy of mass production for *F. intonsa* has been determined at 20 ^{0}C. One hundred females produce 800 eggs per cage daily. Due to 90% egg collection efficiency and 70% hatch rate, 500 larvae can be reared per cage. When female ratio and emergence rate of *F. intonsa* are assumed to be 70% and 90%, respectively, 300 females will emerge in two weeks after egg laying. Females of *F. intonsa* lay eggs continuously for more than 30 days with a survival rate of more than 80% at 20 ^{0}C (Murai & Ishii, 1982). This enables us to use adult females for production of eggs for more than two weeks. Thus, more than 4000 females of the next generation per 100 females per cage can be produced during two weeks. Moreover, handling time for

carrying out the rearing processes, such as egg collection, larvae collection, and providing water and foods takes less than 5 minutes per cage per day.

Ceranisus menes lays more than 40 eggs a day (Loomans & Murai, 1994). By increasing the thrips- parasitoid ratio or exposure time, higher parasitisation levels per unit may be expected. Also differences in acceptance and larval development between different strains of *C. menes* parasitising *F. intonsa* and *F. occidentalis* may affect the productivity of parasitoid (Murai & Loomans, 1995). The level of superparasitism and host feeding was not important under the conditions used, but further study is needed. Mass rearing of *C. menes* in a box cage needs further investigation.

The method described here for mass rearing of thrips and parasitoids has several advantages over those using fresh plant material. It reduces a possible exposure to insecticides present on plant material, and allows the manipulation and separation of thrips populations from different locations, thus preventing contamination with other thrips species or strains of the same species. Pollen can be stored for long periods at low temperature and maintains its quality over long periods of time, making rearing conditions independent of variable greenhouse and host-plant conditions during summer and winter. The method permits certain modifications for experimental requirements. For example, when using a water-agar layer on top of a single stretched film, as an alternative to the regular water layer, eggs are fixed for subsequent embryological and histological studies (Gerald Moritz, University Halle-Wittenberg, personal communication). Size of the cage and number of insects reared can be easily adjusted for specific experimental purposes: in a slightly modified form (smaller cylinders) we have used this method for life-history studies and parasitisation testing (Loomans & Murai, 1994; Murai & Loomans, 1995). On the other hand, there is a limit to the size of the cage and the maximum number of larvae which can be reared to maturity per cage or the number of adults allowed to oviposit during more than one day. At densities above 500 larvae or adults per ring cage, the stretched film sometimes gets damaged. Feeding larvae may cause puncture holes, thus causing the film to break or causing condensation inside the ring and the pollen to mould, and thereby decreasing its efficiency drastically.

The method described here can also be used for other purposes, such as collection of eggs for establishing cell and tissue cultures (Nagata et al., 1997), testing the effects of different secondary host-plant substances (de Jager et al., 1995), enzyme-inhibitor activity or chemicals, like antibiotics, on host-plant acceptance, feeding behaviour and life-history studies.

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Chapter 4

Host selection by thrips parasitoids: effects of host age, host size and period of exposure on behaviour and development

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Abstract

Detailed behavioural observations were carried out on the host selection process by *Ceranisus menes* (Walker) and *Ceranisus americensis* (Girault) (Hymenoptera: Eulophidae), two solitaty endoparasitoids of thrips larvae. When exposed in a no-choice situation to 7 different age and 7 different size classes of larvae of western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), host acceptance was strongly correlated with age and size of the host. For *C. americensis* and *C. menes* (yellow) two distinct groups of size classes could be distinguished, coinciding with the first and early second instar of western flower thrips. For females *C. menes* (brown) host acceptance decreased gradually along host size classes. With an increase in larval size and age the attack-success-ratio and the insertion-success-ratio decreased significantly for both species and strains observed. Differences were observed in behaviour between species and within *C. menes* between strains: of the two colour-types used, a yellow strain was more effective than a brown strain. About 50 % of the hosts that a female of *C. menes* (brown, Hyères) encountered, were actually inserted when they were 1-2 days old. Larvae older than 3 days were attacked only for 16%, were inserted very rarely and the average insertion time was much shorter. When young host larvae were offered in different size classes, small larvae (0.8 mm and less, about equal to the size of the parasitoid which is 0.7 - 0.8 mm long), were preferred. *C. americensis* and a yellow type of *C. menes* ('Brignoles') were more successful in completing an attack than a brown type of *C. menes* ('Cabrils'). Large larvae (0.9 mm or more) were more readily attacked by 'Brignoles' than by 'Cabrils', but the insertion ratio was similar for both strains.

Host acceptance of different aged and sized larvae is limited by behavioural defensive reactions of *F. occidentalis* larvae. When encountering small sized larvae a parasitoid can overcome these defensive reactions, but when larvae are larger than the parasitoid herself, encounters are often interrupted, and larvae managed to escaped from being inserted once attacked. The difference in apparent preference of different sizes of larvae between the colour-types of *C. menes* can also be due to differences in the duration of an encounter and an attack: yellow types spent less time in completing each of the different steps of the attack cycle than brown types. Especially encounter time is longer for the last group. Observations on host acceptance by *C. americensis* show that this parasitoid is able to attack and parasitise older and larger-sized larvae more successfully. Once inserted, not always an egg is laid: a wasp can either reject a larva after internal probing or the larvae manages to escape from being parasitised before oviposition took place.

Observations on wasps exposed to batches of 25 *F. occidentalis* larvae for a period of 8 hours showed that the number of hosts parasitised by *C. menes* (yellow strain from 'Yolo' USA) decreased significantly in the course of time. The numbers and the times of host-handling events and the success in completing the oviposition sequence gradually decreased in time. There was a great difference between wasps in total number of larvae parasitised when exposed to 25 larvae during the full period and those exposed to a new batch every hour: 11.2 and 28.3 hosts were parasitised respectively. *C. americensis* parasitised 17.5 hosts on average after being transferred, but in a different set-up. The host acceptance ratio, the number of hosts containing an egg, and activity of the wasp decreased gradually over time for both species. The influence of host acceptance by both parasitoid species on thrips population dynamics and their potential effectiveness in biological control is discussed.

Introduction

In order to complete her reproductive cycle, an insect parasitoid first has to search, find and select a potential host. Once it has physically contacted that host, she has to determine whether the host is the appropriate species and growth stage to use for development of her offspring. Knowledge of this host selection process (Vinson, 1976, 1977) contributes not only to an understanding of its efficiency and preference, but also of the population dynamics of the host (pest) and the parasitoid and its foraging behaviour. Basic knowledge of the attributes that govern a parasitoid's efficiency and preference in selecting her hosts is, therefore, critical for the development and its successful application as a future biological control agent in IPM programs. Pre-introductory evaluation criteria that have been developed for natural enemies (van Lenteren, 1986; Minkenberg, 1990)) use this knowledge for selection of biological control agents. Synchronisation of a natural enemy with its target host is an important criterion during this pre-introduction selection process. The preference for certain stages or age and the distribution of offspring along the range of juvenile stages of the host, which can be used by the female parasitoid for feeding or oviposition, plays a significant role in the synchronisation of host-parasitoid populations.

The host acceptance process may include different steps such as host encounter, antennation, probing, oviposition and marking (Van Driesche & Bellows, 1996) during which the host is examined, externally and internally, and accepted or not. Different stimuli may be necessary to elicit this sequence of behaviour: parasitoids may use movements and vibrations by the host, chemical cues and physical features of the host size, shape and texture (Vinson, 1977; Van Driesche & Bellows, 1996). On the other hand, a non-sedentary host may counteract the parasitoid's actions by behavioural reactions to an attack, trying to avoid parasitisation (Gross, 1993). In a specific parasitoid - host system, this may result in differences in vulnerability and preference of the parasitoid for a certain age, stage or size of the host, and also in a refuge for the host. These refuges may be either physical, spatial, or temporal, or may simply result from invulnerable classes of hosts. Differences in acceptance and suitability of host ages may have a significant impact on the stability of predator-prey (Hassell & May, 1973) or parasitoid-host interactions (Kistler, 1985). Evaluation of different parasitoid species and populations, not only will allow us to select that natural enemy that performs best on a specific host. As a side effect, it will also give insight whether and how parasitoid species or strains that share the same host species are able to coexist.

Ceranisus menes (Walker) and *C. americensis* (Girault) are two solitary endoparasitoids of larvae of western flower thrips. *C. menes* is distributed worldwide and has been recorded from a wide range of thrips species: larvae of more than twenty species belonging to genera such as *Frankliniella*, *Thrips*, *Taeniothrips* and *Megalurothrips* (Thysanoptera: Thripidae) have been recorded as hosts (Loomans & van Lenteren, 1995). *C. americensis,* on the other hand, has only been found in association with *F. occidentalis* in the western parts of the USA (Trjapitsyn & Headrick, 1995; see chapter 2). Its relation with its host is still largely unknown. In the process of evaluating the potential of *C. menes* and *C. americensis* as biological control agents of *Frankliniella occidentalis*, the efficiency by which the different phases of the host selection process (Vinson, 1976, 1977) are completed, can be considered as important selection criteria as well.

The life-cycle of western flower thrips and closely related species can be divided into six different stages: an egg phase, a first and a second stage larva, a prepupal and pupal phase and the adult stage (Tommasini & Maini, 1995; Lewis, 1997). From these 6 stages only the larvae are prone to attack by *Ceranisus* parasitoids: the egg is laid in the soft plant tissues, whereas the pupal stages are hidden in the soil. At the end of the larval stage, the thrips larvae search for a site to pupate and move away from the plant parts (leaves, flowers) to the soil. During their feeding period, larvae hide and feed on places where they are difficult to access by their natural enemies. In glasshouse conditions *F. occidentalis* can oviposit continuously throughout the year. Generations will soon overlap

after the initial infestation and larvae of different age and size will be available continuously. *C. menes* and *C. americensis* females searching for hosts will thus encounter host larvae of various ages. Differences in acceptance and suitability of these various host ages might have a significant impact on its ability to control *F. occidentalis* infestations. Preliminary observations on the parasitoid-host relationship between *C. menes* and *F. occidentalis* (Loomans, 1991; Murai, 1988), showed that *C. menes* prefers first and early second stage larvae of its hosts. As size of *F. occidentalis* larvae is between 0.4 and 1.1 mm, and the size of *C. menes* is about in the middle, host acceptance is expected to be affected by the size, activity and vigour of reaction by the host.

This study investigates the various components of the parasitoid's attack and oviposition behaviour and examines the effects of differences in age on host acceptance by *C. menes* and *C. americensis.*Direct observations on the frequency and timing of the behavioural components involved in host acceptance allow us to create a general picture of the host acceptance and oviposition sequence (van Lenteren *et al.*, 1980; van Lenteren, 1994). In this paper, we show that the combination of its searching efficiency and/or interactions with its host or prey, once encountered (host-acceptance behaviour) will determine whether the interaction between a natural enemy and its host will be effective or not.

Material and methods

Cultures and origin

Cultures of thrips hosts, *Frankliniella occidentalis*, were established in the laboratory from individuals collected in glasshouses at Wageningen University. Cultures were either maintained on bean pods in glass jars or on pine pollen as described by Loomans & Murai (1997) and Murai & Loomans (2001, see chapter 3) respectively. For the method of rearing host larvae and parasitoids (*C. menes*), see Loomans (1991), except that *F. occidentalis* larvae were reared on cucumbers. Strains of *C. menes* were collected from *Centaurea officinalis* (yellow - 'Brignoles', brown - 'Hyères') in France in 1990 (Loomans, 1991; see chapter 2), and from carnation (brown - 'Cabrils') in Spain in 1991 (Riudavets *et al.*, 1993), infested with *F. occidentalis* in glasshouses and in the field respectively. Parasitoids were reared in the laboratory since then on the light colour-form of *Frankliniella schultzei* (Trybom) using the bean pod method and tested in 1991 (age) and 1992 (size). *C. americensis* ('Willcox') was collected in Arizona – USA, May 1993, and kept on *F. occidentalis,* cultured on pine-pollen and honey-water until testing in 1995.

Preparation of hosts and parasitoids

We performed three types of experiments for strains of both species of parasitoids: 1. age class experiments, 2. size class experiments and 3. a time related experiment.

1. Age experiment: The pollen rearing method (Murai, 1990) was used to synchronise host-age. Larvae of *F. occidentalis* reared at 25 ^{0}C were divided into 7 age classes of 24 hrs and offered to a single female of *C. menes*. In addition a group of prepupae and pupae was tested. Using the pollen rearing method, at 25 ^{0}C age classes of 0-24, 24-28 hrs and part of the 48-72 hrs correspond with the first larval stage, and 48-72 hrs up to 144-168 hrs correspond with second stage larvae. Females of strain 'Hyères' were used as test material. In the experiment females were 2 days old and were experienced on the first day, i.e. they had at least one oviposition experience prior to testing. For each age class 10 females (*C. menes*, Hyères) were tested. Once-inserted larvae were not replaced by a fresh larva.

2. Size experiment: *F. occidentalis* larvae were divided into seven different size groups ranging from 0.5 mm to 1.1 mm. Size is correlated with age (see figure 4), in particular until day 3. Larvae of size classe of 1.0 and 1.1 mm were selected amongst groups of different ages (age: 3-5 days). Females of two strains of *C. menes* (brown abdomen, collected in Cabrils (Spain), September 1991) and strain AB (yellow abdomen, collected near Brignoles (France), September 1990), reared in the laboratory on *Frankliniella schultzei* Trybom, were used as test material. Only experienced two day old females were used, and they had at least one oviposition experience 4-8 hrs ('Cabrils') or

20-28 hrs ('Brignoles') prior to testing. For every host size class five females of each strain, size 0.7 mm, were observed. For *C. americensis* 10 females were followed in a similar set-up; they were experienced on their first day and stored overnight in a glass vial with some honey.

3. Time experiment (eight hour period exposure): In this experiment host acceptance behaviour was observed and egg-laying capacity measured for both species for a continuous period of 8 hours. A single female was placed in an arena with 25 host larvae, 24-48 hours old *F. occidentalis*, for one hour. In a first series the behaviour of the female was observed and registered continuously: time spent on host handling components, walking and standing still. Each hour she was transferred to a new, similar cell. Larvae were taken out immediately after they were inserted and replaced by the fresh one. Inserted larvae were dissected simultaneously. In a second series a similar procedure was followed, except that no behavioural observations were made. In a control series we ran parallel a female was left with 25 larvae for the whole 8 hour period. Larvae were dissected and checked for eggs immediately thereafter. This experiment was performed for 10 females of a yellow strain of *C. menes* ('Yolo' - USA) in November 1993 and for 13 females of *C. americensis* ("Willcox') in May 1994, except that for the latter only the second transfer series was performed. Experiments with *C. menes* were performed in a Munger-cell (25 mm diameter, 10 mm high), with a sweet pepper leaf as host substrate. Those with *C. americensis* in small Petri dishes (50 mm diameter, 20 mm high) with gauze on the top and a bean leaf disc (*Phaseolus vulgaris*) (40 mm diameter) floating on water.

Experimental set-up

As observation units in we used a Munger-cell modified after Tashiro (1967). Twenty-five host larvae of one size class were introduced with a fine brush (000) into the cell - 25 mm diameter, 10 mm high. The underside of a sweet pepper leaf was used as a host substrate. One to two hours later, after the larvae had settled, a single female parasitoid was introduced. Immediately after introduction the wasp's behaviour was observed continuously with the use of a stereomicroscope. In the age experiment wasps were followed for 1 hour, in the size experiment for the first 10 encounters (contacts) with host larvae (*C. menes*) and for *C. americensis*, the first 10 insertions as well. Parasitised larvae were removed during the size experiment, but not during the age experiment. Wasps that did not start searching within 20 minutes were discarded and replaced by a new female. All observations were done in a climate room, 21 ^{o}C ± 1 ^{o}C.

Behavioural components of Ceranisus

Host-handling events were subdivided in an encounter (antennal contact), attack, insertion and host-feeding. These are defined as follows: when a female parasitoid contacts a host with her legs and/or antennae ('encounter') she bends her abdomen towards the larva, overpowers the host larva in a short struggle, extends her ovipositor and tries to insert it into the larva's body ('attack'). After inserting the ovipositor a *C. menes* female is turning 180^{0}, lifts the larva up in the air ('lifting') or remains in a 'tail-to-tail' position ('tailing'), attempting to oviposit ('insertion': the period during which the ovipositor remains inside the larval body) (figure 2). When after an insertion the wasp turns around and starts feeding on the larval body fluids this is considered as host-feeding; repeatedly stinging and feeding can occur in one sequence. In addition to the specific host-handling events we also registered walking activity, standing still and preening behaviour. A detailed scheme of the different behavioural components of the encounter and attack sequence of *C. menes* is given in figure 1. *C. americensis* has a basically different approach in her attack and parasitisation sequence of host larvae: while *C. menes* quickly turns around after insertion of the ovipositor, lifting the larva in the air or tailing it behind her, *C. americensis* stays in the original insertion position, bending her ovipositor between her legs. This is consistent for the different strains and over the range of hosts we tested. All behavioural components were recorded using The Observer 2.0 (Noldus IT - Wageningen) to register

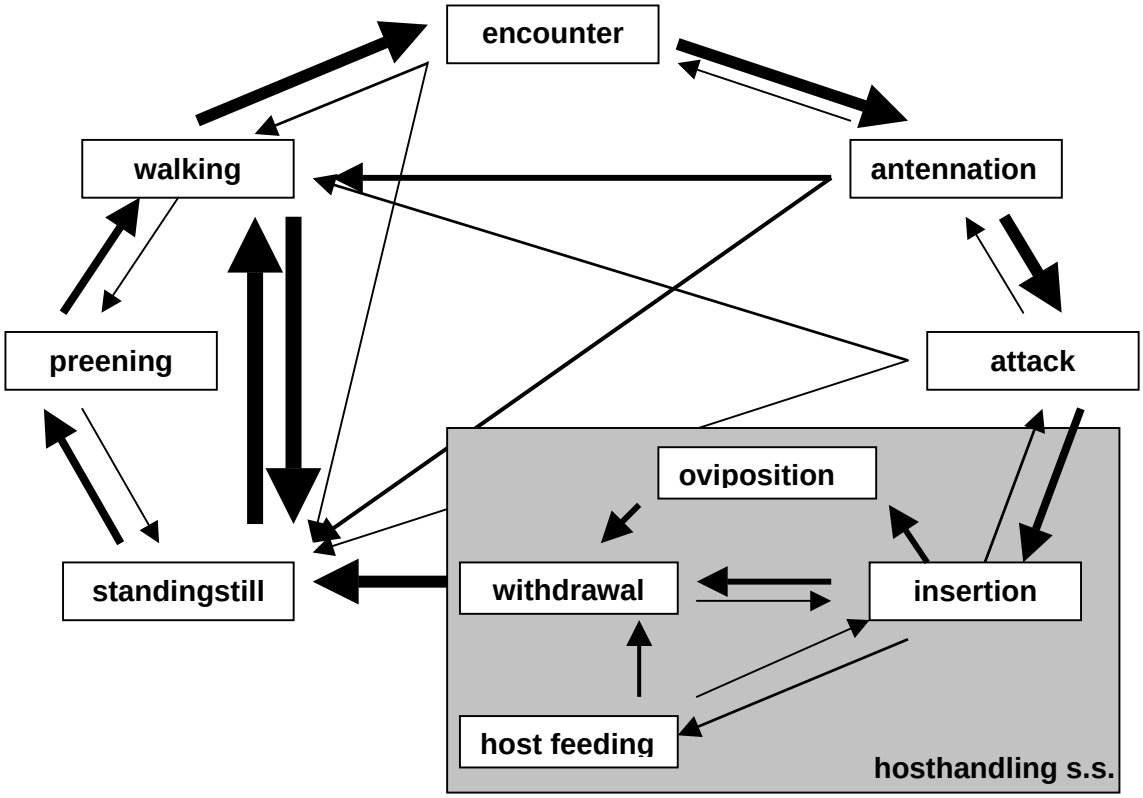


Figure 1. Sequence of behavioural components of *Ceranisus menes* and *Ceranisus americensis*, when searching for and handling of thrips host larvae. Thickness of the arrows indicates the relative frequency of events.

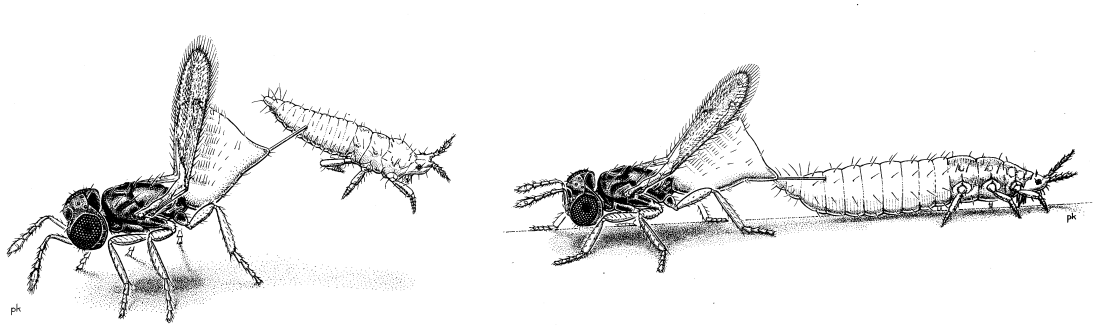


Figure 2. Oviposition postures of *Ceranisus menes* (yellow, Brignoles') parasitising a thrips larva. Lifting an L_1 (left), tailing or dragging an L_2 (right) (from Loomans & van Lenteren, 1995; drawing Piet Kostense).

and calculate the number, kind, sequence and times of contacts with the hosts. When an inserted larva was taken out of the arena, it was transferred into a reaction tube with pollen and a honey-solution (size experiment *C. menes*) or a sweet pepper leaf disk (size *C. americensis*) in a multi-well (Greiner) 24 compartment cells. All observations were carried out in a climate room, temperature 21 ± 1^0C, humidity >80%, between 9:00am and 6:00pm.

Statistics
From the observations on host acceptance and egg-laying, we calculated the host attack-ratio (the ratio of hosts attacked per encounter) and the insertion-ratio (the ratio of inserted hosts per number of hosts attacked). Attack and insertion-ratio result in the external host acceptance-ratio: the ratio of hosts inserted per encounter. In case larvae were checked for eggs by dissection, we include an oviposition ratio as the number of eggs per number of inserted hosts (internal host acceptance ratio).Finally, an overall host acceptance-ratio was calculated: ratio number of eggs per host encountered. Results were tested statistically between size classes within strains (Kruskall-Wallis tests, $p< 0.05$ and multiple comparison test when significant) and within size classes between strains (Mann-Whitney U or Kruskall-Wallis, $p< 0.05$).

Results

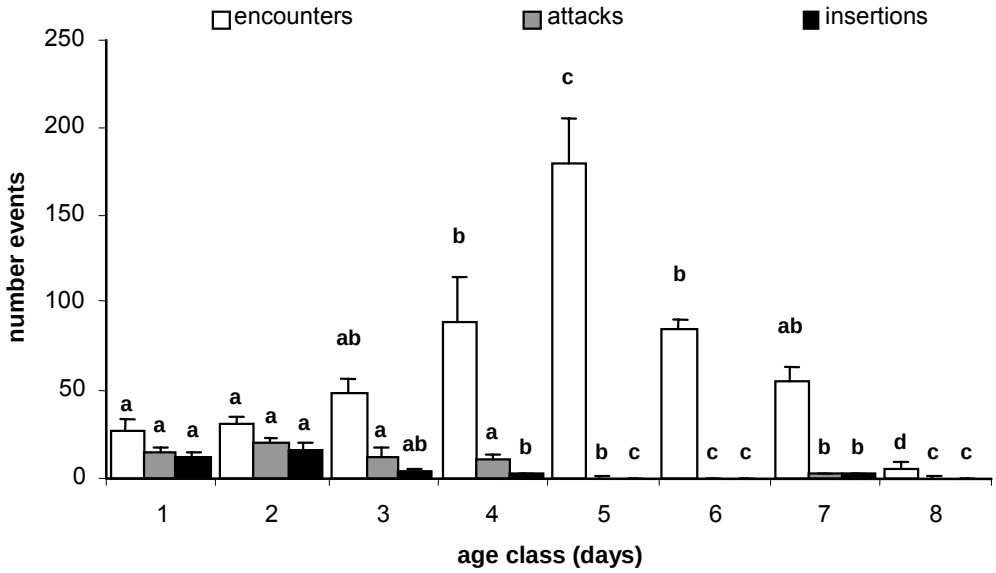


Figure 3. Average numbers of encounters, attacks and insertions (± s.e.) by females of *C. menes* (brown strain, Hyères) when offered different age classes of larvae of *F. occidentalis* during one hour. Significant differences between age classes per behavioural component are indicated by different letters (Kruskall – Wallis test, $p< 0.01$ and multiple comparison test).

1. Age classes
When interacting with *F.occidentalis* larvae of a different age, the numbers of encounters between host and parasitoid are related to the age of the larvae (figure 3): increasing numbers of encounters with age till day 5, and subsequently decreasing thereafter.,That female wasps were less able to parasitise larvae from a certain age class, was mainly due to an increase in activity of thrips larvae (table 1). Larvae which are ready to pupate (day 8) show less activity and number of encounters was very low: Some were attacked, but this was never followed by an insertion. Results show that *C. menes* (Hyères) mainly attacked the youngest age classes (up to day 3, corresponding with first stage larvae) and that host acceptance - measured as insertion of the ovipositor - was most successful in the youngest 2 age classes (table 1). When we consider the extent to which a host is accepted at first (attack/encounter rate, table 1) and the extent to which an attack is completed successfully (insertion/attack rate, table 1), this even becomes more clear. Upon encountering a larva of the first 2 age classes, 60 % of the encounters resulted in an attack, but the attack success-ratio rapidly declined when thrips larvae were older, because they managed to interrupt the attack and escape. The same is true for the insertion success ratio: older larvae are more difficult to insert, indicating that the parasitoid had some difficulty in inserting its ovipositor into these hosts.

Table 1. Average (± s.d.) number of success ratios, times of attack and ovipositor insertion and % of total host handling time by females of *C. menes* (strain Hyères, brown), when exposed to various age classes of *F. occidentalis* larvae/pupae during one hour (Kruskall-Wallis test: $p < 0.01$ all columns; times indicated with different letters are significantly different after multiple comparison test); [a] = average time of successful interactions only, p = pupae.

F. occidentalis Age (days)	# ♀	*C. menes* (brown) average success ratio attack/enc.	insert/attack	average time (sec) [a] total	insertion	hosthandling % total time
1	7	0.60^{a} ± 0.23	0.90^{a} ± 0.07	33.0^{a} ± 37.6	27.8^{a} ± 37.4	14.4^{b} ± 4.3
2	6	0.63^{a} ± 0.13	0.82^{a} ± 0.21	49.7^{a} ± 84.2	38.6^{a} ± 71.4	24.7^{a} ± 7.2
3	8	0.33^{b} ± 0.23	0.47^{b} ± 0.29	32.5^{a} ± 24.4	24.9^{a} ± 22.5	9.3^{ab} ± 6.4
4	6	0.16^{c} ± 0.09	0.15^{c} ± 0.14	12.3^{b} ± 10.6	7.9^{b} ± 7.7	5.1^{b} ± 1.8
5	6	0.01^{d} ± 0.03	0.00^{d} ± 0.00	0.0^{b} ± 0.0	0.0^{b} ± 0.0	4.7^{b} ± 1.3
6	4	0.00^{d} ± 0.00	0.00^{d} ± 0.00	0.0^{b} ± 0.0	0.0^{b} ± 0.0	2.3^{b} ± 0.2
7	2	0.05^{d} ± 0.01	0.83^{a} ± 0.17	20.3^{b} ± 8.3	11.7^{b} ± 7.8	3.7^{b} ± 0.6
8p	3	0.03^{d} ± 0.04	0.00^{d} ± 0.00	0.0^{b} ± 0.0	0.0^{b} ± 0.0	0.4^{b} ± 0.4

success ratio's: number of attacks per encounter and number of ovipositor insertions per attack

The time for parasitising a host (time from encounter until the ovipositor was withdrawn) took 32.5 - 49.7 seconds on average in the youngest age classes (day 1-3), but could last up to 551.3 seconds. Insertion time varied from 24.9 - 38.6 seconds in the first 3 age- classes. Young host larvae became motionless shortly after being tailed or lifted in the air (figure 1), larvae older than 3 days were never lifted and host and parasite stay in a 'tail-to-tail' position, often dragging the parasitoid behind them. Average times of attack and insertion are much shorter from 3 day old (second) stage larvae onwards and probably were too short for depositing an egg successfully. Comparing total host-handling time and the actual insertion time (table 1) shows that at least 5 seconds were spent on encountering and attacking hosts. Partly this was due to repeated attacks on the same host, partly because Hyères females took more time to antennate and inspect the host.

2. Size classes

Size (body length) of *F. occidentalis* larvae is strongly correlated with age until day 3 (figure 4). This period of rapid increase in size coincides with the first and early second larval instar. In the medium and late second instar larvae only slightly increase in size. At the end of the larval period and close to pupation, larvae stop feeding, empty their gut and start searching for a place to pupate. A slight decrease in size is the result.

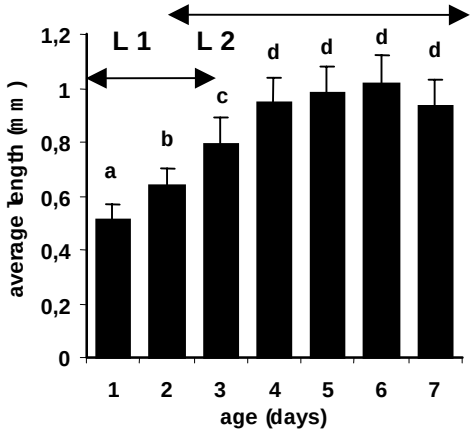


Figure 4. Relationship between the length (mm; ± s.e.) of *F. occidentalis* larvae and the days of juvenile development; at 25 ^{0}C and 16L:8D on a diet of pine pollen and honey-water.

Numbers and ratios

Analysis of the number of events and calculation of the success ratio's (figure 5, table 1) in the different size classes shows that external host acceptance of *F. occidentalis* larvae by *C. menes* and *C. americensis* largely coincides with the size. In *C. americensis* and *C. menes* ('Brignoles') two distinct groups of size classes can be distinguished: sizes smaller and equal to that of the parasitoid (0.8 mm) and sizes which were larger. 'Brignoles' wasps accepted larvae up to 0.8 mm after first contact for 98-84%, 'Cabrils' 85-75%, whereas *C. americensis* attacked almost all larvae encountered (98-92%) (figure 5). Encounters with large sized larvae often were interrupted. The insertion-ratio, a measure for successful completion of an attack, decreased significantly with increasing size for both the brown and the yellow strain of *C. menes,* till 0.39 and 0.17 respectively (table 2). In small sized larvae, 'Brignoles' and 'Willcox' were most successful in completing an attack, 'Cabrils' did so in a gradually decreasing ratio (host insertion-ratio, table 2). In large sized larvae all wasps could finish an attack in 45 % or less of the cases. Attack and insertion ratio result in an overall acceptance ratio (figure 5, black bars). In the first group 98-72% of the larvae encountered were inserted successfully, in the second only as few as 17% (*C. americensis*), 12 % ('Cabrils') and 2% ('Brignoles'). Observations on *C. americensis* up to when 10 hosts were actually inserted shows (figure 6, left) that the number of encounters necessary for that increases sharply from 0.9 mm or larger and as a consequence, it takes 1 hour or more before a wasp completes 10 insertions successfully (figure 6, right) It also shows that females did not easily give up, although a large number of encounters were unsuccessful and not followed by an attack.

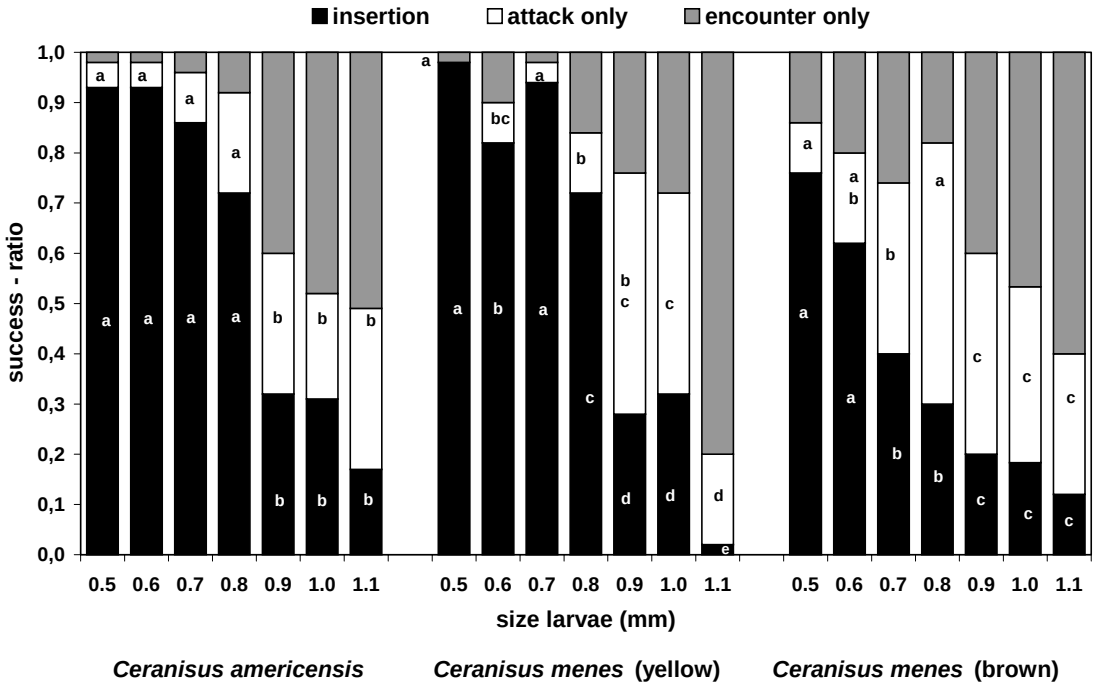


Figure 5. Succes-ratio of different encounter types occurring in host acceptance by *Ceranisus americensis* and two different colour types (yellow – Brignoles and brown - Cabrils) of *Ceranisus menes* and various size classes of *F. occidentalis* for the first 10 encounters with a host. Different letters inside the bars indicate significant differences between size-classes (multiple comparison after Kruskall-Wallis test: $p<0.05$). Average success-ratio's between *C. menes* (both strains) and *C. americensis* (Mann Whitney U-test, Kruskall Wallis test, $p<0.05$) were different for size classes 0.5, 0.7 and 0.8 mm (after Loomans *et al.*, 1997).

Table 2: Host insertion-ratio (fraction of insertions per attack) for *C. menes* ('Brignoles', yellow; 'Cabrils', brown) and *C. americensis* when offered larvae of *F. occidentalis* of different size classes. Averages followed by different letters are significantly different between classes (multiple comparison test, after Kruskall-Wallis test, $p<0.05$) or between strains and species (Mann-Whitney U-test, $p<0.05$), are in bold.

	Larval size class *F. occidentalis*						
strain	0.5 mm	0.6 mm	0.7 mm	0.8 mm	0.9 mm	1.0 mm	1.1 mm
Brignoles	1.00 ±0.00^{a}	0.91 ±0.12^{bc}	0.96 ±0.08^{ab}	0.87 ±0.16^{c}	0.37 ±0.24^{d}	0.46 ±0.28^{d}	0.17 ±0.13^{c}
Cabrils	**0.88** ±0.08^{a}	0.74 ±0.23^{a}	**0.56** ±0.29^{b}	**0.36** ±0.15^{cd}	0.31 ±0.10^{c}	0.43 ±0.22^{bd}	0.39 ±0.38^{cd}
Willcox	0.95 ±0.08^{a}	0.95 ±0.08^{a}	0.89 ±0.14^{a}	0.77 ±0.15^{b}	0.44 ±0.34^{c}	0.58 ±0.21^{bc}	0.36 ±0.34^{c}

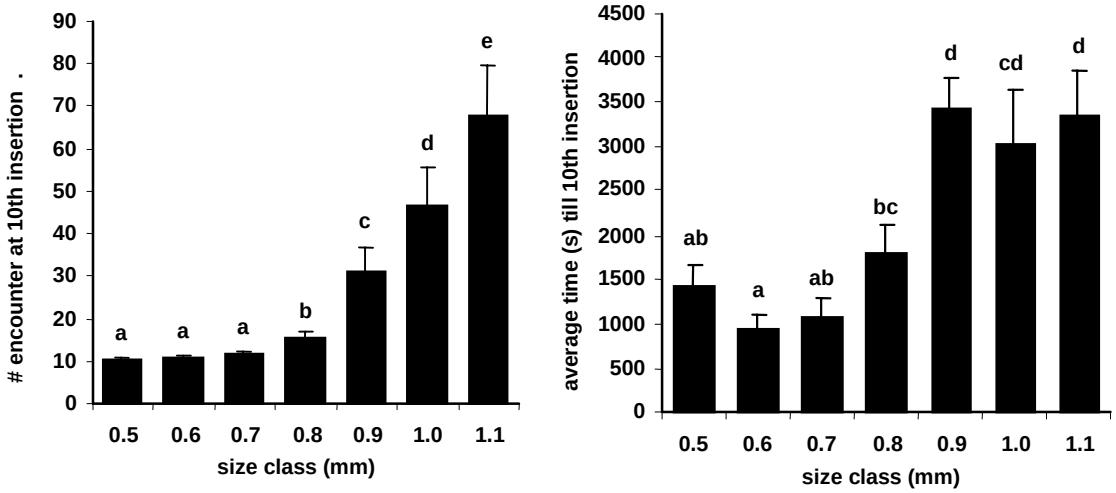


Figure 6. Average number of larvae (± s.e.) encountered (left) by *C. americensis* and average time needed till 10th host was inserted successfully (right); in class 1.0 and 1.1 mm 9 and 6 wasps were used respectively, others failed to insert 10 hosts within the observation maximum of 90 minutes (Kruskall-Wallis test, $p < 0.05$).

Duration of behavioural components

Calculations on the duration of the three host-handling components – encounter, attack and insertion – presented in figure 7 shows that *C. americensis* and *C. menes* 'Brignoles' females in general spent less time contacting and attacking a host than 'Cabrils' females. Of the host handling components, the time of an encounter did not differ regardless if a larvae was attacked or not, except for 'Cabrils' in 2 size classes. Attack times differed, however, between size classes for both *C. menes* strains, but not for *C. americensis* (figure 7). The time taken for an attack generally increased with increasing host size: it took the parasitoid two attempts or more in a row to attack and overpower a host. In both *C. menes* strains an unsuccessful encounter and attack even lasted longer than a successful one in small larvae (0.7 mm or less) because of repeated attempts (figure , bottom)In *C. americensis* the unsuccessful ones took somewhat longer but not significantly. Once the host larva was overpowered, insertion times did not differ significantly between sizes for all wasps, only 'Cabrils' took less time for a larvae of 0.5 mm and of 1.1 mm. There were clear differences, however, between both strains of *C. menes* . Overall host handling times varied from 7.4 - 229.5 seconds for 'Cabrils', and from 2.8 - 150.6 seconds for 'Brignoles'.Extreme insertion times occurred in sizes up to 0.8 mm. In all larvae insertion times were shortest for *C. americensis* (average14.7 – 18.0 seconds), intermediate for *C. menes* 'Brignoles' (16.6 – 28.2 s), whereas 'Cabrils' females took significantly more time (29.2 – 57.2s; figure 7). Larvae of all sizes were lifted (figure

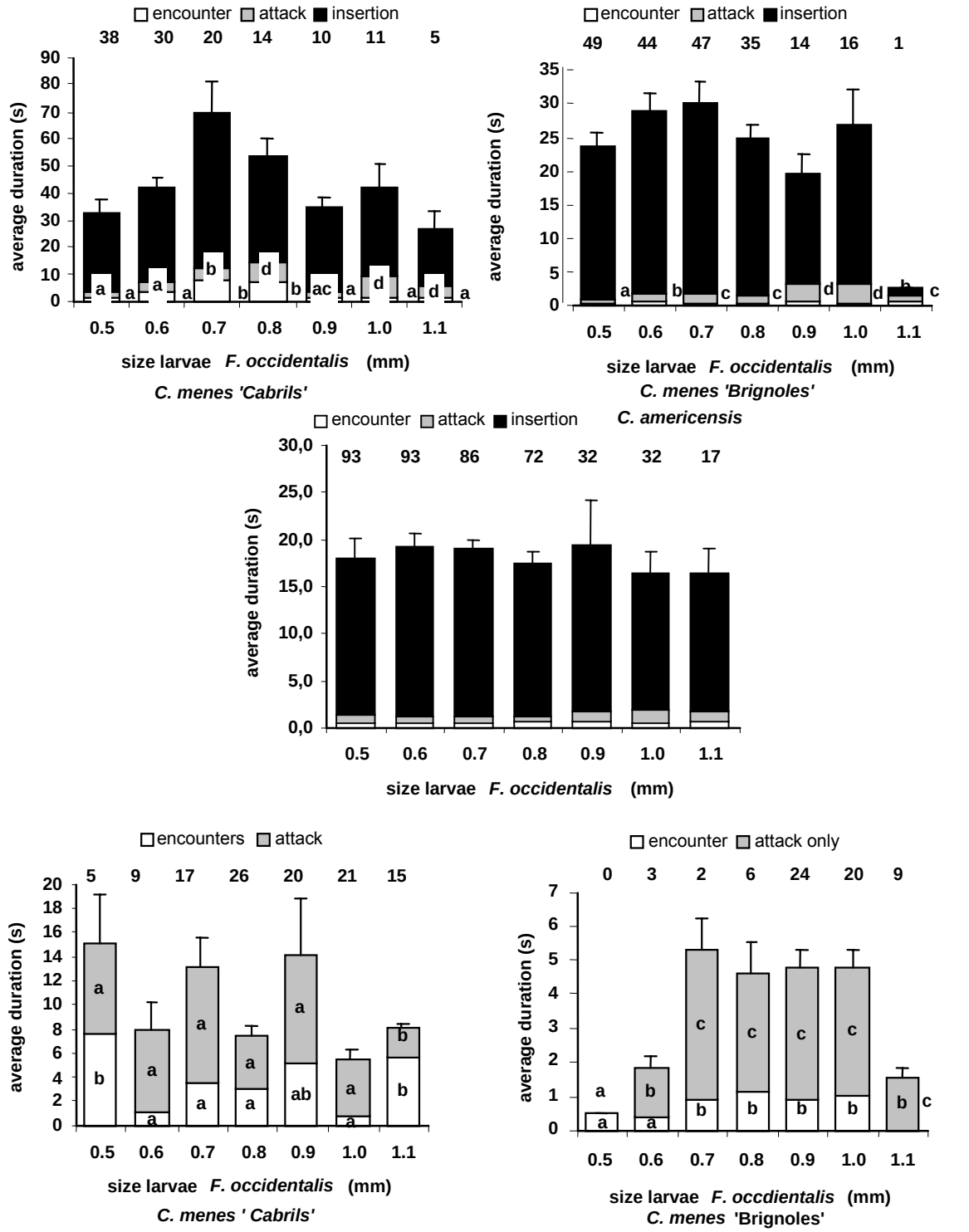
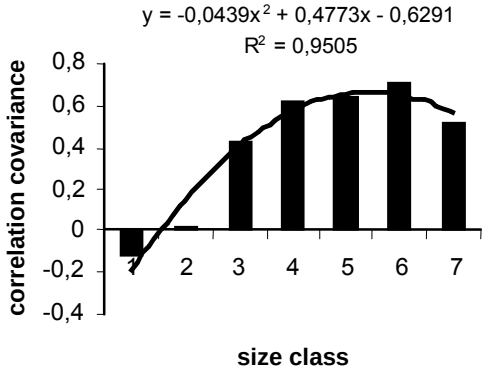


Figure 7. Average duration (± s.d.) of the different behavioural components occurring during host acceptance by two strains of *C. menes* (brown Cabrils', top-left; yellow, 'Brignoles, top-right) and *Ceranisus americensis* 'Willcox' (middle), when exposed to various size classes of larvae of *F. occidentalis*, for the first 10 encounters per female. Durations of unsuccessful attacks are given for 'Cabrils' (bottom left) and 'Brignoles' (bottom right). Others were not significant. Averages followed by different letters within each column are significantly different between classes (multiple comparison after Kruskall - Wallis test : $p < 0.05$); number of events are indicated in top of the graph (n=10 females) Insertion times preceding host-feeding ('Brignoles' 226.0 ± 38.7 sec (n=3), for 'Cabrils' 251.7 ± 105.2 sec (n=7), for *C. americensis* 311.3 ± 53.4 sec, n=9) are excluded.



$$x,y = \frac{Cov\ (x,y)}{\sigma_x * \sigma_y} \quad (1)$$

$$Cov\ (x,y) = \frac{1}{n} \sum_{i=1}^{n} (x_i-\mu_y)(y_i-\mu_y) \quad (2)$$

x_i = duration insertion
y_i = oviposition (0 or 1)
μ_i = expectation valuse duration oviposition
μ_y = expectation value oviposition success
σ = deviation
n = number of samples

Figure 8. Comparison of the correlation (coefficient of covariance) between the duration of (ovipositor) insertion by *Ceranisus americensis* and the value of oviposition success (egg found) for different size classes of *F. occidentalis* larvae for the first 10 encounters with a larva. The trend-line indicates the relation between the size of the larvae and the correlation coefficient (n=285 larvae).

2) by females of both *C. menes* strains (40-70 % of the encounters, 10-30 % in size-class 0.5 mm), but with increasing size larvae had to be lowered more often. When host and parasitoid were in a tailing position, larvae tried to escape by crawling away, dragging the wasp behind her (figure 2). Large sized, physically strong larvae thus managed to reduce insertion time.

Dissections

Because of a strong drop in relative humidity in the climate cell, the attempts to rearing the larvae individually failed for both *C. menes* strains, and because no significant numbers of dissections could be made on dead larvae, we cannot present any oviposition results. Results for *C. americensis* show that 88% of the 0.6 mm larvae that were inserted and 37 % of the largest size class, actually contained an egg (figure 9). Covariance analysis shows that the occasion in which an egg is found in different size classes of *F. occidentalis* is correlated to the duration of ovipositor insertion by the female (figure 8). The hyperbolic trend indicates a size dependent relationship: no correlation at the 2 smallest size classes (L1 - larvae), a strong correlation for the larger size classes (L2 - larvae). When trying to parasitise large larvae, insertion time for a *C. americensis* female to lay an egg is too short: the larvae manages to wriggle and drag itself out. Although the

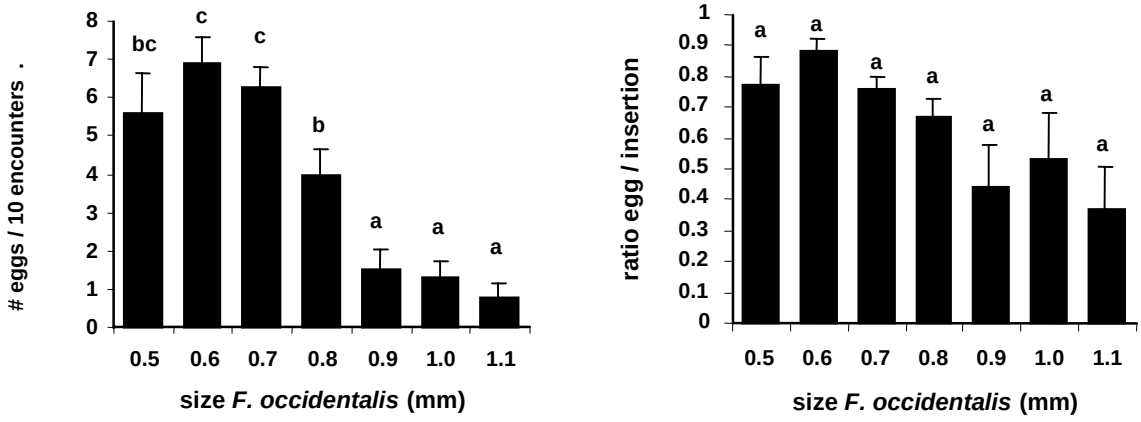


Figure 9. Average number of eggs (± s.e.) for *Ceranisus americensis* during the first 10 encounters with larvae of different sizes of *F. occidentalis* (left) and egg / insertion ratio (number of eggs per successful insertions right); different letters indicate significant differences between size classes (Kruskall – Wallis, $p < 0.01$) (trendline egg / size: R^2=0.87 left and R^2 = 0.82 right)

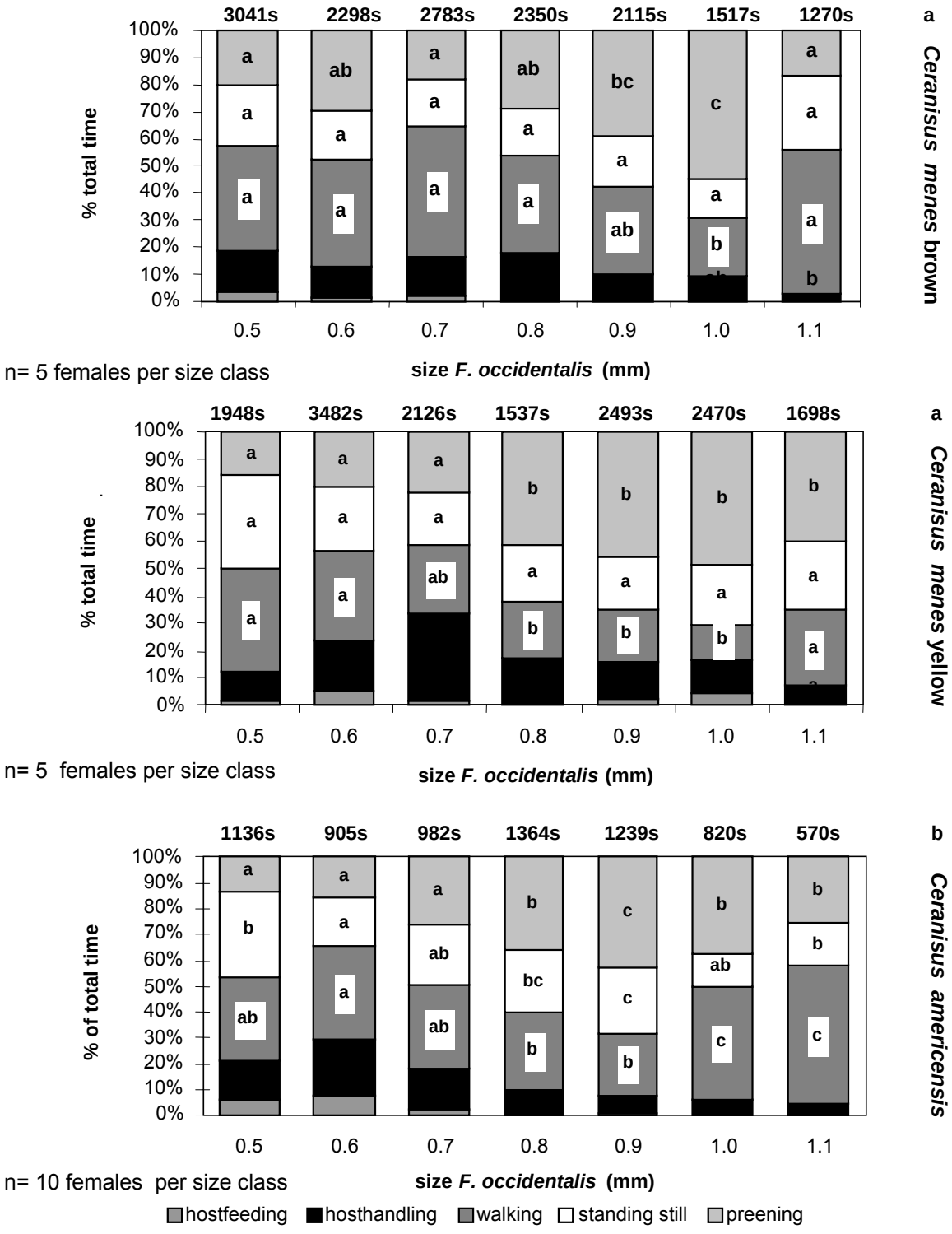


Figure 10. Relative distribution of 5 catagories of behavioural components for *Ceranisus menes* (brown type 'Cabrils' - top and yellow type 'Brignoles' - middle) and *Ceranisus americensis* (bottom) for the first 10 encounters with larvae of *Franklineilla occidentalis* in 7 different size cohorts (0.5-1,1 mm body length). Per species letters indicate significant differences per behavioural component between different size classes (Kruskall - Wallis test, $p < 0.05$). Average total times per size class are mentioned on top of each bar.

minimum time needed to lay an egg was 1.0 seconds and maximum time needed was 57.3 seconds, the relative frequency of insertion times in the larvae with 'no-egg' was more skewed than for larvae with an 'egg' (Mann-Whitney U-test, $p < 0.01$). Dissection results show that the egg – insertion ratio tends to decrease with size: there is an overall decrease in oviposition from 68% in small larvae to 10 % or less in large larvae (figure 9, left).

Overall searching time

The overall searching time that wasps needed to encounter 10 larvae of *F. occidentalis* in a row varied per strain and species, and the larval size group involved (figure 10). Overall, *C. americensis* spent less time than both *C. menes* strains. In part this was due to direct differences in times necessary for handling hosts, but largely in a general searching pattern of a specific strain: the relative time distributions of wasps of a certain strain within a certain size class looks similar. From size class 0. 8 mm onwards, relatively less time is spent on interactions with the hosts and searching on the host substrate, and more time is spent on preening. This is a direct result of host larvae actively resisting against being attacked and defending themselves and by producing anal droplets. All strains needed less time to encounter 10 larvae of the 2 largest size groups, largely because encounters were not completed and wasps refrained from attacking the host or were incapable doing so.

3. Time classes

Parasitoid activity as a measure for external host acceptance was the first aspect considered in this experiment. Behavioural observations show that *C. menes* females spent 90-95% of their time on walking and standing still and this only changed slightly at the end of the 8 hour period, when about 60% of the time wasps were standing still (figure 11, left). Also the total time they spent on host handling decreased from 10% in the first two hours, to 5% at the end of the period. Insertion time was a major part of the time handling hosts, but only during the last two hours insertion occurred about 10 times less than at the start (table 3). Wasps spent increasingly more time on host feeding (figure 11, right). In general, wasps became less active and when insertion was successful, more host-feeding occurred thereafter.

That parasitoids were less active is also shown by the total number of encounters: these significantly decreased from the 1st till the 8th hour (table 3). A decrease in interactions with the host larvae already started after the first two hours, but after 4 hours this became significant (table 3). In absolute numbers, hosts were less frequently encountered, less larvae were attacked and less insertions occurred during the last 4 hours. Wasps were also relatively less active (less attacks followed upon encounter) and were somewhat, but not significant, less successful in finishing an attack, resulting in an overall decrease of hosts inserted per encounter with 60% (table 3, figure 12 left). At the same time, once a wasp accepted a larvae and started an attack, she was similarly able to insert the larva, regardless the time interval. It suggests that a host larvae is able to escape, mostly during external examination, when females have only antennal contact. This could be either due to rejecting more hosts or that hosts were escaping more often upon contact.

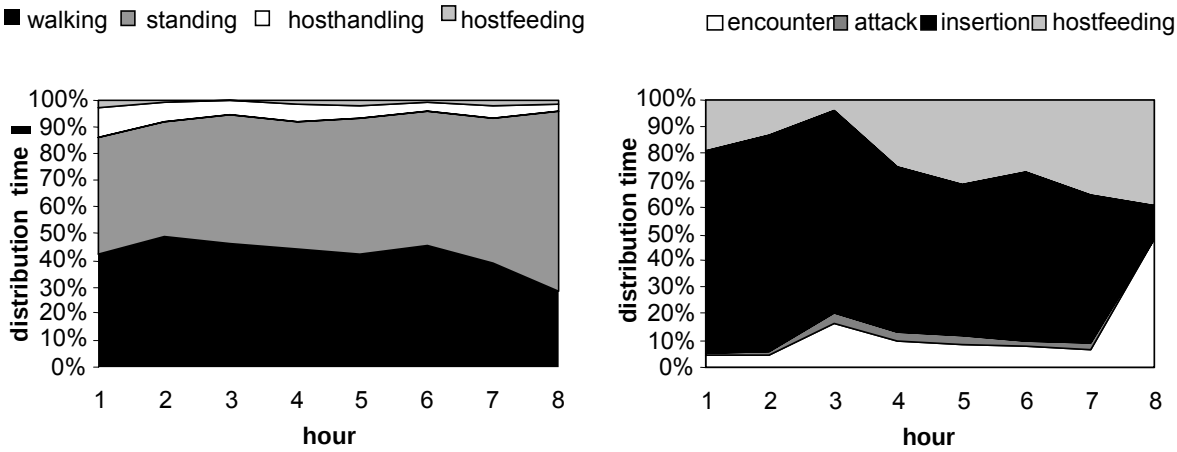


Figure 11. Behavioural data for *C. menes* (yellow, 'Yolo') when exposed to batches of 25 first stage larvae of *F. occidentalis* for a continuous period of 8 hours; every hour wasps were transferred to a new batch of larvae. Changes in total searching (number of events: top - left) and relative time distribution (within handling components 'encounter'–'attack'–'insertion'-'hostfeeding': top - right).

Table 2. Averages (± s.e.) of frequencies of events and calculated individual ratio's for the behavioural components 'encounter'-'attack'-'insertion' per block of 2 hours over an 8 hour period per 10 females (*C. menes*, strain 'Yolo'). att/enc = attack ratio per encounter, ins/att = insertion ratio per attack, ins/enc = insertion ratio per encounter. Significant differences between hours is indicated by different letters (Kruskall –Wallis test, $p < 0.05$).

	frequencies events			calculated ratio's		
time	encounter	attack	insertion	att/enc	ins/att	ins/enc
1-2	27.6 ± 3.2 ^{c}	23.8 ± 3.3 ^{c}	22.2 ± 3.4 ^{c}	0.84 ± 0.04 ^{c}	0.91 ± 0.03 ^{a}	0.77 ± 0.05 ^{c}
3-4	28.2 ± 2.1 ^{c}	19.8 ± 2.6 ^{c}	16.9 ± 3.0 ^{c}	0.66 ± 0.07 ^{a}	0.85 ± 0.07 ^{a}	0.56 ± 0.08 ^{b}
5-6	19.4 ± 3.0 ^{b}	13.0 ± 2.1 ^{b}	10.6 ± 0.6 ^{b}	0.65 ± 0.04 ^{a}	0.71 ± 0.08 ^{a}	0.47 ± 0.07 ^{ab}
7-8	10.7 ± 2.0 ^{a}	3.0 ± 0.6 ^{a}	2.6 ± 0.6 ^{a}	0.42 ± 0.09 ^{b}	0.78 ± 0.12 ^{a}	0.34 ± 0.09 ^{a}

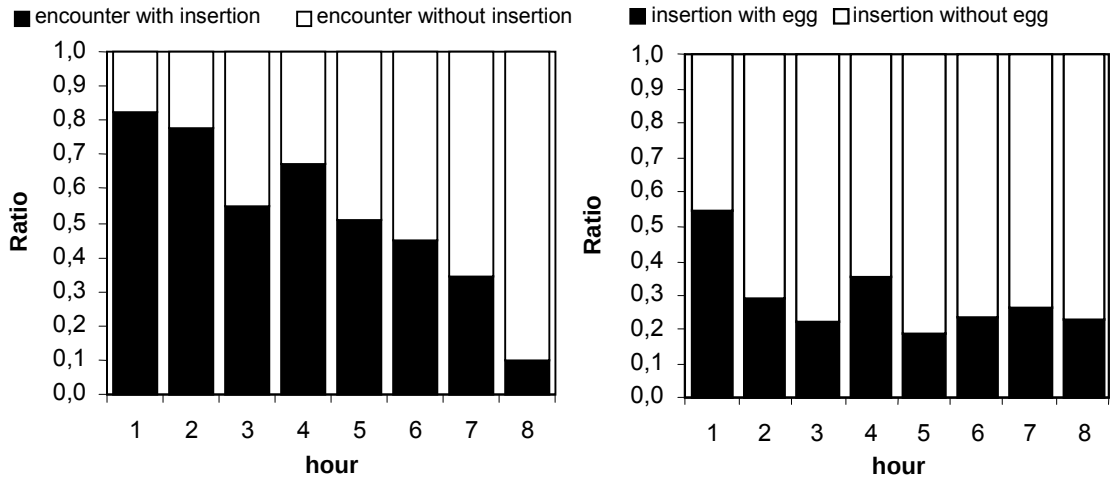


Figure 12. Ratio of successful insertions (left) and successful ovipositions (right) during an 8 hour period by *C. menes* (strain 'Yolo', yellow), per interval of 1 hour; linear regression of insertion/encounter ratio and time is $y = 0.885 – 0.542x$, $R^2 = 0.294$, $p < 0.01$; linear regression of egg/insertion ratio and time is $y = 0.488 - 0.409x$, $R^2 = 0.167$, $p < 0.01$.

Acceptance upon internal examination, as measured by the ratio of egg-laying, also decreased in time, but less drastically then after external examination (figure 12, right; linear regression analysis of insertion / encounter ratio and time: $y = 0.885 – 0.542x$, $R^2 = 0.294$, $p < 0.01$; linear regression of egg/insertion ratio and time: $y = 0.488 - 0.409x$, $R^2 = 0.167$, $p < 0.01$). During the first 2 hours about 60% of the insertions was followed by an oviposition. After this time the egg / insertion ratio decreased to 20-30%. This could be explained either because females were less motivated after the first 2 intervals or that they became egg limited: the number of matured eggs decreased rapidly and females did not lay eggs in every larvae they inserted. That females ran out of mature eggs is also indicated by an increase in host-feeding: at the end of the period host-feeding became more apparent: the ratio increased about two times (18% in the beginning to 38 % at the end; figure 11, right). When dissecting thrips larvae that were host-fed, we never found a parasitoid egg.

Analysis of our observations and calculations shows that, within *C. menes*, the total number of eggs found after dissection largely differed with the type of exposure (figure 13): when transferred every hour, significantly more eggs were found (28.3 eggs / female) than when parasitoids were left with the same hosts non-stop for the full 8 hour period (11.2 eggs / female) . The observed females scored intermediate. The difference is due to a difference in number of total hosts offered during 8 hours: 200 in the transfer and 200 + 463 replacements in the observation series and 25 in the non-transfer series (*C. menes*). In the latter series, after a short time (based on the outcome from the transfer series, between 1 and 2 hours, see figure 14) all host larvae have likely been encountered and inserted. As *C. menes* is able to refrain from egg-laying when encountering previously parasitised hosts (Banasik, 1994), they soon will have become inactive. Dissection results confirm that females refrained from laying eggs: during 8 hours more than 1 egg was found on 2 occasions only for *C. menes* (out of 164 parasitised larvae) and no case of superparasitism occurred in *C. americensis*. The difference between the transfer with and without observation (28.3 and 16.5 eggs / female respectively) is likely due to the disturbance by the observer, taking out inserted larvae and replacing them with a new one. On average 17.5 parasitised larvae were found per female *C. americensis* during 8 hours.

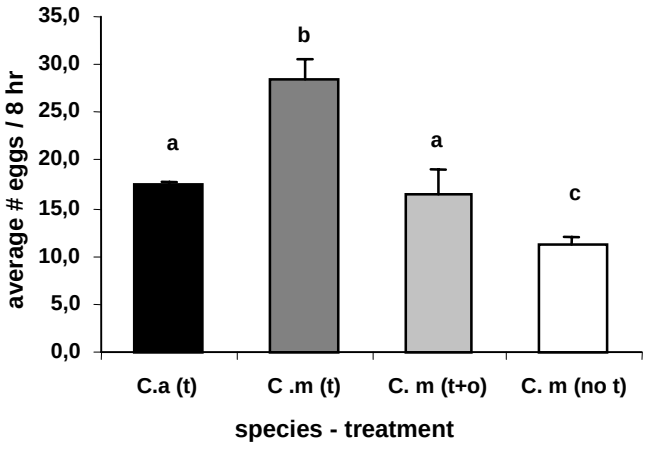


Figure 13. Average total number of eggs (± s.e.) laid by *C. menes* ('Yolo') and *C. americensis* ('Willcox') when exposed to 25 larvae L_1 of *F. occidentalis* during a continuous period of 8 hours in different treatments: 't+o' = behavioural observation and hourly transfer of parasitoid females, inserted thrips larvae were replaced by fresh larvae upon insertion; 't' = hourly transfer of parasitoid females, no observation; 'no t' – no transfer, continuous exposure for 8 hours. Significant differences between species – treatments are indicated by different letters (Kruskall- Wallis test, $p < 0.05$).

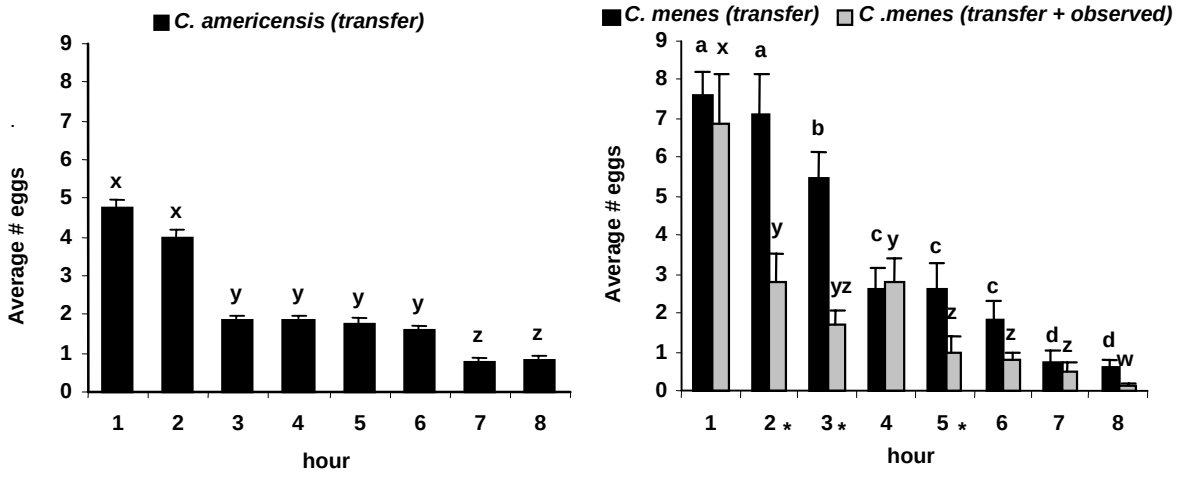


Figure 14. Average number of eggs found (± s.e.) per hour by *C. menes* ('Yolo') and *C. americensis* ("Willcox') over a continuous period of 8 hours and different treatments. Significances are indicated between species (*): M-W ($p < 0.001$) and within a species between hours (abc, wxyz) Kruskall-Wallis ($p < 0.001$); Linear regression: *C. americensis:* $y = +5{,}393 - 0{,}639x$; $R^2 = 0.537$; *C. menes* (transfer) $y = +8.496 - 0.778x$; $R^2 = 0.606$; *C. menes* (transfer+observed) $y = +4.560 - 0.537x$; $R^2 = 0.408$.

Table 3. Average duration (in seconds ± s.e.) of different behavioural components of *C. menes* (strain 'Yolo') upon successful insertion of a *F. occidentalis* larva; every hour wasps (n = 10) were transferred to a new group of larvae (25 L_1). No significant differences were found between separate behavioural components when an egg was deposited or not (Mann-Whitney U test); Kruskall - Wallis test revealed no significant changes in duration between individual hours during the 8 hour observation period.

Hour	Nr. larvae total	(-egg, +egg)	Duration (s.) encounter	attack	insertion	total handling
1	122	(54-, 68+)	1.1 ± 0.4	0.3 ± 0.0	19.7 ± 3.1	21.1 ± 3.2
2	93	(66-, 27+)	0.6 ± 0.1	0.4 ± 0.0	16.8 ± 2.6	17.8 ± 2.6
3	74	(57-, 17+)	0.7 ± 0.1	0.4 ± 0.0	20.3 ± 4.9	21.4 ± 4.9
4	86	(58-, 28+)	1.2 ± 0.2	0.5 ± 0.1	11.7 ± 1.3	13.2 ± 1.3
5	54	(45-, 9+)	0.8 ± 0.2	0.4 ± 0.0	20.3 ± 5.3	21.5 ± 5.3
6	34	(24-, 10+)	0.8 ± 0.2	0.3 ± 0.1	12.8 ± 2.0	13.9 ± 2.0
7	19	(15-, 4+)	1.0 ± 0.3	0.4 ± 0.1	20.4 ± 4.1	21.9 ± 4.2
8	5	(4-, 1+)	0.4 ± 0.1	0.3 ± 0.1	14.7 ± 4.3	15.6 ± 1.4
Total	487	(323-, 164+)	0.9 ± 0.1	0.4 ± 0.0	17.4 ± 1.4	18.6 ± 1.4

Observations made in the transfer series shows that the number of hosts receiving an egg decreases significantly over time for *C. menes* (figure 14, right) and *C. americensis* (figure 14, left). Unfortunately, we cannot directly compare the absolute number of eggs laid by both species, because the set-up and larval density in both experiments were different. For *C. americensis* 1963.5 mm^2 = 78.54 mm^2 was available per larva in the Petri dish, whereas for *C. menes* this was 490.87 mm^2 = 19.64 mm^2 per larva in the Munger cell. The 4 times higher density for *C. menes* will have had its effect, especially in the first hours when larvae were more easy to find. During the second half the *C. menes* females refrained from searching and less encounters occurred and less encounters were completed successfully (table 3) .

Comparing the duration of different behavioural components of *C. menes* ('Yolo') over time (table 4) shows that upon successful insertion, no significant differences were found between the individual behavioural elements when an egg was deposited or not (Mann-Whitney U-test, $p > 0.05$). This did not change during the 8 hour period. Overall (Kruskall – Wallis test) no significant differences were found in duration of an insertion, with or without an egg.

Discussion

The results on host acceptance indicate that during a small part of juvenile development thrips larvae are vulnerable to parasitism by *Ceranisus* species. However, the actual host range of a parasitoid depends on the probability of a host being found (ecological host range), host defensive reactions (behavioural interactions) and host suitability (physiological host range). On the other hand, when the parasitoid is unsuccessful in locating a host, in laying an egg and in regulating its development inside a host, the host has "obtained" an ecological, behavioural and physiological refuge. Asynchronous development of the subsequent generations of hosts and parasitoids can add a temporal refuge as well. Host-age structure can provide a refuge from parasitism (Kistler, 1985) and predation (Hassell & May, 1973). Differences in parasitoid egg distributions found may be the result of several, different processes (van Lenteren, 1994), including morphological factors, behavioural interactions and encounter probability. Differences in host age quality and suitability for development and parasitism may be biased as a result of a combination of these factors (Harvey *et al*., 1994). We will in detail discuss the relevance of these aspects to our parasitoids below.

Behavioural interactions

Behavioural observations on different age and size classes show that for both *Ceranisus* species their host preference is the result of actions by the wasp and reactions by the host she encounters. This makes that both species are limited in their host choice and are restricted to the acceptance of small sized, young *F. occidentalis* larvae. The 8 hour time series indicates that relatively more larvae can escape from parasitism when encountered late and egg-load is depleting: the activity of *C. menes* the wasps decreases already after a few hours, resulting in a few ovipositions at the end of that period. The increase in host-feeding we observed towards the end of the period, and thus the need for nutrition (Jervis & Kidd, 1986), is an indirect indication for this as well. Both species are syn-ovigenic (sensu Jervis *et al.*, 2001), but the amount off eggs and the egg-maturation rate are lower in *C. menes* than in *C. americensis*. However, for *C. americensis* the absolute number of ovipositions was lower, which is partly explained by an additional searching component, because the arenas were 4 times as large. Still, the decrease in numbers of hosts accepted over time can only be explained by a decrease in motivation due to the interaction with the host larvae. Learning could be involved as a reaction to series of unsuccessful encounters and attacks, as seen by a decrease in activity by *C. menes* towards large sized hosts. A difference in body cuticle thickness of both host stages, making penetration by the ovipositor impossible, might be relevant for thrips as well, as sometimes we observed in wasps they had difficulties to insert their ovipositor. But because these larvae resist heavily we could not separate both factors clearly. Offering immobilised or anaesthesised hosts (Hildebrands *et al.*, 1997) could indicate whether this is relevant for thrips or not.

The host examination and acceptance behaviour found for *C. menes* and *C. americensis* is comparable to that observed in other thrips-parasitoid combinations (Russell, 1912; Williams, 1916; Bailey, 1933; Sakimura, 1937; Saxena, 1971; Carl, 1971; Hirose, 1989): once a host is encountered and examined with the antennae, the ovipositor is thrusted forward between the legs and inserted into the host's thorax or abdomen. Most parasitoid species stay in this position, but *C. menes* immediately turns 180^0, lifting the

vigorously moving larvae up in the air (Carl, 1971; Murai, 1988; Galazzi & Bazzocchi, 1993; figure 2). Lifting the larva up in the air, allows the parasitoid to have better control over it. With large larvae, wasps often stay standing tail-to-tail to their host (figure 2), but insertion times were not significantly shorter (figure 7). *C. americensis* stays in the original insertion position. Once inserted, first stage larvae become paralysed or immobilised, but second stage larvae keep wriggling and resisting, dragging the female behind her, trying to escape. In other experiments (chapter 5), however, we did not find any correlation between the duration of an insertion and the presence of an egg in 1-2 day old larvae.

Our behavioural observations show that acceptance of *F. occidentalis* larvae by *C. menes* and *C. americensis* decreases with size. As age, and thus larval instar, is strongly correlated with size, parasitoids do not succeed in parasitising larvae of 4 days and older. Age class experiments with another *C. menes* strain (yellow from Pescia, Italy) (Fourez & van Impe, 1995) largely coincide with the results we found for the brown strain from Hyéres, in that parasitsation is most effective during the first 3 days. In some cases parasitoids do not seem to prefer any particular size or age (*C. menes: K. pisivorus*- Bühl, 1937; *F. intonsa* - Sakimura 1937; *T. tabaci* - Carl, 1971; *C. russelli*: *C. fasciatus*- Russell, 1912; *C. nubilipennis*: Williams, 1916). Other records state a certain preference, even within the same host-parasitoid combination: parasitoids prefer large (Saxena, 1971 - *T. tabaci*; Bailey, 1933 - *C. fasciatus*) or medium sized larvae (Daniel *et al.* 1983; Daniel, 1986 -*Toxothrips ricinus, Zaniotrhips ricini* and *Retithrips syriacus*). Except that the host acceptance process will be specific for each individual host-parasitoid combination, most records are qualitative and authors do not mention or did not observe interactions over a wide range of size and age classes of the thrips host.

Differences in host-handling times of various strains of *C. menes* parasitising thrips larvae have not been specified before. Times recorded for *C. menes* in general, while handling larvae from other host species fall within a similar time range, and varied from 17-69 seconds (Hirose, 1989) for *Thrips palmi*, 30-60 seconds (Carl, 1971) and 60-180 seconds (Sakimura, 1937) for *T. tabaci*. For *C. russelli* attacking *Calitothrips* oviposition time ranged from 15-240 seconds (Bailey, 1933), but 20-50 seconds according to Russell (1912). *C. americensis* takes less time to parasitise *F. occidentalis* (14-20 seconds) than *T. tabaci* (45 seconds) larvae of the same age (chapter 5). When host feeding occurs (*C. menes, C. americensis, C. loomansi; C. russelli, C. nubilipennis*), no egg is laid, stinging and feeding follow one another repeatedly, up to 12 minutes is spent handling the host and eventually the larva is killed.

A difference in vigour of reaction of the host to the probing of the parasitoid resulting in premature termination of the oviposition process most likely explains the parasitoid's host preference. Because of our direct observations on the parasitoids, we now know that the distribution among host larval age and size is the result of a choice made by the parasitoid and behavioural defensive measures by the host. Of the 3 host handling components we observed, the time of an encounter for a certain species or strain did not differ regardless if a larva was attacked or not. Only times needed for an attack differed between size classes for *C. mene*s strains and *C. americensis,* and generally increased with increasing host size, because it took the parasitoid two attacks or more in a row to overpower a host. Because of this, unsuccessful attacks lasted longer than successful ones in small larvae in *C. menes* (0.7 mm or less; figure 7). However, once the host larva was overpowered, insertion times did not differ significantly between sizes. Each strain and species observed had its specific characteristics in handling hosts. Females of the yellow *C .menes* strain in general spent less time contacting and attacking a host and insertion times were shorter than for females of the brown strain, in particular in the middle size class range. Lifting of larvae was largely restricted to young and small hosts. With an increase in size, larvae had to be lowered more often. When host and parasitoid were in a tailing position larvae tried to escape by crawling away, dragging the wasp behind her. Large sized, physically strong larvae thus managed to reduce insertion time and oviposition results as found for *C. americensis* (figure 8).

The effect of behavioural reactions of the host on differences in acceptance by the parasitoids is most clearly illustrated by the parasitisation success ratio's. All sizes of *F. occidentalis* reacted either by abdominal movements as a defensive response, by excretion of anal exudates or just by moving away upon contact. When this was not effective and the larva was attacked, it tried to escape by wriggling and dragging herself away when inserted. In small sized larvae (0.8 mm, day 3) the wasp could overcome these defense measures, but in larger sized hosts only in a decreasing number of cases: encounters often were interrupted or larvae escaped by running away. Once being attacked, vigorously moving larvae managed to escape increasingly with size, due to their increase in strength. Defensive reactions (wagging, violent abdominal movements, shaking off the attacker) and escape behaviour (walking away, dropping off plants) have been observed in many other thrips species when disturbed (Lewis 1973, 1997; Gross, 1993; Diop, 1999; chapter 7), or when attacked by phytoseiid predators (van der Hoeven & van Rijn 1990; Bakker & Sabelis, 1989). Adult thrips react to encounters with anthocorid predators by running, walking or flying, this in decreasing order (Isenhour & Yeargan, 1978). Behavioural defensive reactions by old and large thrips larvae that prohibit parasitisation have been reported for a number of species (Bailey, 1933; Saxena, 1981; Carl, 1971), and in particular for host species whose larvae are more active and easily disturbed like *T. tabaci*, *F. tritici* (Russell, 1912), *F. occidentalis, Megalurothips usitatus* (Fullaway & Dobroscki, 1934) or *M. sjostedti* (Diop, 1999). If insertion occurs, the larva is dragging the wasp along (Williams, 1916), trying to escape (figure 1). Asian strains of *C. menes* attacked all sizes of larvae of *Frankliniella intonsa* (Sakimura, 1937) and *Thrips tabaci* (Carl, 1971, Sakimura, 1937) indiscriminately, and these showed no violent defense measures. Saxena (1971) recorded a preference for second stage larvae of *T. tabaci*. *C. menes* however failed to complete parasitisation in larvae of *Taeniothrips alliorum* and *Haplothrips floricola* (Sakimura, 1937) and large sized larvae of *T. tabaci* often escaped parasitisation (Saxena 1971), because of vehement defense. *C. menes* attacked *Haplothrips chinensis* (Murai, 1990), but could not develop. *F. schultzei* larvae, which are smaller and defend themselves less violent, are attacked by *C. menes* in both larval stages. Larvae can also defend themselves by excreting anal droplets containing a pheromone. Adults and larvae of *F. occidentalis* produce this alarm pheromone upon disturbance (Teerling *et al.*, 1993ab), e.g. resulting in a (slight) increase in the number of larvae dropping themselves of the plant. Attacking larger hosts thus makes wasps vulnerable to defensive behaviour, especially when small wasps attack host larger then themselves.

As shown here, defensive behaviour of large western flower thrips larvae is rather effective: although attacked initially, few are actually parasitised and wasps gave up and refrained from further attacks. Whether this is actual rejection of a host which is not suitable, adaptive learning or a result of the mere defensive behaviour is not clear. Attacking large hosts likely includes 'costs' for the parasitoid: in addition to extending the total handling time, it also reduces her searching efficiency as more time is spent on non-searching behavioural elements like preening and standing still. In some cases a parasitoid might be injured or unable to search for long periods because of anal excretions that sticks to her body. Larvae of a number of Panchaetothripinae (*Retithrips*, *Caliothrips*, *Selenothrips*, *Heliothrips*, *Rhipiphorothrips*) constantly keep their abdomen in an uplifted position bearing a droplet of intestinal liquid, enclosed by the whorl of anal bristles (Loomans & van Lenteren, 1995) and in other species the abdomen is partly covered with liquid excrements. *C. russelli* observed in the open on a croton leaf while attempting to oviposit in larvae of *H. haemorrhoidalis*, was frequently caught by the sticky excrements produced by this species, and only with great difficulty succeeded in freeing itself (Russell, 1912). *C. menes* attacking early second stage larvae of the same species, ran into the anal excretion droplets, resulting in prolonged periods of preening and unsuccessful attacks. After removing the droplets, *C. menes* stung 6 out of 10 larvae, but oviposition did not occur.

When *T. semiluteus* on the other hand nears a larva of *H. haemorrhoidalis*, it moves around the tip of the abdomen, lifts its middle leg and puts it on the anal droplet, pushes it down with its middle and hind leg and stings the larva shortly.

Developmental interactions

In sessile hosts, such as whiteflies (van Lenteren *et al.*, 1980), scale insects (van Lenteren, 1994), woolly aphids (Mueller *et al.*, 1992), acceptance or rejection of a parasitoid for a particular host size, age or stage is the result of differences in external morphology and internal host quality or suitability for parasitioid development. In free moving hosts such as aphids, lepidopteran larvae and thrips preference of a parasitoid is the result of differences in reaction vigour of the host as well. Size and strength of the wasp relative to the host, and speed become relevant factors.

Both *Ceranisus* species are koinobiont endoparasitoids: parasitised larvae continue to feed and grow during parasitism. Resources for parasitoid growth are not fixed, and development largely depends on feeding rate and capacity for growth during the interaction (Harvey *et al.*, 1994). Parasitised thrips larvae cannot be distinguished in shape or in size from unparasitised larvae until pupation starts. The preliminary results presented above, indicate that once a thrips host of any size is parasitised, the parasitoid herself or the developing egg or larva directly affects or regulates the host physiology, and that host quality is not a direct function of host size at parasitism (Harvey *et al.*, 1994).

Although in our experiments *C. americensis* and the yellow strain ('Brignoles') of *C. menes* were behaviourally more efficient than a brown strain ('Cabrils'), other factors which influence successful parasitism, like internal defense measures by the thrips host and differences in suitability of larvae of different size and age, should be taken into account as well. Encapsulation has not been observed yet, but also it has not been thoroughly checked. Because in both the size and age experiment of *C. menes* we had problems with rearing individual larvae, the relation between size of the larva and oviposition and subsequent developmental success could not be established. Preliminary experiments that we carried out for *C. americensis* also suffered from a high larval mortality, both in the test and in the control series, but still show some interesting results. In a first series, where we exposed 50 larvae in 7 different age groups to a female wasp, results indicate that *C americensis* is able to parasitise and complete development in hosts of all ages, but that the number of parasitoid pupae decreased with increasing age of the larvae the wasp was exposed to (figure 15 right). Experiments we carried out in a

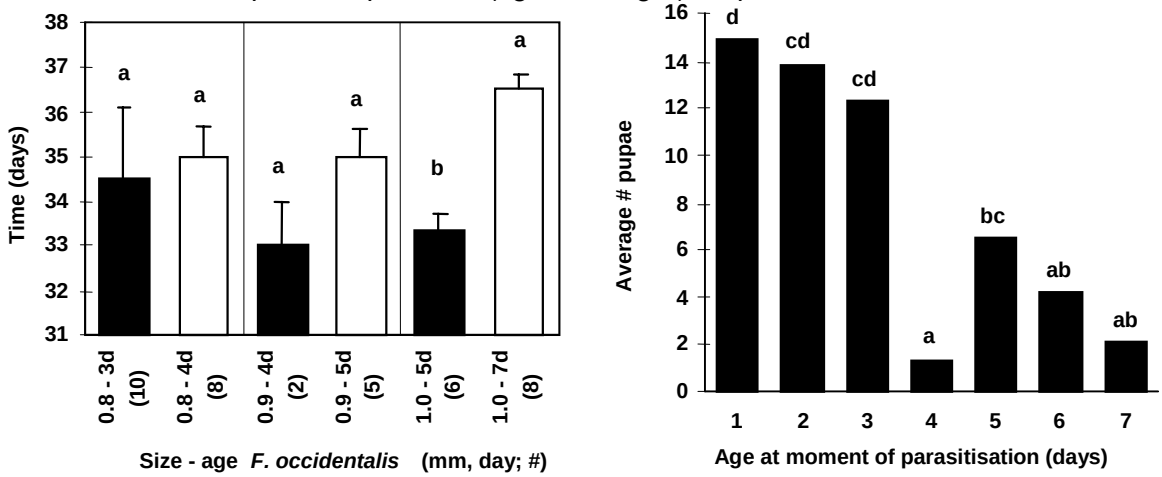


Figure 15. Average number of *C. americensis* pupae developing from *F. occidentalis* of different age groups (right: n= 10 wasps per age class, exposed to a group of 50 larvae each) and developmental time (days ± s.d.) of pupae that developed from same sized larvae, but different in age (left: n= 30 inserted larvae per treatment). Significances according to Mann-Whitney U test (left) and Kruskall - Wallis test (right), $p < 0.05$.

second test on *C. americensis* inserting larvae of a similar size but different in age, also indicate that she was able to develop from larvae up to 7 days old (figure 14, left). Developmental time was not different, but also these results could not be substantiated, because of high levels of mortality in the test cultures. Records for *C. menes* (Murai, 1988) indicate that this species can incidentally develop from thrips larvae that are parasitised which are close to pupation.

How the apparent preference for the 1st larval and early second instar will be translated into their actual parasitism in the greenhouse, will depend on the searching abilities in different crops and thrips infested host plant substrates. The balance between the vulnerability window to the parasitoid and enemy-free space the host creates will determine whether natural enemy will be effective as a biological control agent or not.

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Chapter 5

Host selection by *Ceranisus menes* and *C. americensis*: inter- and intraspecific variation between populations of parasitoids and their thrips hosts.

Antoon J.M. Loomans

Abstract

Host selection studies were performed for *Ceranisus menes* (Walker) and *Ceranisus americensis* (Girault) (Hym.: Eulophidae), solitary koinobiont endoparasitoids of larvae of various thrips species (Thysanoptera: Thripidae). Interactions with first stage larvae of three *Frankliniella* species - *Frankliniela occidentalis* (Pergande), *F. schultzei* Trybom and *F. intonsa* (Trybom) – and of *Thrips tabaci* Lind. were investigated by behavioural and developmental observations, in no-choice experiments. Differences in the behaviour and biology of both the host and the parasitoid species strongly influenced their development and fitness, which was related to a variation on the population level as well. (1) On the host species level, populations of *C. menes* differed in host acceptance, the number of parasitised offspring and parasitoid developmental time. When *T. tabaci* was involved the size of the parasitoid pupae (and adults) was different as well. Parasitisation success of *C. menes* encountering larvae of *F. occidentalis* or *T. tabaci* was related to differences in the colour-type and geographical origin of the population: females of the yellow colour-type of *C. menes* reacted similar to larvae of both species, whereas females of the brown colour-type were more successfully parasitising *T. tabaci* than *F. occidentalis*. *C. americensis* performed better on *F. occidentalis* than on *T. tabaci*.: during one hour more larvae were attacked, more larvae were parasitised of the first, but on *T. tabaci* they were smaller in size and the developmental time was shorter. With respect to different *Frankliniella* species, behavioural differences were much less pronounced, but developmental times differed per host species. (2) On the host population level, parasitoid strains did not differ in the number of parasitised offspring on 2 different populations of *F. occidentalis*, but did so in the size of their pupae and in their developmental time. With respect to *T. tabaci*, effects were clearly stronger: strains of both parasitoid species were less efficient in parasitising *T. tabaci* from Egypt than that from The Netherlands. In conclusion: *C. americensis* preformed best on its original co-evolved host *F. occidentalis*. *C. menes* consists of a large complex of regional populations, that either reproduce sexually or asexually. They differ morphologically, geographically, behaviourally and physiologically in their response to different geographical populations of thrips species, each of them having its unique characteristics. The consequences of variability between pests and parasitoids, on the species and population level, for the selection of natural enemies and the biological control strategies involved, is discussed.

Introduction

Over 5600 species of thrips are described to date from across the world (Lewis, 1997), but just a few per cent of these are of economic importance. The western flower thrips, *Frankliniella occidentalis* (Pergande, 1895), and the onion thrips, *Thrips tabaci* (Lindeman, 1889), are the most important thrips pest species on ornamental and vegetable greenhouse crops in Europe (Tommasini & Maini, 1995). Populations of these very polyphagous species are distributed all over the world, but vary geographically in biological, physiological and ecological traits. In its area of origin, the western part of the USA, *F. occidentalis* is variable in colour and size of the body, and all of these forms have originally been described under a number of different names (Tommasini & Maini, 1995). The three colour forms are sympatric in distribution and interbreed readily in the laboratory (Bryan & Smith, 1956), the pale and

dark form being similarly able to transmit TSWV (Sakimura, 1962). In the field, subspecific host plant relations occur: a New Zealand strain of *F.occidentalis* is highly specific for *Lupine*, it is susceptible to pesticides (Martin & Workman, 1994) and its reproductive potential is significantly lower than that of European strains (De Kogel *et al.*, 1997, 1998). It seems though that only the intermediate form, which is extremely polyphagous and highly resistant to various pesticides (Brødsgaard, 1994), has spread around the world since the early 1980's (de Kogel *et al.*, 1997). Using molecular based methods, Gillings *et al.* (1995), however, detected two genetically different populations of *F. occidentalis* in Australia, whereas and Brunner *et al.* (2002) found that the within species variation in Europe was low.

Populations of *Thrips tabaci* can also widely differ in life-history (Murai, 1990b) and specimens vary in colour and body size and these forms can naturally co-occur in the same region (Priesner, 1960; Schliephake, 1984). Their host-plant range (Zawirska, 1974, 1976) and the ability to transmit viruses (Zawirska, 1976; Wijkamp, 1995) is related to a different mode of reproduction (arrhenotokous or thelytokous) and its sex-ratio varies with locality and season (Kendall & Capinera, 1990). Molecular diagnosis by Jenser *et al.* (2001) and Klein & Gafni (1996) for *T. tabaci* populations in Hungary and Israel respectively have shown that genetic differences coincide with these clear differences in morphological and biological traits. Although in greenhouse grown crops infestations with the indigenous *T. tabaci* have been largely replaced by the introduced *F. occidentalis*, mixtures of both species often co-occur. In summer *T. tabaci* naturally invades greenhouse crops and is part of the thrips pest complex (see Chapter 7). In a number of crops both pest species can be controlled biologically, either by the release of pirate bugs *(Orius* spp.), of predatory mites (*Amblyseius* species) or a mixture of both (Riudavets, 1995). In others, there still is no satisfactory solution available. It is unknown, however, if variability between populations of these pest species is of any relevance to/for biological control.

Thrips parasitoids are currently evaluated for their efficiency to control thrips pests in European greenhouse systems (Loomans & van Lenteren, 1995). Strains of two eulophid parasitoid species have been collected, *Ceranisus menes* (Walker) and *Ceranisus americensis* (Girault) from different parts in the world (Chapter 2). *C. menes* is distributed worldwide, wheras *C. americensis* finds its origin in the (western part of) the USA (Loomans & van Lenteren, 1995; chapter 2). Both species are solitary endoparasitoids of the larval stages of thrips (subfamily Thripinae). *C. menes* is known to parasitise more than 20 thrips species, some of which are important pest species of greenhouse crops like *F. occidentalis*, *Frankliniella schultzei* Trybom 1910, *T. tabaci* and *Thrips palmi* (Karny, 1925) (Loomans & van Lenteren, 1995). Its host range probably still can be extended: on wild plants it has been found regularly in association with a mixture of populations of *Frankliniella*, *Thrips* and *Taeniothrips* (Loomans, 1991). Different colour-types exist and populations differ in their mode of sexual reproduction according to geographic origin: yellow and brown asexual types co-occur in the western hemisphere (Europe, Americas) whereas asexual yellow and bicoloured sexual types co-occur in the eastern hemisphere. *C. americensis* has only been associated with *F. occidentalis* (Seamans, 1923), but its actual parasitisation was established only recently (Loomans & van Lenteren, 1995; chapter 4). Little is known however about the actual physiological host preferences and ecological host range. Establishing rearing cultures of *C. menes* and *C. americensis* on *F. occidentalis* and *T. tabaci* as hosts in the laboratory, indicated that different parasitoid strains produced different numbers of offspring consistently over a number of generations.

Here I report on differences in behavioural and biological performance among populations of *C. menes* and *C. americensis*, collected from different geographical origins, parasitising different species and strains of thrips. In particular I address the importance of using behavioural traits in the parasitoid evaluation process and question whether different thrips species - and populations of these - affect parasitisation efficiency, and whether geographic variability between parasitoid populations affects the host selection process.

Material and methods

Origin and cultures of thrips and parasitoids

The species and strains of thrips and parasitoids we used in the experiment originated from different places in the world. 'Strain' is used in the sense of Diehl & Bush (1984): 'the cultured offspring of a sample taken from a field population at a certain time and locality'. Dutch strains of *F. occidentalis* and *T. tabaci* originated from greenhouse chrysanthemum and field onions respectively. An Egyptian strain of *T. tabaci* was accidentally introduced with infested beans, the Australian strain of *F.occidentalis* (Perth) was collected from chrysanthemum. Strains of *T. tabaci* differed in colour and body size: females of the Dutch strain were dark in colour and size ranged from 1.0-1.10 mm in length, whereas females from Egypt were pale and measured 0.75 - 0.85 mm. *F.occidentalis* strains could not be distinguished by colour or body size (females 1.3-1.45 mm, males 0.9-1.0 mm). *Frankliniella schultzei* (Trybom, 1910) (1.0-1.1 mm long) is well known in subtropical and tropical areas. The light colour-form was accidentally introduced in our laboratory early 1990 through infested beans originating from the Mediterranean area. *Frankliniella intonsa* (Trybom, 1895) (length between 1.3-1.4 mm) is palaearctic in distribution. The population we used was introduced from Japan in 1991 and was kept in containment on pollen for evaluation trials till 1995. Except for *F. occidentalis* all strains and species tested here reproduced asexually. *T. tabaci* was reared on leek and bean pods, *F. schultzei* on bean pods as well and *F. intonsa* and *F. occidentalis* on pollen and honey-water (see Chapter 3), unless specified otherwise.

The *C. menes* complex can be divided in three abdominal colour-type groups: a yellow, a browntip and a bicoloured form and from each type different strains were cultured and tested. For host specificity testing we used strains of the yellow type *C. menes* ('Brignoles'-France, 'Lodi'-USA, 'Yolo'-USA, 'Dreumel'-Netherlands and 'Shimane'-Japan and slightly different yellow-buff type from 'Holambra'-Brasil), of the brown type *C. menes* ('St.Maximin'-France, Hyères-France, 'Cabrils'-Spain and 'Irvine'-USA) and of *C. americensis* (strain 'Willcox' and 'Camp Verde' - Arizona). Strain names are related to the locality were the founder specimens have been collected. *C. menes* was reared on *Frankliniella schultzei* (light form), using French beans (cf. Loomans *et al.*, 1995) or on *T. tabaci* using leek leaves or French beans. *C. menes* (Japan) was reared on *F. intonsa* and *C. americensis* on *F. occidentalis*, both using the artificial method (Murai, 1990a) for about 20 and 10 generations respectively at 25 ^{0}C (see Chapter 3). All parasitoid strains reproduced asexually.

Behavioural observations

Three series of observations were carried out. In a first series we compared two *C. menes* strains, one from Japan and one from Brasil, and tested these on their original hosts, *F. intonsa* and *F .schultzei* respectively, and compared these with the new host species *F. occidentalis*. In a second series we used two other *C .menes* strains, one from France (yellow, 'Brignoles') and one from Spain (brown, 'Cabrils') and tested these both on *F. schultzei* and on *F. occidentalis*. In a third series we used the same yellow *C. menes* strain ('Brignoles') and a brown one from France ('Maximin') together with *C. americensis* ('Willcox') and observed their behaviour when encountering larvae of *F. occidentalis* or *T. tabaci.* In all cases larvae 24-48 hours old were used. All observations were performed, using a modified Munger-cell (30 mm diameter, 10 mm high) as an experimental arena with a sweet pepper leaf (*Capsicum annum* L. cv. 'Mazurka') or bean leaf (*Phaseolus vulgaris* L., test 2) as a host substrate. The arena remained in a horizontal position, the underside of the leaf directing upwards. A two days old inexperienced female of each parasitoid strain was introduced into the arena with 25 or 30 larvae of the respective thrips species or strain in the preferred first larval stage (24-48 hours old, Chapter 4) and observed continuously.

The behaviour of each wasp and encountered thrips host larvae was recorded by using a portable event recorder and 'The Observer' (Noldus IT - Wageningen) as a registration and calculation program. The following behavioural components were recorded: host-handling events, walking, standing still and preening. Host-handling events were subdivided in an

encounter (antennal contact), attack (start of the oviposition posture and going into a short struggle to subdue the thrips larva), insertion (ovipositor is stung into and remains inside the larval body) and host-feeding (repeatedly stinging and feeding), (for definitions see Chapter 4; after any insertion of the ovipositor in the host body lasting 2 seconds or more we considered a larva as being inserted). Larval reactions that prevented (escape) or interrupted (movement, anal droplets) the process were recorded as well. In the first 2 series every inserted larva was replaced by a fresh larva until 10 insertions per female were accomplished. This was done for 10 females. In this way 100 insertions were made for every parasitoid-host combination. In series three, we followed a similar procedure (replacement when inserted), but waps were observed for 1 hour. Each inserted larva was transferred into a reaction tube with pollen and a honey-solution (test 1 and 2) or a sweet pepper leaf disk (test 3). All observations were carried out in a climate room, temperature 21 ± 1 ^{0}C, humidity >80%., between 9:00 AM and 6:00 PM. One set of treatments was repeated once per observation day as much as possible for each parasitoid-host combination From the registered behavioural components of the parasitoid we calculated the time spent walking, standing still and/or preening and the number and duration of each interaction with a host larva: encounter, attack, insertion and host-feeding. From the numbers we also calculated the successive success-ratios (see also Chapter 4): the attack-ratio (number of attacks per encounter), the insertion-ratio (insertion / attack) and the acceptance-ratio (insertion / encounter) per parasitoid-host combination and used this as a measure for host acceptance.

Post-insertion observations

Dissections: After insertion we divided the larvae randomly in 2 cohorts and estimated the oviposition ratio in one by dissecting the inserted larvae by squashing it on a microscope slide and verifying the presence of eggs per host larvae 1-3 days after insertion. The remaining cohort we used to establish the parasitisation success by following them through time: the number that survived and the time they needed to develop. Individuals were either recognised as being parasitised in the pupal stage of the parasitoid or not. The ones that developed into thrips adults were considered as being unparasitised The parasitisation rate was calculated as: the number parasitised / (total inserted larvae - dead larvae) and used this as an indication for host suitability.

Developmental biology: In addition to the experiments mentioned above, and because in a number of cases (series 2 and 3) the individual rearing of larvae failed, we included a separate set of experiments to followed the development of parasitsed host larvae over time. For testing effects between different populations of *F. occidentalis*, a single two day old, virgin female parasitoid was placed in a plastic ring of (8 cm diameter, 5 cm high) with 75 thrips larvae, 24-48h old. After 24 hrs. parasitoids were removed and larvae were reared on pollen and honey-solution. Each combination was repeated 25-35 times. Possible strain effects within *T. tabaci*, were tested in a similar set-up. Brown strains of *C. menes* were tested singly on bean pods in stead of pollen to rear the larvae, 10 times per combination. For the yellow strains, 10 females, conditioned as above, were exposed to 100 larvae, fed with pollen in a plastic ring. After 8 hours parasitoid females were removed and larvae reared till maturity. Each combination was repeated 3 times.

For comparison of the host suitability of the 3 *Frankliniella* species we used a slightly different set-up: females of various parasitoid strains were exposed individually to 30 host larvae in a Munger cell with a bean leaf (*Phaseolus vulgaris*) as host feeding substrate. Every inserted larva was replaced by a fresh larva until 10 insertions per female were accomplished. This was repeated 10 times. In this way 100 insertions were made for every parasitoid-host combination. Of the inserted larvae, 50 were checked for the presence of eggs by dissection, the other 50 larvae were allowed to develop until the pupal stage of the parasitoid or adults of thrips.

In all cases development was followed over time, parasitoid prepupae were put on moist filter paper in a glass vial and checked daily for pupation and hatching adults. Experiments were carried out in climate rooms: the single female experiments at 25 ± 1^{o}C,

the multi female experiment also at 21°C ± 1°C (16L:8D). When pupal size was measured the length and width of the pupae (see figure 1) was measured and the width / length - ratio calculated.

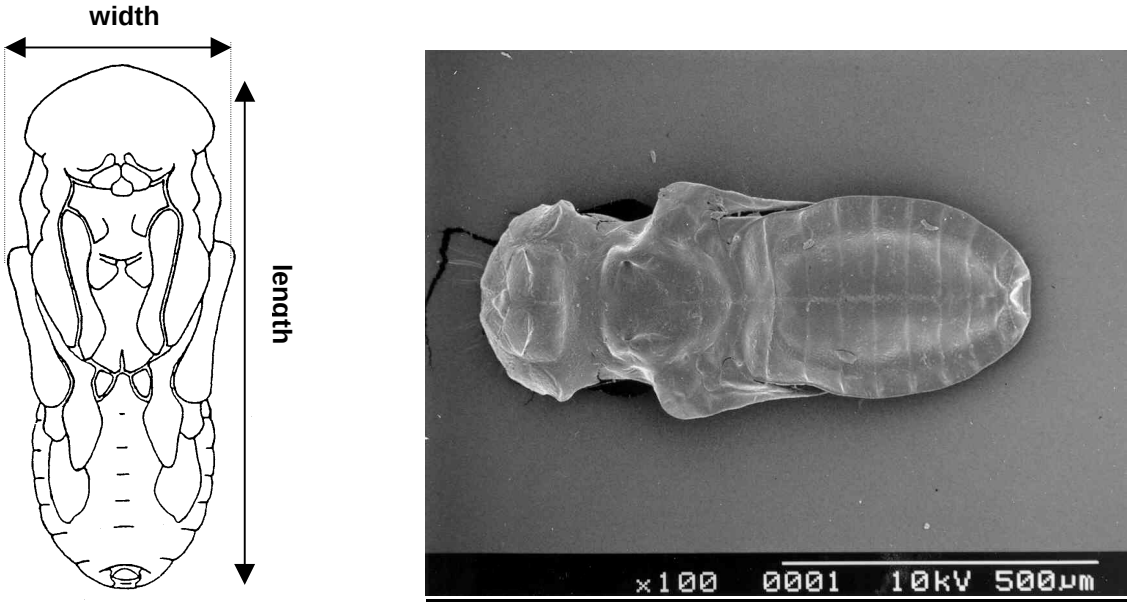

Figure 1: Size measurements of parasitoid pupae (left): length (mm and width (mm) at the wing-pad, as a measure for parasitoid fitness (drawing from Sakimura, 1937; 100*). Right: electronmiscroscope scan of a pupa of *Ceranisus menes* ('Brignoles', yellow strain) (photograph Günther Tschuch, University Halle –Wittenberg, Germany).

Statistic analysis

Wasps that did not meet a standard of 10 insertions within 2 hours or that did not respond within 30 minutes after introduction into the arena were excluded from further calculation. Before statistical analysis, behavioural data were all pooled for the female wasps in each treatment and are all expressed as the mean times, numbers or duration. All behavioural interactions with one individual host larva in the same sequence of events was calculated as being one single event and thus summed up for that host. For instance when a wasp pursued a host larvae that tried or managed to escape by running away, the subsequent contacts were considered as one encounter. Host-handling time was calculated by adding the times needed for an encounter, attack and/or insertion thus covering the time between first antennal contact and release of the host. Host-feeding events were excluded from statistic analysis on duration of events, because of it extreme long periods of time (5-15 for the normal insertion time). The mean percentage of all times, numbers and/or ratios of different behaviours were calculated per female per treatment and statistically analysed.

Data from treatments performed within the same period of time and experimental series were analysed for differences in number of events, in duration and success-ratios between parasitoid strains by the Mann-Whitney U-test (between host species) and the Kruskall-Wallis test (within host species), the latter followed by a Multiple Comparison test, when significance occurred ($p < 0.05$). Series belonging to different experiments were not compared statistically.

Results

Overall searching time

The overall searching time parasitoid strains needed to insert 10 host larvae in the first 2 series varied from 30 - 50 minutes in the first to 60 - 80 minutes in the second series (figure 2). And this was only in part due to direct differences in times necessary for handling hosts. Although the time needed for inserting 10 larvae seemed more characteristic for a specific parasitoid strain in that arena than its interaction with a certain *Frankliniella* host (figure 2), searching and host-handling behaviour proofed quite variable, which makes it difficult to compare the different test series by themselves. For instance the Japan strain showed a much higher number of host-feeding events than the Brasilian strain, probably due to differences in rearing conditions of the parasitoid (21^0C for Japan, 25^0C for Brasil). Some periods wasps were quite active (figure 2 left) in others relatively inactive and standing still a lot (figure 2 right4). Whether this behaviour was related to the host larvae present is not clear from our data. For inserting 10 host larvae of a similar size class, *C. americensis* took much less time: 904.5 ± 169.7 seconds (see chapter 4). However, when *C. menes* strains were exposed for one hour to larvae of *T. tabaci*, more time was spent handling these larvae than those of *F. occidentalis* (table 2). When encountering larvae of different *Frankliniella* species (figure 2), differences were largely coinciding with differences in the parasitoid strain.

Table 2 Time (sec ± s.e.) spent handling hosts during 1 hour of exposure to larvae of *F. occidentalis* or *T. tabaci* by *C. menes* (yellow and brown colour-types) and *C. americensis*.

Species	*F.occidentalis*		*T. tabaci*	
strain	time	percenttime		percent
C. menes - yellow ('Brignoles')	387.0	10.8	913.6	25.4
C. menes - brown ('Cabrils')	614.7	17.1	756.8	21.0
C. americensis ('Willcox')	472.8	13.1	558.2	15.5

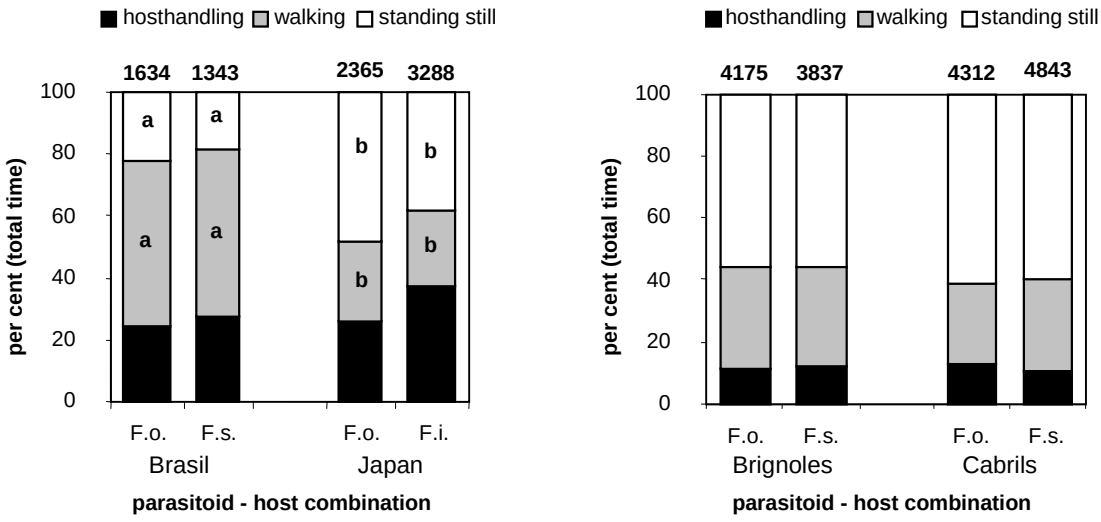

Figure 2: Relative time distribution of 3 behavioural components (walking, standing still including preening and handling hosts) for 4 strains of *C. menes* searching for larvae of *F. occidentalis* (F.o.), *F. schultzei* (F.s.) or *F. intonsa* (F.i.) until 10 insertions took place; 30 first stage larvae available with replacement (left), 25 (right); the total observation time (sec.) needed for 10 insertions is indicated on top of the bars. Significant differences in time distribution are indicated by different letters (Kruskall-Wallis, $p< 0.05$).

Host-handling times

Females of the various strains differed in the amount they spent searching and the time they took for handling the host. Once a host is contacted, the average time spent on the subsequent interactive events with the host differs according to the strain of the parasitod and the host species. In series 1 (figure) times between for an encounter and attack depended on the parasitoid strain and not on the *Frankliniella* species involved: The Japan strain took more time for all three subsequent interactive events – encounter, attack, insertion - than it took the Brasilian strain. This was only significant when attacking *F. occidentalis* by the Japan strain than by the other 2 species of hosts. In series 2 both strains of *C. menes* did not differ in the time they needed to overpower ('attack') the host and also the time of insertion was similar. However, the brown strain ('Cabrils') significantly took more time for an encounter of the host larvae, regardless the species (4.8 ± 0.8 s, n=140 F.o.; 4.5 ± 1.1s, n=127 F.s.) than it took the yellow type ('Brignoles') to proceed (0.8 ± 0.1s, n=199 resp. 0.8 ± 0.1, n=126) (figure 4). The long encounter time for 'Cabrils' was not the overall result of pooling separate encounters with a larva trying to escape, but the result of a prolonged time they took for external inspection with the antennae. Although a pursuit occasionally occurred, after a first miss the larva usually managed to escape.

In series 3, *C. americensis* spent less overall time on an encounter, attack and insertion of *F. occidentalis* larvae, than both colour-types of *C. menes* (figure 6). We also see that remarkable differences exist in the separate behavioural interactive events with the different host larvae. For the yellow *C. menes* strain ('Brignoles') it takes a similar very short time (0.7 ± 0.1 s.e. s, n=115 and n=119) from first contact (encounter) to start an attack on both hosts, whereas for the brown *C. menes* ('Maximin'), though still short, it took more than double the time (1.8 ± 0.1 s, n=175 for *F. occidentalis* and 1.7 ± 0.1, n=183 for *T. tabaci*). For *C. americensis* however the encounter time depends on the host: fast (0.7 ± 0.1 s, n=256) for *F. occidentalis* and slower for *T. tabaci* (1.1 ± 0.1 s, n=101). The attack times are similar for *C. menes* yellow strain (1.0 ± 0.1, n=107 and 0.8 ± 0.1, n=99) and *C. americensis* (0.8 ± 0.1 s, n=221 resp. 42), while for *C. menes* (brown) it takes double as much time to overpower a host larvae (1.5 ± 0.1 s, n=138 for *F. occidentalis* and 1.4 ± 0.1 s, n=148 for *T. tabaci*). In particular *C. americensis* took a short time for an insertion (16.0 ± 1.8 s) when compared with *C. menes* yellow (32.0 ± 3.9 s) and brown (43.2 ± 3.7 s). When *T. tabaci* is offered as a host, host handling time characteristics were shorter for the brown-type of *C. menes* (35.7 ± 3.7 s) compared to the yellow (61.6 ± 11.6 s) and *C. americensis* (48,1 ± 11.3 s). Thrips host species also affected host handling time by the parasitoid. *C. americensis* spent significantly more time handling *T. tabaci* host larvae than *F. occidentalis* host larvae, whereas the average duration of behavioural steps was similar for the *C. menes* yellow and brown strains. The number and duration of host feeding events did not differ, each parasitoid strain or the thrips host species. Average duration of an insertion followed by host-feeding, is significantly longer (see figures 3, 4, 6).

Number of behavioural activities

Ceranisus menes and *C. americensis* have a basic different approach in their attack and parasitisation of host larvae: *C. menes* quickly turns around after insertion of the ovipositor, lifting the larva in the air or tailing it behind her (Chapter 4), while *C. americensis* stays in the original insertion position, bending her ovipositor between her legs. This is consistent for the different strains and over the range of hosts we tested. When involved in host-feeding, however, *C. menes* remains in its initial position, and stings the host from between the legs repeatedly. The incidence of host-lifting largely depends on the size and age of the host, first stage larvae being lifted in 40-60 % of the insertions. This can be different, however, for the different parasitoid host – combinations we observed during the period they were allowed to insert 10 hosts: Brasil – *F. schutzei* (n = 11 females; 4,2 ± 0,4 s.e.), Brasil - *F. occidentalis* (n = 14; 5,5 ± 0,6), Japan – *F. intonsa* (n = 11; 5,7 ± 0,6), Japan – *F. occidentalis* (n=9; 7,2 ± 0,4) but results were not significant between species.

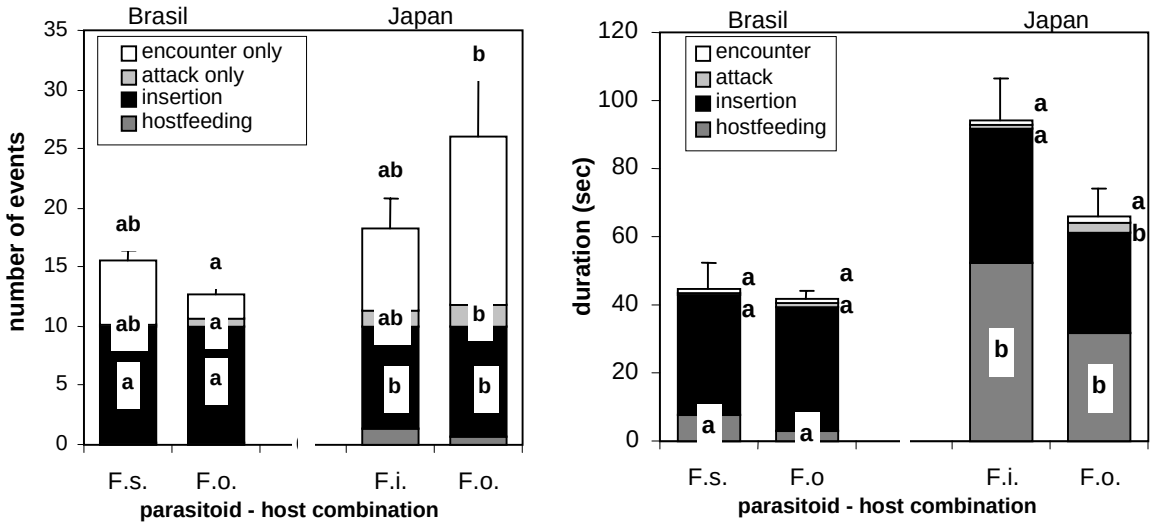

Figure 3. Average number (left) and duration (right) (± s.e. of total) by *Ceranisus menes* strains Brasil and Japan needed for 10 insertions of host larvae, when encountering different *Frankliniella* species (*F. occidentalis* = F.o, *F. schultzei* = F.s., *F. intonsa* = F.i.). Significant differences between parasitoid – host combinations are indicated by different letters (Kruskall - Wallis test, $p < 0.05$).

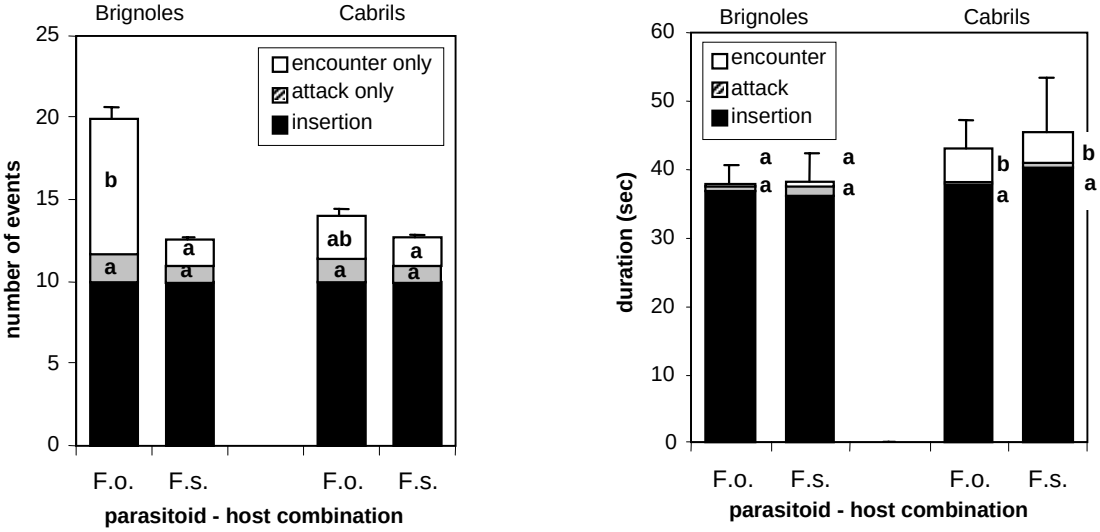

Figure 4. Average number (left) and duration (right) (± s.e. of total) by *Ceranisus menes* strains 'Brignoles' and 'Cabrils' needed for 10 insertions of host larvae, when encountering different *Frankliniella* species (F.o. = *F. occidentalis*, F.s. = *F. schultzei)*. Significant differences between parasitoid – host combinations are indicated by different letters (Kruskall - Wallis test, $p < 0.05$). Host-feeding occurred twice for each parasitoid - host combination, 'Cabrils' (n=4, 344.8 ± 311.8 s.) and 'Brignoles' (n=4, 164.8 ± 84.8 s.) but is not included.

When different species of *Frankliniella* were involved (figure 3 and 4), we see that within the same test series, differences in number of larvae were minor, and that differences were consistent within *C. menes* strains. In all series, the number of total encounters with F. occidentalis to get to 10 insertions was larger than with larvae of the other host species, but results were only significant for the 'Japan' (figure 3) and 'Brignoles' (figure 4) strain: less hosts were accepted upon an encounter with *F. occidentalis* than with the other host species larva, either *F. schultzei* or *F. intonsa.* This can be either due to rejection by the wasp or because the encounter was interrupted by a reaction of the attacked host larva.

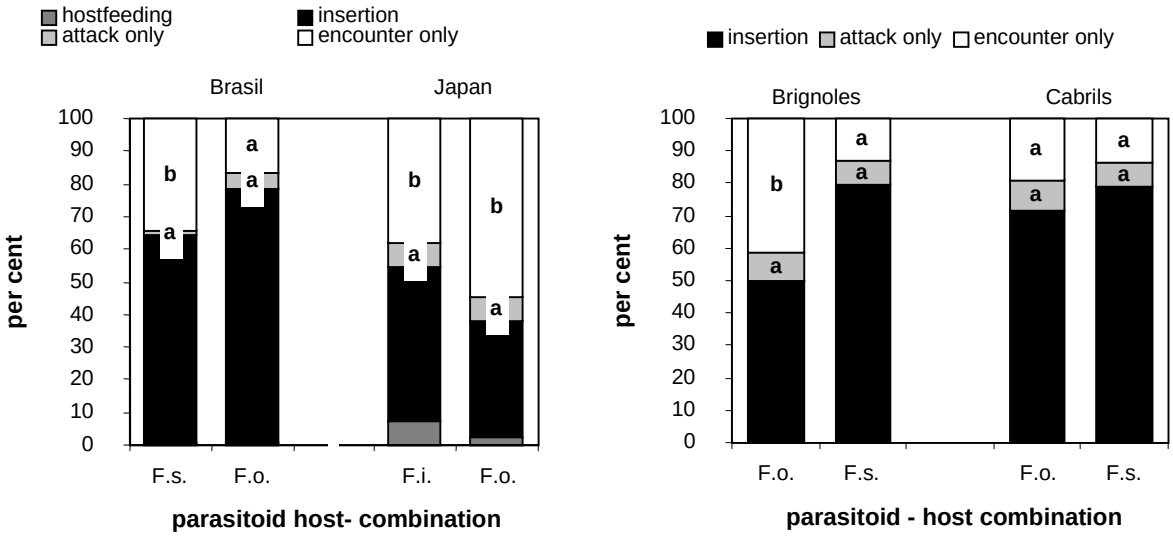

Figure 5 Overall parasitisation success ratios of host acceptance events for *C. menes* strains, when encountering different *Frankliniella* species. *F. occidentalis* (F.o), *F. schultzei* (F.s.) and *F. intonsa* (F.i.) until 10 insertions of host larvae had been completed. Significant differences between parasitoid – host combinations are indicated by different letters (Kruskall - Wallis test, $p < 0.05$).

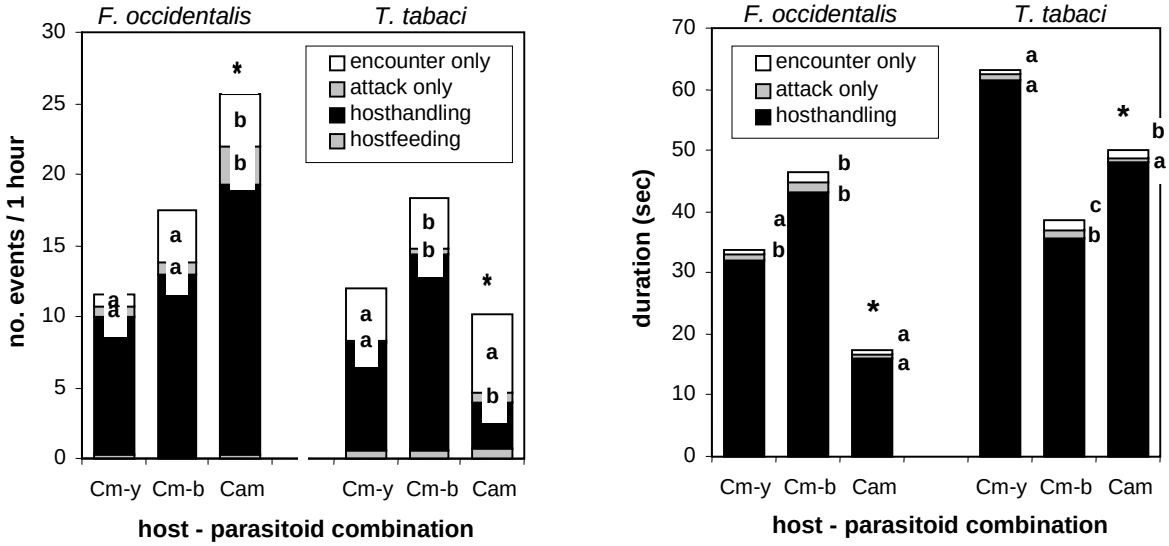

Figure 6. Average number (a) and duration (b) of hosthandling events of *C. menes* (Cm-y = yellow Brignoles and CM-b = brown type Maximin) and *C. americensis* (Cam), parasitising larvae of *F. occidentalis* and *T. tabaci*. The duration of host-feeding events is not included in the graph: Brignoles (n= 3*Fo: 160.5 ± 47.2 s; n = 6*Tt: 327.1 ± 135.0 s), Maximin (n = 0*Fo; n = 5*Tt: 384.0 ± 143.5 s) and *C. americensis* (n = 3*Fo: 291.9 ± 26.9s; n = 7*Tt = 508.5 ± 157.3 s). Significant differences between parasitoid strains are indicated by different letters (within host species, KW-test) or stars (between host species, M-W U-test), $p<0.05$, 10 replicates per parasitoid-host combination.

Parasitoid species, however, clearly differed in the acceptance of larvae when either *F. occidentalis* or *T. tabaci* were offered. The thrips host species clearly affected the number of events: *C. americensis* 'Willcox' encountered, attacked and inserted a much larger number of *F. occidentalis* larvae those of *T. tabaci*. For both colour-types of *C. menes*, however, the number of encounters was rather constant for both host species (figure 6). This difference is not due to a difference in success handling a first stage larva as a host. When we compare the three strains within the same host group, *C. menes* (brown type 'Maximin') encountered,

attacked en inserted more larvae than the yellow one, but *C. americensis* clearly had less interactions with larvae of *T. tabaci* during the hour of observation (figure 6).

Parasitisation success rates

Besides the number of host a wasp encounters, attacks, etc., the ratio by which it is successful in proceeding to the next step in the host acceptance process is important. How successful is a wasp managing to finish the process, once it attacks. Therefore, we calculated different success ratio's of the behavioural sequence of encounter, attack, insertion, egg-laying and defence measures and escapes by the host larva. This was used as a measure for the level of acceptance and parasitisation by the female wasps.

Upon encountering larvae of *Frankliniella* species (figure 5), *C. menes* strains varied in their success of subsequently attacking and inserting the encountered host larva. In the first series (figure 5 left) females of the Brasil strain were able to end 80% of their contacts of a *F. occidentalis* larvae with successful insertion of that larva, whereas in the other combinations wasps were much less successful: only 40-60% of the hosts they met were actually inserted. In the second series (figure 5 right), the yellow type ('Brignoles') was less successful than the brown ('Cabrils') when encountering *F. occidentalis* larvae: only half of the contacted hosts ended in an actual insertion. Both strains did not differ in their success rate towards *F. schultzei* larvae where 70-80% was successful. In most case the sequence was already ended immediately after contact.

Upon an encounter with larvae of *F. occidentalis* or *T. tabaci* (figure 7) in the third series, *C. menes* (yellow) and *C. americensis* accepted larvae of *F. occidentalis* to a higher extent than those of *T. tabaci* (white bars). Once an attack has been initiated ('accepted'), the proportion of wasps being able to insert the hosts is similar for all parasitoid strains (striped bars): all three strains were equally successful in finishing an attack, and inserting a host larvae, regardless the species. For *C. americensis* this results in a significant higher overall insertion rate (ratio of inserted larvae per encounter) for *F. occidentalis* (0.77) than for *T. tabaci* (0.48). Although *C. menes* (yellow) initiates attacks on relatively more larvae of *F. occidentalis* than on those of *T. tabaci* after first contact, it is less successful in finishing such an attack, resulting in a comparative overall result (insertion / encounter) for both host species (figure 7 black bars).

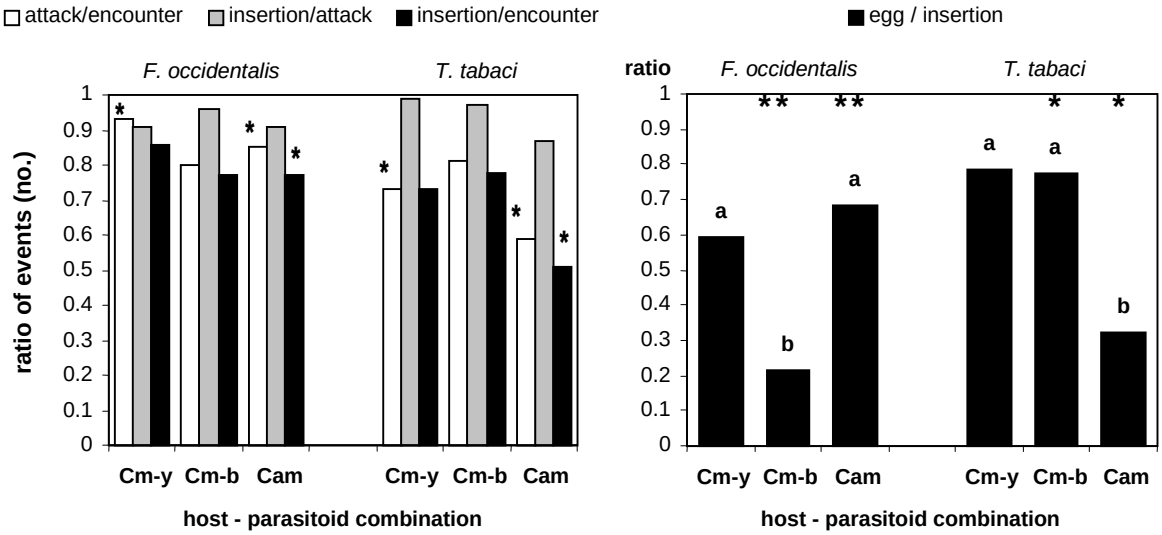

Figure 7. Success ratio's in different steps of the host acceptance process by *C. menes* (Cm-y = yellow and Cm-b = brown type) and *C. americensis* (Cam), parasitising larvae of *F. occidentalis* and *T. tabaci* after external (left) and internal (right) inspection over a period of 1 hour. Significant differences between parasitoid strains are indicated by different letters (within host species, Kruskall–Wallis - test) or stars (within parasitoids and between host species, Mann-Whitney U-test); $p<0.05$.

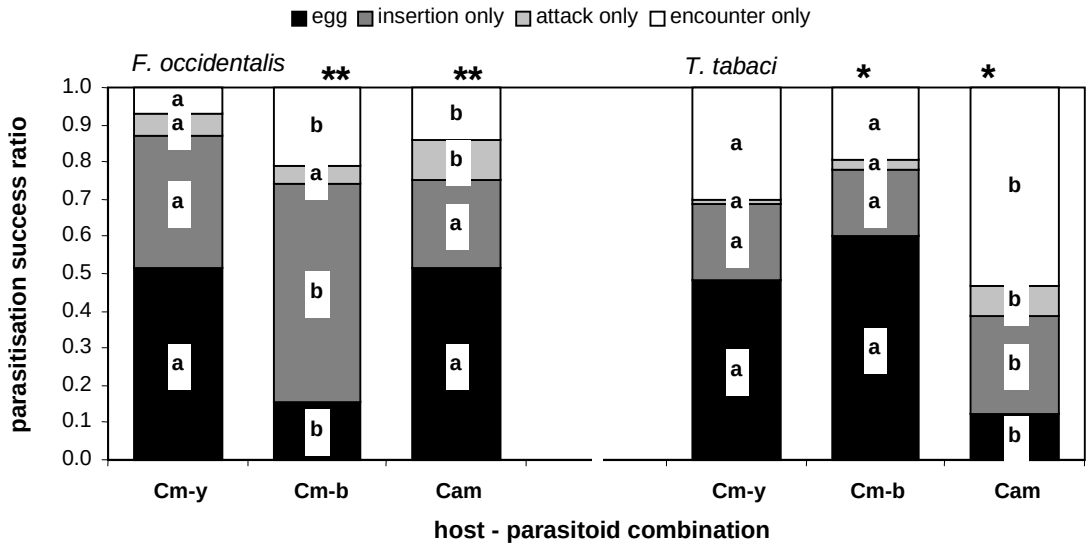

Figure 8: Overall combined success ratio's of the different steps in the host acceptance process. Abbreviations and statistical tests like described in figure 7.

Post-insertion results

Dissections - Cultures on individual larvae, set-up after our behavioural observations in series 2 collapsed almost overnight as result of a steep drop in relative humidity % and larvae could not be dissected properly anymore. Therefore, a separate experiment was set-up, in which 100 larvae of 3 different *Frankliniella* species had been inserted, as described in the methodology. Subsequently this group was split into 2 cohorts: one which was dissected and another which we reared till the pupal stage. From the first series, we see (figure 9) that the number of hosts that had been subjected to insertion, and that actually contained an egg varied from 52 for Brasil to 90% Japan, both on *F. occidentalis* with intermediate values for the 2 other combinations. For the second series, we see a similar variation in hosts actually containing an egg, especially for the *C. menes* strains: Brasil 52 –80 %, Brignoles 53-77 % and Hyères 71-85%, whereas hosts inserted by *C. americensis* contained an egg in 82 % or more cases: *C. menes* rejects more *Frankliniella* hosts after internal inspection than *C. americensis* does.

In series 3, host acceptance after internal inspection (ovipositor probing), measured by dissection, differs clearly with the parasitoid - host combination (figure 7 right). Also here not every host which had been stung, oviposition occurred. In contrast with the previous series we see that a much lower percentage is parasitised by *C. menes* (brown) inserting *F. occidentalis* larvae (21%) and by *C. americensis*, inserting *T. tabaci* (32%) (figure 7). A combination of the graphs in figures indicates (figure 8) that 50 - 60 % of the encountered larvae are actually parasitised, except for *C. menes* (brown) that only parasitises 16% of the encountered *F. occidentalis* larvae and for *C. americensis* parasitising 15% of the *T. tabaci* larvae. *C. americensis* showed the highest parasitisation level when *F. occidentalis* larvae are offered, a maximum of 25 larvae in 1 hour, and a maximum of 11-12 larvae for *C. menes*, when *T. tabaci* was offered. When an insertion is followed by host-feeding, oviposition has never been found, for either one of the parasitoid species.

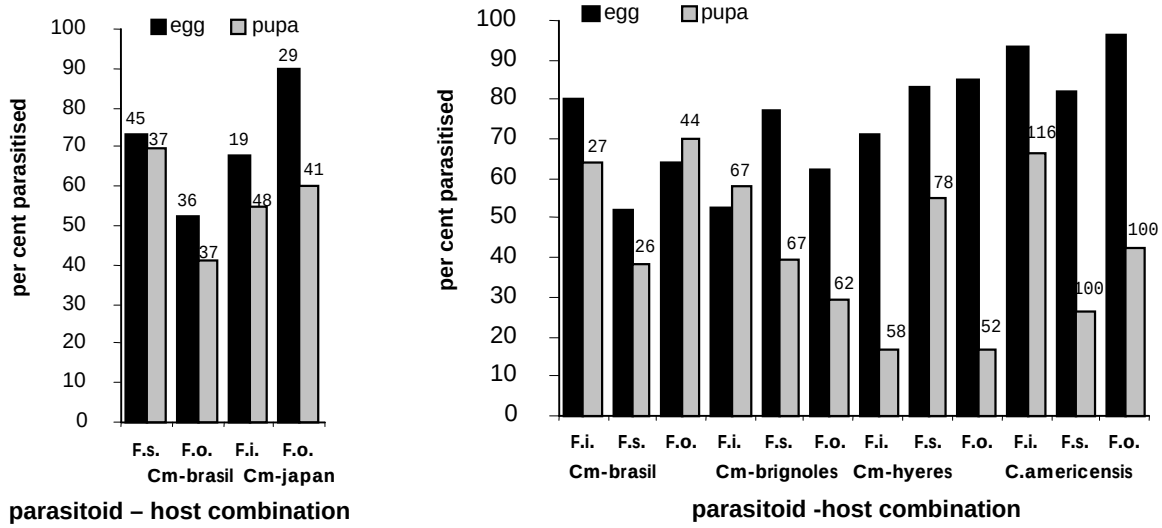

Figure 9 : Parasitisation success of *Ceranisus* strains parasitising different *Frankliniella* (*F. intonsa* = F.i., *F. schultzei* = F.s., *F. occidentalis* = F.o.) species derived from dissections (black bars) and developmental studies (grey bars) in series 1 and 2; above each bar the original numbers are given for calculating the % parasitism, for dissection and development (right) we used 50 inserted *C. menes* – 'Brasil', 100* *C. menes* yellow, 100* *C. menes* brown, and 150* *C. americensis* per strain per treatment)

Development

Once a host larvae is parasitised and a parasitoid develops successfully, this cannot be distinguished externally from unparasitised ones until the moment the larvae start to pupate. The pupation process has extensively been described for *C. menes* by Sakimura (1937), parasitising *T. tabaci.* The characteristics are similar for other strains of *C. menes* and for *C. americensis* as well, also when different thrips species are parasitised. Yellow and brown strains of *C. menes* and *C .americensis* can already be distinguished from each other by the size (see below) and colour of the maturing pupa.

Parasitisation success (development until the pupal stage of the parasitoid) varies largely: internal acceptance of ahost not necessarily leads to successfull development within that host. For almost all parasitoid - host combinations this leads to less parasitoids that develop: the combinations Brasil - *F. occidentalis* (70%), Brignoles – *F. intonsa* (58%), Hyères – *F. schultzei* (55%) ands *C. americensis* – *F. intonsa* (67%) were most successful. The last three combinations performed poorly on *F. occidentalis* in this respect and showed to be the least suitable host. When we take the time to develop in consideration as a measure for suitability, parasitoids develop most quickly on *F. intonsa* and take more time 2-4 days) on *F. occidentalis* (tables 3 and 4).

In a second group, of non-behavioural, experiments we specifically looked into the influence of the variability between different populations of certain species of thrips, in particular of *F. occidentalis* and *T. tabaci*. The number and percentage of hosts parasitised (parasitoid prepupa), pupal size and developmental time were used as parameters for strain and host fitness effects. Table 5 shows that both parasitoid species, *C.. americensis* and *C. menes* (yellow 'Brignoles') clearly differed in numbers they parasitised in one day. On both strains of WFT, parasitoids however did not differ in the number of progeny. They differed however in size of the pupa (length and also width, but not in ratio) and the total time to develop from egg to adult. Offspring produced on the Australian western flower population was larger, but it took 1 day more to develop.

Table 3. Developmental time (days ± s.d.) of parasitised thrips juvenile stages of 2 different parasitoid strains of *Ceranisus menes* ('Shimane–Japan, Holambra-Brasil) at 25 ^{0}C (16L:8D); *Frankliniella occidentalis* = F.occ, *F. schultzei* = F.sch, *F. intonsa* = F. int. Significant differences between host species are indicated by different letters (multiple comparison test after Kruskall Wallis test, $p < 0.05$); result series 1.

Strain	host	#	egg + larva	propupa	pupa	total
Brasil	F. sch	21	7.2 ± 0.6	1.9 ± 0.6	16.3 ± 0.5 ^{a}	25.4 ± 1.3 ^{a}
	F. occ	24	7.6 ± 1.0	2.0 ± 1.0	15.9 ± 0.9 ^{a}	25.5 ± 1.8 ^{a}
Japan	F. int	40	6.5 ± 0.5	1.9 ± 0.4	18.4 ± 3.0 ^{ab}	26.8 ± 2.9 ^{ab}
	F. occ	34	7.1 ± 1.0	2.0 ± 0.6	18.1 ± 1.3 ^{b}	27.2 ± 1.3 ^{b}

Table 4. Developmental time (days ± s.d.) of parasitised thrips juvenile stages of different parasitoid strains of *Ceranisus menes* (yellow 'Brignoles', brown 'Hyères') and *C. americensis* ('Willcox') 25 ^{0}C (16L:8D); *F. occidentalis* = F.occ, *F. schultzei* = F.sch, *F. intonsa* = F. int. Significant differences between host species within the same parasitoid strain are indicated by different letters (multiple comparison test after Kruskall Wallis test, $p < 0.05$). N = larvae at start, n = number parasitised, different for egg-pupa and for pupa + egg-adult because of pupal mortality.

Strain	host	N	egg-propupa	n	(pro)pupa	n	egg-adult
Cm-y	F.int	150	8.4 ± 0.9 ^{a}	62	17.5 ± 0.8 ^{a}	31	25.7 ± 0.8 ^{a}
(Brignoles)	F.sch	150	10.0 ± 1.3 ^{b}	36	17.7 ± 1.0 ^{a}	30	27.0 ± 0.8 ^{b}
	F.occ	150	9.5 ± 1.6 b	49	18.5 ± 1.4 ^{a}	40	27.8 ± 1.2 ^{b}
Cm-b	F.int	100	7.7 ± 0.0 ^{a}	10	17.0 ± 0.3 ^{b}	5	24.4 ± 0.5 ^{a}
(Hyères)	F.sch	100	9.7 ± 0.5 ^{b}	43	15.1 ± 0.6 ^{a}	9	24.3 ± 0.9 ^{a}
	F.occ	100	11.0 ± 0.0 ^{c}	9	17.9 ± 0.3 ^{b}	5	28.8 ± 0.5 ^{b}
Cam	F.int	150	8.4 ± 1.6 ^{a}	84	16.0 ± 1.3 ^{a}	77	24.1 ± 1.1 ^{a}
(Willcox)	F.sch	150	9.0 ± 0.8 ^{b}	25	18.7 ± 0.8 ^{b}	15	27.9 ± 0.9 ^{b}
	F.occ	150	9.7 ± 0.4 ^{b}	44	18.6 ± 0.8 ^{b}	26	28.3 ± 1.1 ^{b}

Table 5: Parasitisation of F. occidentalis strains Australia (Au) and Netherlands (Nl): average (s.d) number and size and developmental time of parasitised offspring per female C. americensis (Willcox-Arizona) and C. menes (France, Brignoles-AB, yellow type), 25^{o}C. Mann -Whitney U between strains of the same thrips host ($p<0.05$).

parasitoid	strain nr. F.occ		pupa nr.	(s.d)	pupa nr.	length (s.d.)		dev.time days (s.d.)	
C. americensis	Au	23	37.3^a	(14.3)	700	0.91^a	(0.07)	28.2^a	(1.6)
(Willcox)	Nl	23	40.1^a	(18.9)	684	0.86^b	(0.06)	27.2^b	(1.5)
C. menes yellow	Au	31	22.6^b	(10.5)	575	0.91^a	(0.07)	28.9^c	(1.4)
(Brignoles)	Nl	35	27.6^b	(11.5)	707	0.82^c	(0.06)	27.9^a	(1.1)

For *T. tabaci* the results are summarised in tables 6 and 7. Although conditions were different (multi-female test on pollen at 20^{0}C; the single female tests on bean pods at 25^{0}C), the experiments show that 3 out of 4 yellow and both brown colour-types of` *C. menes* produced more offspring on the Dutch *T. tabaci* population than on the population from Egypt. Parasitoid pupae were also significantly larger on this strain, represented here by their length, than on the Egypt strain. All parasitoid strains performed rather poorly on F. occidentalis, although in 3 out of 4 cases size of the remaining pupae was larger than on T. tabaci. Table 8 shows that the developmental time for the various life stages of parasitoids, depended largely on the temperature, the parasitoid strain involved and on the thrips host offered. Developmental time varied between strains of *C. menes* (table 8), according to their phenotypic appearance (abdominal colour-types: yellow versus brown) and geographical origin. Yellow strains show a large variation in overall developmental time, whereas brown types do less. This variation is even more pronounced at 20 ^{0}C: developmental time is much longer, especially the Dutch strains have a very long development time. Values are even underestimated as more than 80 % did not emerge within 130 days. At both temperatures emergence distribution curves of yellow strains show two peaks at a regular interval, the second peak being twice as long as the first. The Japanese strain however, showed a more regular distribution. Overall, the yellow strains we followed through time. Developmental time in the different life stages and overall, was for most parasitoid - host combinations 2-4 days shorter on *Thrips tabaci* than on *F. occidentalis.* At 20 ^{0}C this was much less pronounced. For 2 brown types (table 6) this was again shorter on the strain from Egypt than on the one from The Netherlands at 25 ^{0}C.

Table 6: Parasitisation of *Thrips tabaci* strains from The Netherlands (NL) and Egypt (EG): larval mortality and averages (s.d) of size and developmental time of parasitised offspring per female of *C. menes* (brown colour-types – 'Maximin', France and 'Irvine', USA), 25^{o}C. Mann - Whitney U within strains of the same thrips host ($p<0.05$).

Combination	host	%mortality	%paras.	npupa	lenght pupa	dev.time
Maximin	*T. tabaci* Nl	9.5	78.9^a	207	0.90^a (0.07)	25.2^a (0.5)
(France)	*T. tabaci* Eg	11.2	11.9^b	52	0.80^b (0.03)	26.3^b (0.9)
Irvine	*T. tabaci* Nl	10.6	73.2^a	175	0.90^a (0.07)	24.9^a (0.4)
(USA)	*T. tabaci* Eg	12.0	8.9^b	43	0.78^b (0.04)	25.9^b (1.1)

The relatively high larval mortality (table 7) is probably due to the transfer of newly hatched larvae from bean pods to pollen. Also in control cages mortality of thrips was high 41 % for *T. tabaci* (Egypt), 44 % *T . tabaci* (Netherlands) and 47 % for *F. occidentalis* (3 units each). Developmental times of the yellow colour-type *C. menes* at 20^{0}C were shorter in 3 out of 4 cases for the Egypt strain, but it took a long time to develop and they all showed a large variation. For the brown colour-types it took one day more to develop from the Egypt strain at 25^{o}C than from the Dutch *T. tabaci* (table 3). Our results confirm previous parasitoid rearing experiences: high offspring numbers of brown strains on a Dutch *T. tabaci* strain, but very low offspring numbers when reared on *T. tabaci* from Egypt. Some parasitoid strains (brown type) got extinct while culturing them on the small sized strain of *T. tabaci* from Egypt. When hosted again by the Dutch strain, cultures of brown strains slowly recovered again and remained consistent over a number of generations, suggesting a certain incompatibility between thrips and parasitoid strains.

Table 7: Parasitiszation results by *Ceranisus menes* (yellow strains), when offered first stage larvae of *T. tabaci* (strains from the Netherlands and Egypt) and *F.occidentalis*; 3 units per combination on pollen and honey, 10 females per 100 larvae/unit, 20^0C. Mann -Whitney U test between strains of the same thrips host ($p < 0.05$).

Combination	host	%mort.	%paras.	# pupa	lenght pupa		width pupa	
Brignoles	*F.occidentalis*	27.3	69.7[a]	148	0.94[c]	(0.07)	0.38[b]	(0.02)
(France)	*T. tabaci* Nl	50.0	75.3[a]	108	0.93[a]	(0.05)	0.39[b]	(0.01)
	T. tabaci Eg	41.5	46.2[b]	50	0.83[b]	(0.02)	0.35[a]	(0.02)
Yolo	*F.occidentalis*	52.5	44.2[b]	39	0.89[b]	(0.07)	0.36[c]	(0.03)
(USA)	*T. tabaci* Nl	42.3	55.5[a]	91	0.90[a]	(0.02)	0.34[b]	(0.02)
	T. tabaci Eg	50.0	38.0[b]	41	0.80b	(0.02)	0.26[a]	(0.01)
Lodi	*F.occidentalis*	62.5	42.6[c]	29	0.86[a]	(0.06)	0.34[a]	(0.03)
(USA)	*T. tabaci* Nl	39.5	90.8[a]	136	0.90[b]	(0.02)	0.36[b]	(0.01)
	T. tabaci Eg	60.0	67.5[b]	53	0.90[b]	(0.02)	0.34[ab]	(0.01)
Dreumel	*F.occidentalis*	57.6	46.4[b]	58	0.91[c]	(0.03)	0.37[b]	(0.02)
(Netherl.)	*T. tabaci* Nl	59.6	74.4[a]	74	0.85[b]	(0.03)	0.36[b]	(0.02)
	T. tabaci Eg	38.3	71.8[a]	130	0.78[a]	(0.03)	0.34[a]	(0.02)

Size measurements

The size of a parasitoid pupa was measured by its length and by its width (at the wing pads, figure 1). The size of the parasitoid clearly differed according to the host that the parasitoid wasps developed on (table 6, 7 and 8; figure x): relatively small in the small sized hosts (T. tabaci from Egypt, table 6, 7 and 8), compared to the larger hosts (*T. tabaci* and *F. occidentalis* from the Netherlands). From the latter groups it showed that the pupae developing form F. occidentalis larvae were a bit robuster (as calculated form the width / length ratio) than from *F. occidentalis* (figure 10). The difference in size between the Australian and Dutch strain of *F. occidentalis* is surprising and a bit more difficult to relate to host size. Except for a relatively short adaptation to new rearing conditions, the larval population of Australia may have been strongly male-biased. Although this did not occur in the control experiments, it was difficult to check whether predominantly the males had been accepted for parasitisation, as few adult thrips emerged from the cages. The direct relation between pupal size and adult size and fitness was not established, but indirect evidence from our rearing experiences on the offspring of brown parasitoid strains when exposed to the *T. tabaci* cultures from Egypt, indicates this was likely the case.

Discussion

The extent to which a female parasitoid accepts and is able to parasitise and develop in a certain host species, can not only influence the fecundity, longevity and host finding ability of herself, but also the developmental time, sex-ratio, female size, and even morphology of her offspring (Godfray, 1993; Visser, 1994). It therefore is of crucial importance for a wasp to choose a proper host. For biological control purposes this is of great relevance too, because the ability of a parasitoid to locate her potential hosts successfully ánd the ability to develop on that hosts, largely affects the outcome of the control measures. Behavioural experiments on host selection (i.e. host acceptance) and developmental studies on host suitability can contribute to understanding the performance on of a parasitoid on a certain host species. Intraspecific variation in insect parasitoid species,

Table 8 Developmental time (days ± s.d.) of parasitised thrips juvenile stages of different parasitoid strains of *Ceranisus menes* (yellow strains) and *Ceranisus americensis* (see table 1) at 20 and 25^{0}C (16L:8D); *Frankliniella occidentalis* (Netherlands) = Focc, *Thrips tabaci* (Netherlands) = Ttab and *T. tabaci* (Egypt) = TtEg. Significant differences between host species within the same parasitoid strain are indicated by different letters (multiple comparison test after Kruskall - Wallis test or Mann - Whitney U-test, $p < 0.05$).

Strain	host	#	egg+larva	propupa	pupa	total
Ceranisus menes						
25^{0}C						
Brignoles	Focc	33	9.6 ± 1.3 ^{b}	2.9 ± 0.8 ^{b}	16.3 ± 1.3	28.8 ± 0.6 ^{b}
	Ttab	211	7.5 ± 0.3 ^{a}	1.4 ± 0.3 ^{a}	16.7 ± 0.5	25.6 ± 0.7 ^{a}
Dreumel	Focc	11	8.0 ± 1.0 ^{a}	2.2 ± 0.3 ^{b}	19.8 ± 0.8 ^{b}	30.0 ± 0.2 ^{b}
	Ttab	107	8.3 ± 0.6 ^{b}	2.1 ± 0.8 ^{a}	18.4 ± 0.9 ^{a}	28.8 ± 1.0 ^{a}
Bologna	Focc	27	9.6 ± 0.6 ^{b}	2.3 ± 0.4 ^{b}	17.8 ± 1.3 ^{b}	29.7 ± 2.6 ^{b}
	Ttab	52	7.1 ± 0.2 ^{a}	1.2 ± 0.3 ^{a}	16.4 ± 0.6 ^{a}	24.6 ± 0.8 ^{a}
Yolo	Focc	32	9.4 ± 0.5 ^{b}	1.8 ± 0.5 ^{b}	17.2 ± 1.9 ^{b}	28.4 ± 0.9 ^{b}
	Ttab	131	7.7 ± 0.4 ^{a}	1.4 ± 0.5 ^{a}	16.0 ± 0.8 ^{a}	25.1 ± 2.1 ^{a}
20 ^{o}C						
Brignoles	Focc	158	16.0 ± 1.1 ^{c}	2.2 ± 0.6 ^{b}	69.9 ± 17.2 ^{a}	88.1 ± 16.6 ^{c}
	Ttab	113	11.8 ± 1.2 ^{a}	1.6 ± 0.5 ^{a}	74.3 ± 26.3 ^{b}	87.7 ± 28.3 ^{b}
	TtEg	51	13.2 ± 0.4 ^{b}	2.6 ± 0.5 ^{c}	67.1 ± 17.2 ^{a}	82.9 ± 17.8 ^{a}
Dreumel	Focc	58	14.8 ± 0.6 ^{b}	2.1 ± 0.5	111.7 ± 31.5 ^{b}	128.5 ± 29.9 ^{b}
	Ttab	90	12.4 ± 0.2 ^{b}	2.1 ± 0.6	115.8 ± 7.6 ^{b}	130.2 ± 7.6 ^{b}
	TtEg	140	13.5 ± 1.1 ^{a}	2.0 ± 0.7	91.9 ± 20.2 ^{a}	107.5 ± 19.0 ^{a}
Yolo	Focc	42	14.7 ± 0.6 ^{c}	2.2 ± 0.5 ^{b}	86.3 ± 10.1 ^{a}	103.1 ± 10.4 ^{a}
	Ttab	96	12.7 ± 0.6 ^{a}	1.8 ± 1.3 ^{a}	100.2 ± 8.0 ^{b}	114.7 ± 13.2 ^{b}
	TtEg	41	13.1 ± 0.8 ^{c}	2.7 ± 0.9 ^{b}	98.2 ± 7.0 ^{b}	114.0 ± 7.1 ^{b}
Lodi	Focc	32	14.0 ± 0.9 ^{b}	3.1 ± 0.3 ^{b}	100.6 ± 4.9	117.7 ± 5.5 ^{b}
	Ttab	140	12.1 ± 0.5 ^{a}	2.2 ± 0.6 ^{a}	96.3 ± 1.9	110.6 ± 8.7 ^{a}
	TtEg	54	13.5 ± 1.2 ^{b}	2.0 ± 0.5 ^{a}	94.6 ± 7.2	110.1 ± 7.1 ^{b}
Brasil	Focc	26	13.6 ± 0.7 ^{b}	2.5 ± 0.6 ^{b}	34.9 ± 5.9 ^{b}	51.0 ± 15.7
	Ttab	22	12.2 ± 0.4 ^{a}	2.0 ± 0.6 ^{a}	30.4 ± 3.7 ^{a}	44.5 ± 2.8
Ceranisus americensis						
25^{0}C						
Willcox	Focc	36	8.9 ± 0.9 ^{b}	2.8 ± 1.3 ^{b}	16.9 ± 1.6 ^{b}	28.6 ± 3.4 ^{b}
	Ttab	26	8.5 ± 0.0 ^{a}	2.3 ± 0.3 ^{a}	14.6 ± 0.6 ^{a}	25.3 ± 0.1 ^{a}
CampVerde	Focc	81	9.8 ± 0.6 ^{b}	1.8 ± 0.5 ^{b}	17.9 ± 2.0 ^{b}	29.4 ± 1.9 ^{b}
	Ttab	156	8.5 ± 0.3 ^{a}	1.5 ± 0.4 ^{a}	15.2 ± 0.7 ^{a}	25.2 ± 0.9 ^{a}
20^{0}C						
Willcox	Focc	201	15.6 ± 1.1 ^{b}	2.8 ± 0.7 ^{b}	47.4 ± 15.6 ^{a}	65.8 ± 15.8 ^{a}
	Ttab	141	12.8 ± 0.5 ^{a}	2.4 ± 0.6 ^{a}	89.4 ± 19.9 ^{b}	104.6 ± 19.8 ^{b}
CampVerde	Focc	127	14.4 ± 0.2 ^{b}	2.6 ± 0.9 ^{a}	54.3 ± 21.5 ^{a}	71.3 ± 23.8 ^{a}
	Ttab	69	13.6 ± 1.0 ^{a}	2.8 ± 1.3 ^{b}	56.4 ± 19.4 ^{b}	72.8 ± 20.9 ^{b}

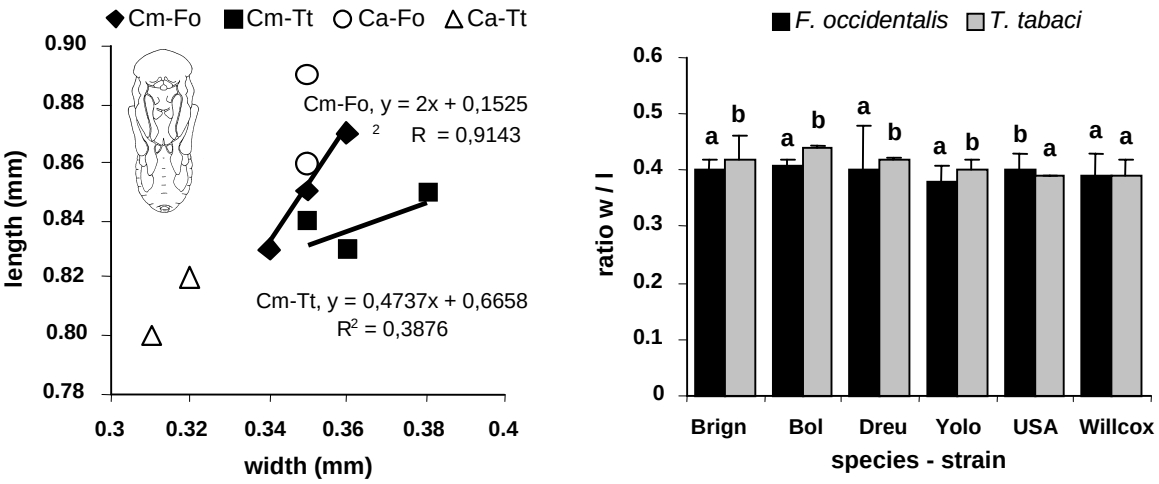

Figure 10. Length - width measurements (left) and width/length - ratio (right) (see figure 1) for parasitoid pupae of 4 different yellow strains of *Ceranisus menes* (Brignoles-France, Bologna-Italy, Yolo-USA and Dreumel-Netherlands) and *Ceranisus americensis* (USA, Willcox) according to the host they parasitise (*Frankliniella occidentalis*, *Thrips tabaci*); linear regression functions given for *C. menes* – host combinations only. Significant differences within a certain parasitoid-host combination are indicated with different letters (Mann – Whitney U, $p < 0.05$).

influencing their impact as a biological control agent, has been reported for many cases (Roush, 1990, Hopper *et al.*, 1993; Unruh & Messing, 1993). Variability may either be morphological, ecological, physiological or behavioural, and often implies either geographical or temporal separated populations. Variablity between strains of pest species has mostly been studied for host plant resistance breeding (Diehl & Bush 1984; Saxena & Barrion 1987; De Kogel *et al.*, 1997), but how it can influence the success of a biocontrol agent has often been overlooked. In biological control programmes involving exotic pests, natural enemies are often introduced from a climatic region similar tot hat of the pest to ensure an ecological synchrony. Hsaio (1993) and Kraaijeveld & van Alphen (1995) show that a lack of physiological synchrony (encapsulation) between the parasitoids and strains of the host, clearly affected suitability and control success.

In thrips, it is well known that populations of polymorphic species may vary considerably in colour, size and structure, which is in part spatial or temporal. In species like *F. occidentalis* and *T. tabaci*, variation is partly phenotypic: e.g. colour-variation induced by temperature (Priesner, 1960), variation in body size due to differences in host plant quality (de Kogel *et al.*, 1999). In our case, pale females of the Egyptian strain of *T. tabaci* became darker after 1 generation or more when transferred from 25^0C to 20^0C and vice versa. Part of this is genotypic like shown for *F. occidentalis* colour types (Bryan & Smith, 1956) and pesticide resistance (Brødsgaard, 1994) and maybe his is true for different *F. schultzei* colour types (Sakimura, 1969) as well. The presence of genetic variation in and between host populations and in the susceptibility to a parasitoid, such as found by Henter & Via (1995) indicates, however, that variability in and between host populations can be very relevant for the outcome of biological control by parasitic wasps. On the other hand, Henter *et al.* (1996) also found large differences in behavioural performance between 2 *Encarsia formosa* strains towards two different species of whitefly hosts, thus showing that there were heritable differences between two populations of asexual wasps. In our experiments we showed that variation occurred both within the host species as well as between parasitoid populations in their performance on populations of this host, based on host selection behaviour and on a physiological compatibility between host and parasitoid strains.

Behavioural observations

Female parasitoids that forage for hosts and evaluate their suitability based on external factors, are influenced in their host acceptance decisions by the age, species, the availability and quality of the host. There is a large amount of evidence in literature that there is a strong correlation between host acceptance on one hand and host suitability on the other hand, in particular for parasitoids of sedentary hosts. However, no evidence is available on external factors playing a role in the evaluation of host suitability by parasitoids of free-moving hosts, that are able to escape by running away or dropping from the plant, such as thrips and aphids. Also in our experiments we find no evidence that external factors play a role in this. A wasp has to "struggle and strike" in order to evaluate the internal quality and suitability of a host species or strain. Also Hildebrand *et al.* (1997) found that the host preference of aphid parasitoids, when offered host races of the same aphid species, was related to differences in physiology of these hosts and not to visual or external chemical cues. From other experiments (Carl, 1971; Banasik, 1994) we know that strains of both colour-types (i.c. 'Bignoles' and 'Cabrils') of *C. menes* are able to discriminate *F. occidentalis* larvae, previously parasitised by congenerics and by herself, from healthy ones after external antennal contact. In our tests here, however, active rejection of healthy hosts seemed rare upon an encounter and that an encounter was not followed by an attack, was largely the result of interruption of the process, because of defence reactions by the host larva, such as swinging a droplet of excrements into the direction of its attacker or just simply by running away upon being touched. Within the range of thrips species we evaluated, active rejection of healthy hosts was rare, attack initiation must be of a more general, subfamily-wide chemical nature. Exposing *C. menes* ('Brignoles') to a non-suitable host from another subfamily of Thysanoptera, such as *Heliothrips haemorrhoidalis* (Bouché), did not lead to any reaction to the host larvae. Wasps encountering larvae by accident, did not react and when counteracted by a defensive reaction of the larva, mostly smearing a droplet of anal exudates on the attacker, they were severely hampered in their search, sometimes even leading to the death of the female.

To what extent are the time a wasp takes for an encounter, attack and insertion, the numbers and times an indicative tool for the level of acceptance c.q suitability of that host species for a parasitoid female? From our size experiments (chapter 4) we learn that wasps take more time to evaluate young hosts externally than old hosts, measured by times of an encounter and attack. Also Diop (1999) found that in sexual strains of *C. menes* the phase of antennating and subsequent attack of *Megalurothrips* larvae lasted longer on young larvae than on older ones. However, within the same age group of larvae, the time of successful and unsuccessful encounters were not significantly different for the parasitoid – host combinations observed. This could be in part due to a limit in reaction and registration time of the observer, especially when an encounter and attack time lasts 1 second or less as it did in the combinations of yellow *C. menes* strains and *C. americensis*. It is then difficult to distinguish whether that split second is just the result of an active interruption by the host or by an active rejection by the parasitoid when not taken by surprise, subdued quickly or lifted from the ground, a thrips larvae has a fair chance to escape. Females of brown colour-types, however, take a relatively long time to inspect a host larva externally (see also chapter 4). This did not differ with respect to the species of host larvae involved: encounter times by 'Cabrils' wasps lasted 4.5-4.8 s for *F. schultzei* resp. *F. occidentalis* and the 'Maximin' females took 1.7 –1.8 s for *T. tabaci* resp. *F. occidentalis*. There is a clear difference though in suitability between *T. tabaci* and *F. occidentalis* larvae for this parasitoid strain. For larvae that resist fiercely against being inserted, the attack time would last longer and insertion / attack ratio be lower, but differences were rarely found for any parasitoid attacking 2 different species of hosts: larvae of all species have a similar chance to interrupt once being attacked. Previous experiments indicated that encounter times decreased during the course of a day (chapter 4), but that attacks became much less frequent, which was due to the motivation / egg load of the female wasp and not so much with the quality of the host. Experiments with different size classes of *C. menes* and *C. americensis* also show that the number of

encounters during a certain period can be large (>160 per hour) regardless of the success on that size class.

With respect to insertion times we found that within the same parasitoid-host combination there was no correlation between insertion times and the parasitisation result (egg laying or not), when 2 day old first stage larvae were used (series 1). For *C. americensis*, however, results indicate this might be true when different species of larval hosts are involved: insertion times were significantly shorter for *F. occidentalis* larvae than for *T.tabaci*, whereas significantly more eggs were laid in the first species than in the latter. Indirectly this indicates that either a wasp needs a certain minimum time for internal inspection of a host larva, ór that there is a difference in host quality or suitability. Our observations on the particular age group involved, which are subdued after a short period and do not resist insertion like older larvae do, make the latter most likely.

Developmental time

Growth and development of insect parasitoids is often markedly influenced by the host species from which they develop and host related variations in size and survivorship are known for many associations. Developmental flexibility and host regulation are important mechanisms that allow parasitoids to develop in a wide range of host instars (Harvey & Thompson, 1995). Parasitoid wasps, while encountering different species and strains of *Frankliniella* and of *T. tabaci,* not only differed clearly in the acceptance and rejection of these species as hosts, but also in time to develop from egg to adult and in the number and size of offspring produced. Under controlled conditions, *C. menes* and *C. americensis* can develop successfully on various thrips species within the subfamily of the Thripinae (Thysanoptera: Thripidae), but our experiments show that parasitoids of different geographic populations may vary greatly inter- and intraspecifically in external and internal host acceptance. In the case of *C. menes*, differences in the biology of the host species strongly influenced their development and fitness (Loomans & van Lenteren, 1995). In previous studies, Murai & Loomans (1995) working with the 'Shimane' strain of *C. menes* and Tagashira & Hirose (2001) working with another local strain of *C. menes*, found no significant difference in pupal duration of the parasitoid among the various host species they studied, *Frankliniella intonsa*, *Thrips tabaci*, *T. hawaiiensis* and *T. palmi*. Our results with asexual strains of the yellow colour-type, which are similar to theirs, show that this largely holds when *Frankliniella* species are involved, but are different when *Thrips tabaci* is parasitised. For the brown colour-types we studied this was the case as well. The developmental process of juvenile *C. menes* is likely affected by the endocrine system of its host and is synchronised with host development. This was shown by a synchronisation of the parasitoid with the host cycle of multivoltine (Murai, 1988) or univoltine thrips host species (Loomans & van Lenteren, 1995). On thrips host species with a relatively short life cycle like *F. intonsa*, parasitoid developmental time is shortest as well. But that only the egg and larval stage are affected by the species of host, as hypothesized by Murai & Loomans (1995) and Tagashira & Hirose (2001), is contradicted by our results, where pupal periods of both *Ceranisus* species vary according to the host species involved (table 8). Also the strong asynchrony between the developmental cycle of *Ceranisus* species and their hosts at 20^0C does not support this hypothesis: whereas the host takes 3-4 weeks to develop, the development of *Ceranisus* species slowed down to 3-4 months or more. The large variation in pupal developmental time at low temperatures has been found before for a yellow strain (Galazzi *et al.*, 1992: Bologna strain on *F. occidentalis*), (Murai, 1990a: 'Shimane' strain on *F. intonsa*).

In many insect parasitoids there is a clear relationship between female body size (often measured as hind tibia length) and egg-load and thus fecundity (Godfray, 1993): large wasps lay more eggs and live longer than small wasps (Visser, 1994). Also thrips species can influence not only developmental time of *C. menes,* but also adult size (Murai, 1988). In our experiments, *C. menes* and *C. americensis*, when developing on either one of the *Frankliniella* species, pupae were significantly larger than those reared on *T. tabaci*. On the

population level we also found differences in size of pupal offspring when parasitoids developed on 2 populations of *F. occidentalis*. Results were much more profound though for *T. tabaci*, in particular for the brown colour-type strains of *C. menes*. Size of the parasitoid correlates with the size of the thrips host species. Size and fecundity in parasitic wasps are partly phenotypical characteristics, depending on environmental factors and hosts and can change when environmental conditions improve. Tagashira & Hirose (2001), comparing the effect of *Frankliniella intonsa* and *Thrips palmi* on development and size of *C. menes* (yellow) found that size of the pupal body clearly differed between the 2 host species, but that there were no significant differences in longevity and total fecundity of the parasitoid. The thrips species it was cultured on did not seem to affect the outcome on the new host species, regardless the original host-parasitoid combination. Although we do not have direct evidence for this ourselves, indirect evidence through our experience when culturing parasitoid strains on different hosts, both confirm and contradict their finding and indicate that the host species and/or strain can strongly affect the parsitoid's fitness. Numbers and size of the offspring of brown colour- types (see table 6) when reared on the Dutch *T. tabaci* strain, decreased drastically when transferred to the *T. tabaci* strain from Egypt. Some parasitoid strains (brown type) were almost lost within 2 generations, because minute wasps were produced in small numbers. When transferred back to the original Dutch strain, cultures recovered from the first generation onwards and remained consistent over a number of generations, suggesting a certain incompatibility between thrips and parasitoid strains. The difference in the level of parasitism and size was not so pronounced for *C. menes* (yellow) and *C. americensis*, but parasitoids were smaller in size too. Likely there is a certain range in host size, relative to the size of the parasitoid, within which a parasitoid can develop successfully and is behaviourally capable attacking new hosts as well.

To what extent behavioural and developmental differences between *Ceranisus menes* populations from various geographic locations are due to phenotypic plasticity or genetic differences can partly be answered. Differences between colour-types in behavioural traits and host preferences on one hand and relative size and developmental times on the other, support a genetic basis. Variation within these colour-types, in particular between the yellow strains, partly have a genetic basis as well, as shown by its consistent differences in developmental time at different temperatures for different geographic populations. Variation in RAPD-PCR polymorphism using total DNA showed the absence of a host-based population structure and a high genetic homogeneity between the different colour-types of *C. menes* on one hand and between geographic populations (Netherlands vs. France) on the other (Loomans, unpublished data) support this. Our results show that inter- en intraspecific differences of the host species affect the growth and development of *Ceranisus* prasitoids. Colour types of the parasitoids clearly differed in their acceptance and suitability of larvae of different host species: number of parasitised offspring, size of the parasitoid pupae (and adults) and parasitoid developmental time. Except by the thrips host species and its mode of voltinism, acceptance and suitability of host larvae, the number and size of offspring as well as developmental time may vary with age, stage, size, quality and sex of the thrips host larvae for colour-types of *C. menes*, but most need further studies to specify these.

Whether environmental variability may influence and perhaps alter suitability, is still largely anecdotal. In the field occasionally high levels of parasitism have been found for biparental *C. menes*, parasitising *T. tabaci* in Japan and *T. palmi* in Japan and Thailand, other records on the same host species show a much lower level of parasitism (Loomans & van Lenteren, 1995). Our host acceptance and suitability experiments can largely explain this. Carl (1971) suggested differences in suitability of *T. tabaci* from Europe and India for *C. menes* from India, and our results give support to this idea. In a natural habitat, mixed populations of both the yellow and brown colour-types of *C. menes* (Europe) can be found on the same plant, infested by a mixture of populations of thrips species belonging to the genera *Frankliniella* (*intonsa, pallida, occidentalis*), *Thrips* (*major, brevicornis, vulgatissimus, fuscipennis,* etc.) or *Taeniothrips* (*hispanicus*), etc. (Loomans, 1991).

Differential host acceptance can give an idea how niche partitioning among parasitoids could reflect their strategies to minimise competition in a natural context. Which host species and how many hosts *Ceranisus* spp. are able to locate however, may also proceed from the foraging behaviour of the parasitoid. If *C. menes* colour-types also show a different searching strategy in their natural habitat or in the greenhouse, and which stimuli are used for host location, is not yet known. In greenhouse crops, usually with a monoculture of host plants infested by one or two thrips species, the situation is less complex. Determination of host-specificity of parasitoids can be used as part of a set of criteria which have to be assessed for a proper evaluation and pre-selection of a candidate species for biological control (van Lenteren, 1995). Our results confirm that intra-specific variation in host-specificity by various strains of parasitoids can be of great importance to possible failure or success in biological control (Unruh & Messing, 1993). We preliminary conclude that *C. americensis* is a better candidate for the control of *F. occidentalis*, the brown colour-type of *C. menes* for *T. tabaci*, and the yellow colour-type of *C. menes* for infestations by either one of both or mixed populations.

What are the consequences of this for biological control of thrips pests? Our findings first show that the result of host-parasitoid interactions are strongly depending on the specific host-parasitoid combination, not only on the species level, but also on the population level. Selecting the proper strain – that is physiologically, biologically ánd ecologically adapted to its target host – and matching this with the population of the host, can be of crucial importance to possible failure or success in biological control (cf. Unruh & Messing 1993; Hsiao, 1993). The differences in host preference between morphological colour-types and between various geographic populations of the parasitoid on one hand and the variability between populations of certain host species on the other, together with the occurrence of mixed infestations, brings about that a tailor made solution by *C. menes* can only be made for a local situation or crop, when all other prerequisites are met. For a globally invasive species like *F. occidentalis*, where there is little variation in biological traits between geographic populations established in the newly invaded areas, a tailor made solution can only be found, by selecting a highly specific natural enemy, applied in a classical biocontrol like approach, with a natural enemy highly specific to its invading host, and as flexible to local conditions as its host. For locally invasive species, like *T. tabaci*, with a high variability between populations in a small geographic area, infestation problems could be solved by a tailor made solution for the local situation. *F. occidentalis,* however, often is the major, but not the only thrips pest around in greenhouse grown crops. Mixed populations often occur and this has consequences for the biocontrol strategy to use. The occurrence of mixed populations of two or more thrips pests in one crop, makes a commercial use of one specialised larval parasitoid species unlikely.

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Chapter 6

Life-history studies on larval parasitoids of western flower thrips[1]

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Abstract

Life-history parameters of two species of parasitoids, *Ceranisus menes* (Walker) and *Ceranisus americensis* (Girault) (Hymenoptera: Eulophidae) were investigated in the laboratory at 20^0C and 25^0C with larvae of western flower thrips, *Frankliniella occidentals* (Pergande) (Thysanoptera: Thripidae) as a host. Of *C. menes* 4 geographical strains were compared, including two morphological types (colour-types: yellow vs. brown abdomen, 'Brignoles – France / 'Shimane' - Japan and 'Cabrils' – Spain). Both species are solitary koinobiont endoparasitoids of thrips larvae, and all strains tested reproduced parthenogenetically. In this study, the influence of temperature on parasitoid development, percent emergence, longevity, fecundity, oviposition frequency and pre- and post-oviposition period was determined and basic demographic parameters, such as intrinsic rate of natural increase (r_m), net reproductive rate (R_0) and generation time (Tc). were calculated.

Developmental and reproductive biology were significantly affected by temperature and characteristic for each species / strain. Immature development increased drastically with a decrease in temperature, in particular in *C. americensis*. Pupal development times varied greatly at both temperatures, whereas egg-larval development varied less. Within *C. menes* there were large differences between strains and colour-types, irrespective of temperature: the yellow type ('Brignoles'-France; 'Shimane' - Japan) showed a large variation in developmental time, whereas the brown type ('Cabrils'-Spain) did not. In *C. menes* fecundity decreased with temperature, but it increased in *C. americensis.* Oviposition frequency (eggs per female during the reproductive period) varied between 3.2 and 12.5 eggs for *C. menes* strains to 17 and 18.7 eggs per female for *C. americensis*. In *C. americensis* the fecundity curve had a maximum on the 4th day after emergence, whereas *C. menes* strains all had a curve that levelled off gradually, which is accounted largely to a difference in ovigeny: steep and short in *C. americensis* versus shallow and long in *C. menes*. The net reproduction (R_0) of *C. americensis* and of the yellow *C. menes* types was much larger than that of the brown one. The intrinsic rate of increase (r_m) for *C. americensis* was 0.0719 at 20^oC and 0.1650 at 25^oC. For *C. menes* the r_m was 0.0487 for the yellow type ('Brignoles') and 0.0848 for the brown type ('Cabrils') at 20^oC and 0.1349 (yellow) and 0.1234 (brown) at 25^oC. Differences between both species largely due to a differences in developmental time and in ovigeny and shows that reproduction at an early phase in life has a greater impact on r_m than reproduction at a later stage.

The value of life-history parameters as an indicative value for a parasitoid's effectiveness as a future biological control agent of *F. occidentalis* and the characterisation of the species and populations are discussed. We argue that absolute values of calculated parameters are of profound, but yet relative value. Survival and fecundity curves are of a very indicative value for the strategic outcome of specific parasitoid-host combination tested and thus as much important a tool in establishing the effectiveness of a particular parasitoid.

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[1] Parts on *C. menes* have been published as : Loomans, A.J.M. and Murai, T., 1994. Comparison of the life-histories of different colour-types of *Ceranisus menes* (Hymenoptera: Eulophidae), parasitoid of *Frankliniella occidentalis* (Thysanoptera: Thripidae), *Proceedings of the section Experimental and Applied Entomology of the Netherlands Entomological Society (N.E.V.), Amsterdam*, 5: 35-40.

Introduction

Western flower thrips, *Frankliniella occidentalis* (Pergande), is an important pest in greenhouse grown vegetable and ornamental crops throughout the world. Population growth can be fast when conditions are favourable. Under the same environmental conditions, differences in the amount and quality of food, such as the availability of pollen, can largely affect population growth differences between crops. Population growth is also not constant during the season: it increases from slow at the early, colonising phase of the crop to fast at the exponential phase from the second generation onwards (Jarošík *et al.*, 1997). This has important implications for the type, timing and release of biological control agents in greenhouse IPM programmes.

Knowledge of the life-time reproductive success of parasitoids can contribute significantly to a better understanding of the evolutionary and demographic parasitoid-host interactions (Godfray, 1993). Understanding the environmental and intrinsic factors that determine the reproductive success of a particular natural enemy, also has more practical implications: population parameters like the intrinsic rate of increase (r_m) have been widely used as indices of the potential performance of natural enemies. Determination and analysis of the life-history parameters is considered an important tool for evaluation of the effectiveness as a future biological control agent by direct comparison (van Lenteren, 1986; Heinz *et al.*, 1993) or as inputs for a simulation model of the population dynamics of the parasitoid (van Roermund & van Lenteren 1993). In order to be effective, a good biological control agent should have a population growth rate that at least equals, but preferably outnumbers that of the target pest. This is considered as an important criterion in the pre-introduction evaluation of effective biological control agents (van Lenteren & Woets, 1988), especially for seasonal inoculative release purposes.

Ceranisus menes (Walker) and *Ceranisus americensis* (Hymenoptera: Eulophidae) are two solitary koinobiont endoparasitoids of larvae of thrips species within the subfamily Thripinae (Thysanoptera: Thripidae). *C. menes* is parasitic on a wide range of hosts, including important pest species like *Thrips tabaci* Lind.,*Thrips palmi* (Karny) and *Frankliniella occidentalis* (Pergande) (Loomans & van Lenteren, 1995). *C. americensis* is known to parasitise larvae of *F. occidentalis*, but its host range is still largely unknown. Within *C. menes*, different morphological types can be distinguished according to the colour of the abdomen: brown, intermediate and yellow (Loomans, 1991, see chapter 2 – figure 2). In material collected in Europe both the yellow and the brown colour-types occur, even on the same collection site and host plant (Loomans, 1991; Galazzi *et al.*, 1992; chapter 2). Collections made in California also showed the presence of both colour-types of *C. menes*, separately as well as on the same site. Material originating from South America show intermediate (Brasil) and brown colour-types (as *Ceranisus rosilloi*, DeSantis, 1961). Specimens originating from Japan (Murai, 1990; Loomans, 1991) belong to the yellow type as well. In the field, sexual and asexual populations are known, but all strains investigated in our laboratory experiments reproduced parthenogenetically. The identification and characterisation of different biotypes of parasitoids can be of great importance to failure or success in biological control (González *et al.*, 1979; Caltagirone, 1985; see chapter 5). According to their colour-type and geographical origin, strains of *C. menes* differed in host acceptance behaviour and host suitability (chapter 5).

In this paper we present data on the life-history of two *Ceranisus* species, including intraspecifical different colour-types of *C. menes,* at two different temperatures, and we compare development time and life-time reproductive capacity to its target host, *F. occidentalis,* as a step in the evaluation of these parasitoids and discuss its significance for future biological control.

Materials and methods

Thrips and parasitoids

Thrips hosts, *F. occidentalis*, were reared according to the artificial method (Murai, 1990), using pine and tea pollen for oviposition and pine pollen and honey solution (10%) for rearing the larvae. Egg-collection and larval synchronisation was done according to a modified procedure as described by Murai & Loomans (2001). Parasitoid females of different and colour-types (yellow and brown) of *C. menes* were compared. Stock material of the yellow type was collected near Brignoles - France ('Brignoles', Aire Barcelone = AB) in 1990 from *Centranthus ruber* and that of the brown type near Cabrils, Spain ('Cabrils') in 1991 from carnation (*Dianthus* spp.) Strains originating from 'Holambra' - Brasil and 'Shimane' - Japan were used as comparison. Since their collection, all strains have been reared in the laboratory on *Frankliniella schultzei* Trybom (light form) as a host, using bean pods and additional bee pollen (Loomans, 1991) as food at 25 ^{0}C, except for the 'Shimane' strain which was reared on pollen and honey-water with *Frankliniella intonsa* (Trybom) as a host. Stock material of *C. americensis* was collected near 'Willcox' - Arizona USA, May 1993, and had been cultured on *F. occidentalis* on pollen and honey-water for about 10 generations.

Experimental procedures

Development - 10 two day old, virgin females of both *Ceranisus* species and strains were put in a plastic ring for 8 hours with 100 *F. occidentalis* larvae, 24-48 hrs old. Ring cages were 8 cm in diameter and 5 cm high. Larvae were reared on pollen and honey-solution 10% until pre-pupation and were then transferred like described above and checked daily for pupation and hatching of adult wapsp. Each combination was repeated twice (20 ^{0}C), three ('Cabrils', 'Willcox') or four ('Brignoles') times (25 ^{0}C). Series were repeated for a variety of *C. menes* strains later on.

Reproduction - Freshly emerged females of *C. menes* and *C. americensis* of each strain were used in the experiments, 15 per strain at two temperatures: 20 ^{0}C and 25 ^{0}C. A single female parasitoid was put in a plastic ring cage, 5 cm in diameter and 5 cm high, with 75 freshly emerged *F. occidentalis* larvae (1-30 hrs) and a thin line of honey for 24 hours. Each female was transferred into a similar new ring every day during her life. Female fecundity was evaluated by the number of pupal offspring. When parasitoid pupae appeared, they were transferred into a glass jar on moist filter paper until eclosure. All life-history experiments were carried out in an Elbanton incubator at constant temperatures of 20 ^{0}C and 25 ^{0}C and at a 16L:8D hr photoperiod. The experiment at 25 ^{0}C was repeated twice.

Life-history parameters - Values of the basic life-history parameters were determined, such as the oviposition period, adult survival (longevity) and reproduction. Fecundity was measured as the number of pupal offspring. Because all strains reproduce parthenogenetically, fecundity equals the female offspring / day.

Calculation of population reproductive statistics - Using the values for life-history parameters mentioned above, life-fertility tables were constructed. From these tables the population growth statistics of the different strains were determined at two temperatures by solving the following equation by iteration (Hulting *et al.*, 1990):

$$\sum_{X=1}^{k} e^{-r_m x} L_x M_x = 1 \text{ (Carey, 1993),}$$

where x is the age in days, k the last day of a females possible life, r_m is the intrinsic rate of increase (population growth rate), L_x the age-specific survival rate and M_x the age-specific fecundity - estimated as the number of parasitoid offspring (pupae) produced per female in each age class x. From this we also calculated the net reproductive rate ($R_0 = \Sigma_x l_x m_x$), and generation time T_g (= ln R_0/r_m).

Statistics

Results were tested statistically, using the Kruskall-Wallis test and a multiple comparison test (total number of eggs and life span of parasitoids, between strains) upon significance and the Mann-Whitney U test (within strains), both at significance levels of $p < 0.05$.

Results

Development.

Ceranisus menes and *C. americensis* are both koinobionts, allowing the host to grow beyond the stage attacked. Parasitised larvae can move about freely and feed normally and cannot be distinguished externally from unparasitised ones and parasitism only becomes evident at prepupation of the host: the absence of prepupal wing buds, a slightly swollen body, a yellow-orange central spot in the prepupa. The pupa is almost white (*C. menes, C. americensis*) when newly formed, becoming dark brown to black. Pupation development takes place outside the larval skin. The site of pupation is related to that of its thrips host, usually the soil. Pupae of both parasitoid species can be distinguished by size and shape and yellow and brown strains of *C. menes* can already be distinguished from each other by the size and coloration of the maturing pupa.

Developmental time from egg-adult (table 1), percent parasitism and percent hatching adults (figure 1, table 2 for a few selected strains) varied between strains, according to their phenotypic appearance (abdominal colour-types: yellow versus brown) and geographical origin (North versus South). Yellow strains of *C. menes* showed a large variation in overall developmental time (figure 2), whereas brown types did less, regardless their origin. This variation was even more pronounced at 20 ^{0}C: developmental time was much longer, especially in the Dutch strains. Values are even underestimated as more than 80% did not hatch within 130 days. American strains of *C. menes* showed developmental times comparable to the Mediterranean strains at 25 ^{0}C (chapter 5), but developmental time at 20 ^{0}C was also much prolonged. *C. americensis* has a developmental time of 28 days at 25 ^{0}C, and 66-71 days at 20 ^{0}C, both comparable to that of *C. menes*. However, the emergence distribution curves show that temperature slows down juvenile development significantly in all *C. menes* strains, but that strains react differently (figure 2). 'Brasil' and 'Cabrils' show a similar but narrow interval at both temperatures, whereas the 'Brignoles' and 'Japan' strains (yellow types) have a much wider interval, with an early and a late, extended peak. For *C. americensis*, however, we see that temperature has a much greater effect on juvenile developmental time: narrow at 25 ^{0}C, and a large variation at 20 ^{0}C.

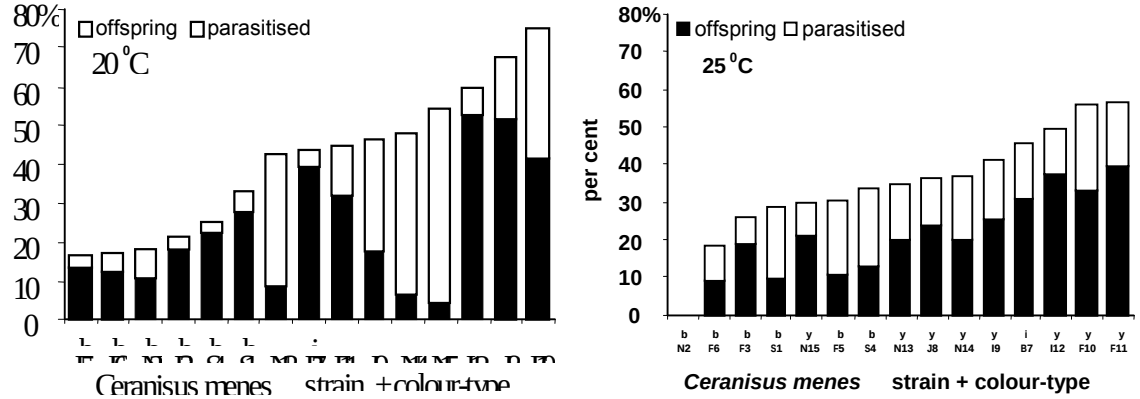

Figure 1. Percentage of hatched wasps (black bars) and parasitisation (black + white bars) of *C. menes* reared on *F. occidentalis* at different temperatures (A, n=200, 20°C; B=300, 25°C). See table 1 for strain symbols.

Table 1. Average developmental time of *C. menes* and *C. americensis* reared on *F. occidentalis* at 20 and 25 (± 1) ^{0}C, n_{20} =200 and n_{25} = 300; geographic origin: B = Brasil: 20 ^{o}S.L.; J = Japan: 35 ^{o}N.L.; F = France, I = Italy, S = Spain:40-45 ^{o}N.L.; N = Netherlands: 52 ^{o}N.L.; C = California: 35 ^{o}N.L.; A = Arizona: 32 ^{o}N.L.); different letters indicate significant differences among strains within temperatures (Kruskall-Wallis, p <0.05)

Strain nr	origin		Colour-type	Developmental time (days ± s.d.) 20 ^{0}C		25 ^{0}C	
Ceranisus menes							
1	S	Incinillas	brown	36.2 ± 1.9	a	26.3 ± 1.6	a
2	N	Kesteren	brown	36.5 ± 1.9	a	*	
3	F	Maximin	brown	38.4 ± 2,8	a	28.5 ± 0.7	a
4	S	Cabrils	brown	38.9 ± 1.6	a	28.4 ± 1.5	a
5	F	Perpignan	brown	39.8 ± 1.5	a	28.5 ± 1.3	a
6	F	Hyères	brown	42.9 ± 7.6	a	27.7 ± 1.0	a
7	B	Holambra	amber	41.5 ± 1.7	a	27.5 ± 1.1	a
8	J	Shimane	yellow	66.2 ± 21.9	b	33.8 ± 7.5	a
9	I	Pescia	yellow	70.7 ± 38.1	b	29.7 ± 3.9	a
10	F	Perpignan	yellow	75.8 ± 37.1	b	29.2 ± 1.5	a
11	F	Brignoles	yellow	82.4 ± 26.7	b	33.4 ± 10.3	ab
12	I	Bologna	yellow	108.0 ± 25.3	bc	36.7 ± 12.8	ab
13	N	Kesteren	yellow	111.4 ± 25.6 ^{u}	c	36.6 ± 10.4	ab
14	N	Dreumel	yellow	119.9 ± 17.1 ^{u}	c	42.1 ± 15.5	b
15	N	Velddriel	yellow	120.5 ± 16.5 ^{u}	c	36.0 ± 11.0	ab
Ceranisus americensis							
1	C	Mendota	-	*		27.1 ± 1.1	a
2	A	Willcox	-	71.9 ± 23.8	b	27.9 ± 1.8	a
3	A	Camp Verde	-	66.3 ± 15.8	b	28.1 ± 3.4	a

^{u}: underestimated, time based on <20 % of hatched pupae within 120 days after parasitisation; *: not tested

Table 2: Average developmental time (days ± s.d.) of selected strains of *C. menes* colour-types on *Frankliniella occidentalis* at different temperatures. Averages are statistically significant when indicated by an * (within colour-types, between temperatures) and by a different letter (between colour-types, same temperature) (Mann-Whitney U, p < 0.05).

temp.	strain colour-type	development time	larvae	parasitised	hatched
C. menes					
20 ^{0}C	'Brignoles' -yellow	82.4* ± 26.7 ^{a}	200	45 %	71 %
	'Cabrils' - brown	38.9* ± 1.6 ^{b}	200	25 %	88 %
25 ^{0}C	'Brignoles' -yellow	33.4* ± 10.3 ^{a}	400	57 %	66 %
	'Cabrils' - brown	28.4* ± 1.5 ^{b}	300	38 %	34 %
C. americensis					
20 ^{0}C	'Willcox'	71.9* ± 23.8 ^{a}	500	46 %	85 %
25 ^{0}C	'Willcox'	27.9* ± 1.8 ^{a}	500	23 %	87 %

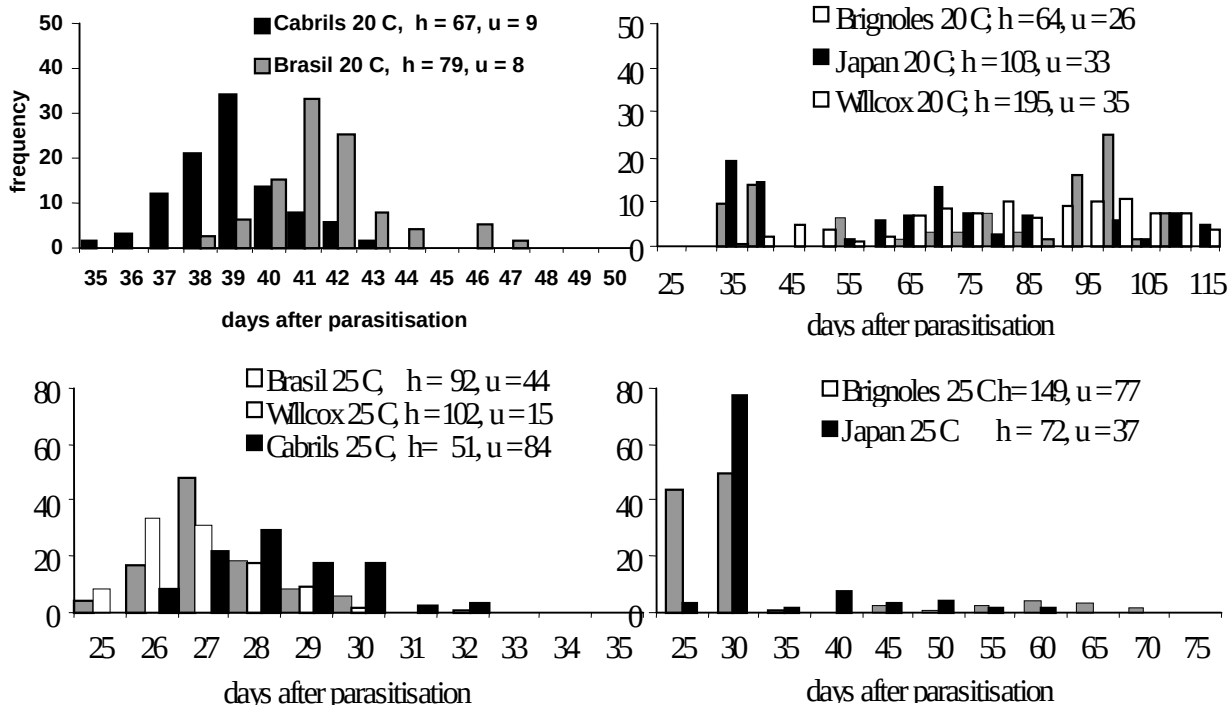

Figure 2: Distribution curves of adult parasitoid eclosure (days after parasitisation) of yellow ('Brignoles', 'Japan'), brown ('Cabrils') and intermediate ('Brasil') colour-types of *C. menes* and *C. americensis* ('Willcox') with *F. occidentalis* as a host at different temperatures (up: 20 ^{0}C; below: 25 ^{0}C); h = number pupae hatched, u = unhatched pupae (healthy or dead).

For both species and most strains in *C. menes*, relatively low levels of parasitism were found (figure 1; table 2) with the brown types on the lower and the yellow type in the upper half. At 25 ^{0}C temperatures the 'Cabrils' and 'Brasil' strains relatively low numbers of adults emerged.

Reproductive capacity

All strains of *C. menes* as well as *C. americensis* we used, reproduced parthenogenetically: only female offspring was produced. The age-specific survival rate and the average daily fecundity per surviving female are shown in figures 3 and 4. Survival curves differ between temperatures: females lived for about 3 (25 ^{0}C) to 4 weeks (20 ^{0}C) in both species. At 20 ^{0}C, female survival was slightly shorter when no hosts were present but in the presence of honey-solution 10% (figure 5) compared to the presence of hosts (figure 3 and 4) (~4 weeks maximum), but decreased drastically at 25 ^{0}C without hosts. No pre-oviposition period was found for *C. americensis*: all females started to lay eggs on the first day (table 3). For *C. menes* there was some variability between strains and temperature ('Brasil', 'Brignoles'), if not on the first day at introduction, all females started to lay eggs on the second day.

Fecundity of *C. americensis* was much higher than that of all *C. menes* strains tested. For *C. americensis* the average daily fecundity was high during the first half of her life-time (figure 3), for *C. menes*, the average daily fecundity gradually declined, however, more gradually with increasing age for all 4 strains (figures 3 and 4). Yellow strains ('Brignoles' and 'Japan') had higher oviposition rates (table 4) than 'Cabrils' (brown) and Brasil (intermediate). When taking the oviposition rate into account – the number of eggs per female per day – *C. americensis* differed markedly from C. menes strains (table 4). *C. americensis* has a short period of relatively high reproduction. The post-oviposition period, in which no offspring was produced, is relatively long for *C. americensis* (7.7 and 8.7 days at 20 and 25 ^{0}C), whereas *C. menes*, had a shorter post-reproductive period of 2-4 days. At 20 ^{0}C the 'Brasil' population was an exception, but in the 'extra time' no reproduction occurred. The age specific fecundity as shown in figures 3 and 4, indicates that both species differ in 'ovigeny' (potential lifetime

egg complement that is mature when females emerge, sensu Jervis *et al.*, 2001) and in egg-maturation rate: both species are syn-ovigenic (emerging with some immature eggs upon emergence), but the extent differs clearly between *C. americensis* and *C. menes.* The first has more mature eggs upon emergence than the second and, in abundance of hosts, the egg-maturation rate is fast, whereas in *C. menes* has less and eggs need more time to mature. Dissection of freshly emerged adult females, confirm this: *C. americensis* had an average of 160 eggs (range 159 –177, n= 5) (full grown and immature) in the ovarioles, whereas *C. menes* ('Brignoles' and 'Cabrils') numbers ranged between 35 and 43 (n=5).

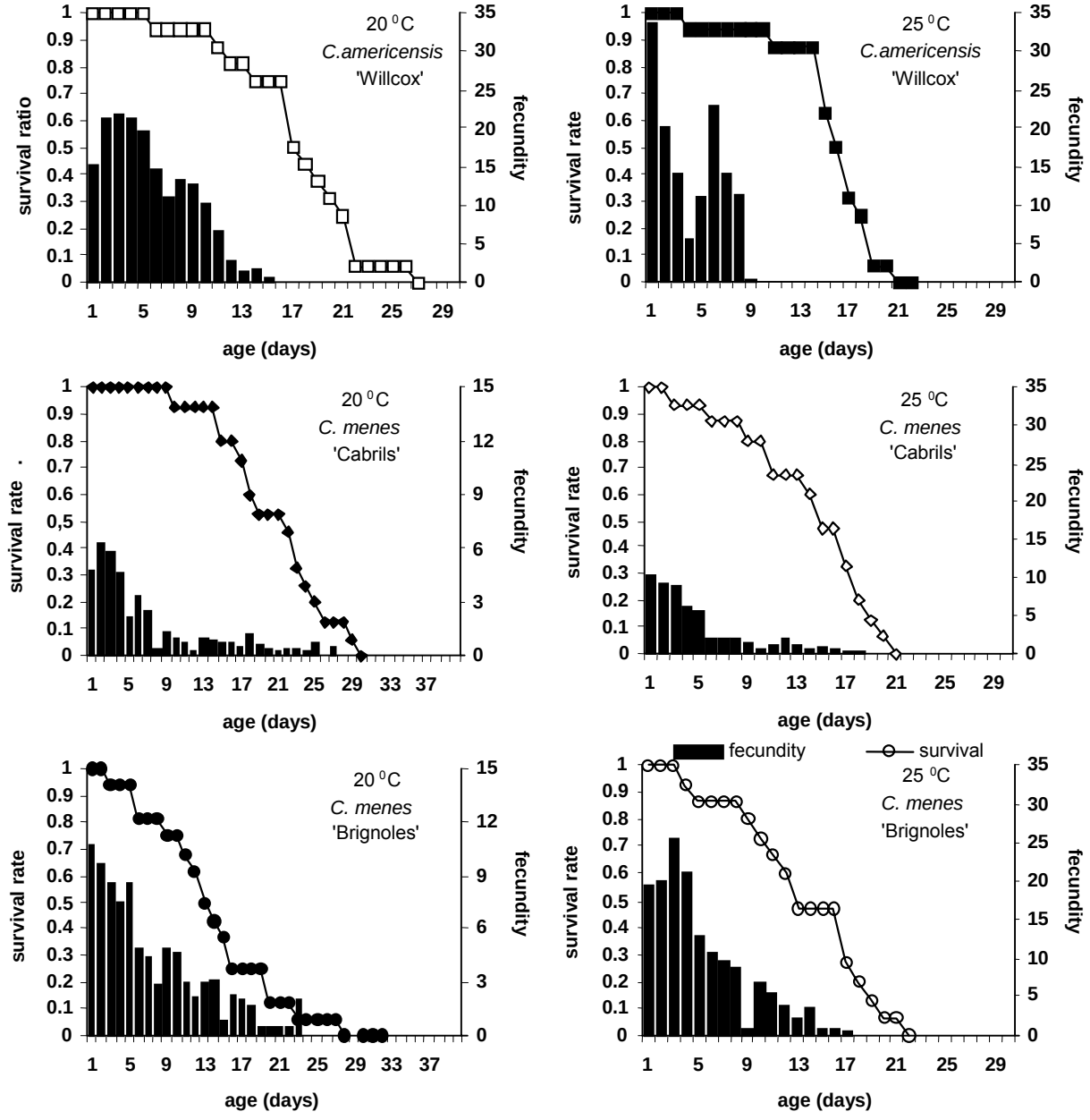

Figure 3. Age-specific survival (left y -axis) and age-specific fecundity (right y -axis) for *C. americensis* 'Willcox' - Arizona (top), a brown ('Cabrils' - Spain; middle) and a yellow ('Brignoles' - France, bottom) colour-type of *C. menes* with 1st stage larvae of *F. occidentalis* as a host at two different temperatures (left: 20 °C; right: 25 °C). Fecundity-values are average numbers of pupal offspring per surviving female (n = 15).

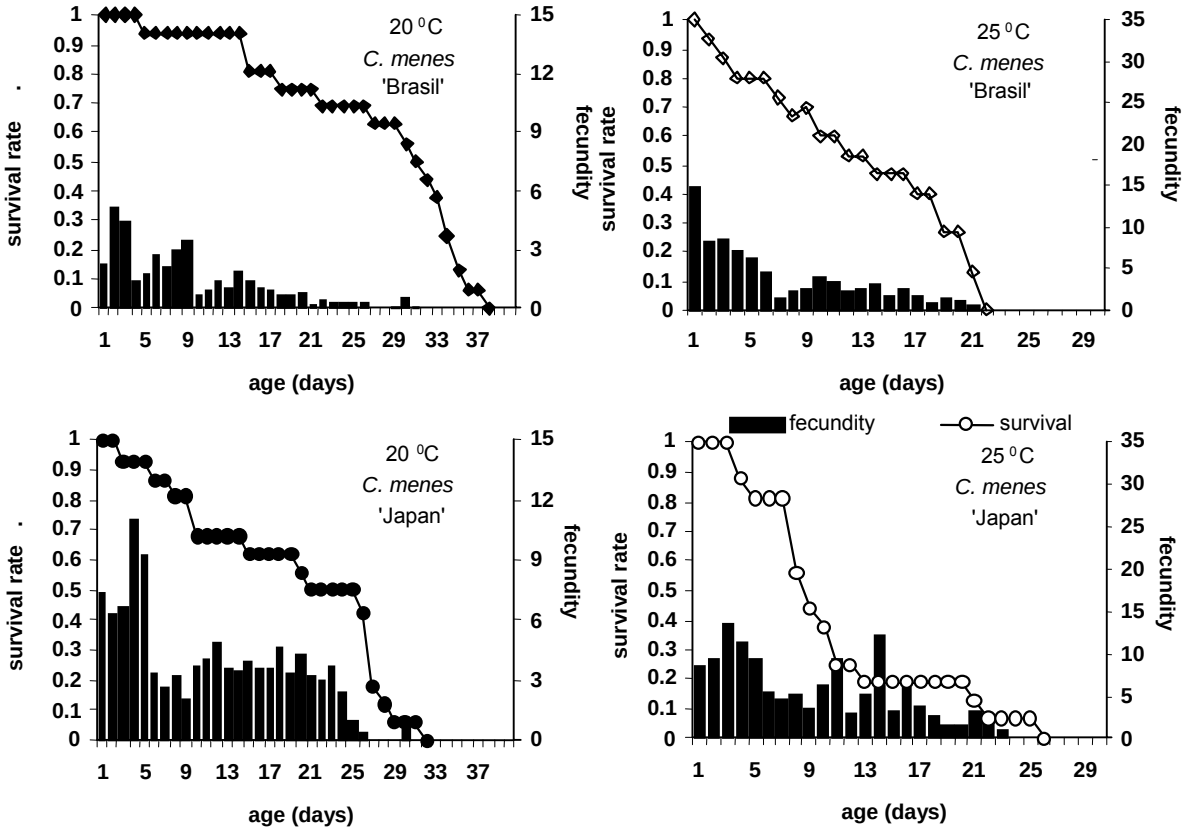

Figure 4. Age-specific survival (lines) and age-specific fecundity (bars) for *Ceranisus menes* strains 'Brasil' and 'Japan' with first stage larvae of *F. occidentalis* as a host at two different temperatures (left: 20 °C; right: 25 °C). Fecundity-values are average number of pupal offspring per surviving female (n = 15); (data 'Japan' from Murai & Loomans, 1995).

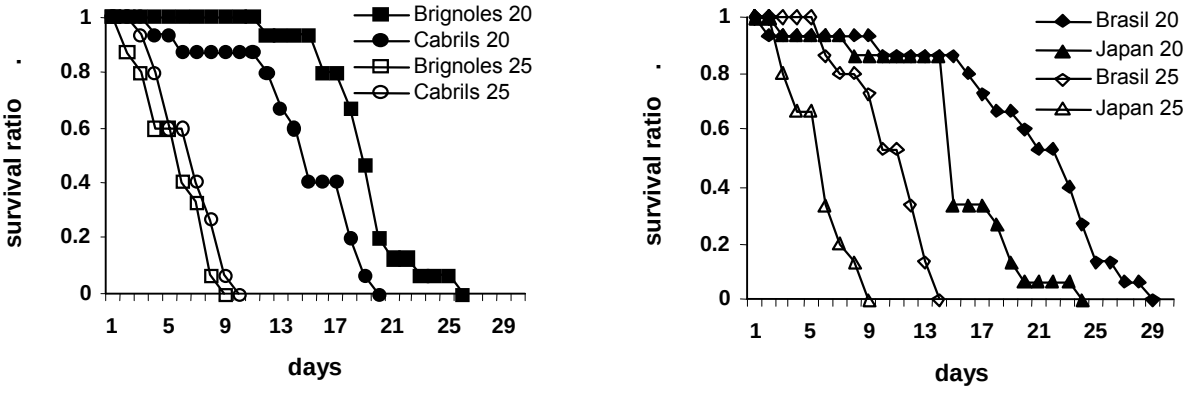

Figure 5. Survival curves of adult *Ceranisus menes*, strains 'Brignoles' and 'Cabrils' (left) and strains 'Japan' and 'Brasil' (right) as a function of age (without hosts, with honey) at 20^{0}C and 25^{0}C. Life span for each strain was significantly different between 20^{0}C and 25^{0}C (Mann-Whitney U- test, $p < 0.05$).

Table 3. The average (± s.e.) female longevity (days), fecundity (eggs/female), pre-oviposition, oviposition and post-oviposition period (days) of *C. americensis* and *C. menes* strains when given a surplus (n = 75) amount of *F. occidentalis* first stage larvae each day throughout their lives at 20 ^{0}C and 25 ^{0}C; pre-oviposition 1 = offspring on the first day; oviposition days = number of days with offspring, post-oviposition = days alive after last offspring occurred). Averages in longevity are significantly different (between strains, same temperature) when indicated by different letters (multiple comparison after Kruskall-Wallis, $p < 0.05$); averages indicated by an * are statistically significant (within colour-types, between temperatures) (Mann-Whitney U, $p < 0.05$)

Species	n	pre-ovip. (days+1)	oviposition (days)	post-ovip. (days)	longevity (days)	fecundity (eggs/female)
20 ^{0}C						
C. menes						
Brignoles-y	16	1.1 ± 0.1	10.8 ± 1.2 ^{a}	2.2 ± 0.4 ^{a}	14.0 ± 1.6 ^{a}	88.4 ± 5.9
Cabrils-b	15	1.1 ± 0.1	12.2 ± 1.0 ^{ab}	3.9 ± 0.6 ^{a}	20.8 ± 1.4 ^{b}	41.4 ± 2.6
Brasil-i	16	1.6 ± 0.1	12.8 ± 1.3 ^{ab}	7.8 ± 1.5 ^{b}	27.4 ± 2.3 ^{c}	40.5 ± 5.1
Japan-y	16	1.0 ± 0.0	16.5 ± 1.9 ^{b}	1.9 ± 0.4 ^{a}	19.9 ± 2.3 ^{b}	108.7 ± 8.7
C. americensis						
Willcox	16	1.0 ± 0.0	9.9 ± 0.6 ^{a}	7.7 ± 0.6 ^{b}	17.3 ± 1.3 ^{b}	168.2 ± 10.3
25 ^{0}C						
C. menes						
Brignoles-y	15	1.0 ± 0.0	11.1 ± 1.0 ^{b}	2.3 ± 0.3 ^{a}	13.8 ± 1.3 ^{a}	139.1 ± 12.0
Cabrils-b	15	1.3 ± 0.3	9.9 ± 1.2 ^{b}	2.3 ± 0.3 ^{a}	14.3 ± 1.3 ^{a}	48.5 ± 5.3
Brasil-i	15	1.0 ± 0.0	10.5 ± 1.5 ^{b}	1.5 ± 0.2 ^{a}	13.3 ± 1.8 ^{a}	59.3 ± 6.6
Japan-y	16	1.2 ± 0.1	8.0 ± 1.3 ^{ab}	2.3 ± 0.2 ^{a}	10.8 ± 1.6 ^{a}	74.2 ± 12.0
C. americensis						
Willcox	16	1.0 ± 0.0	6.9 ± 0.4 ^{a}	8.7 ± 0.7 ^{b}	15.1 ± 1.0 ^{a}	129.1 ± 12.2

Table 4. Calculated life-history parameters for different *C. menes* strains and *C. americensis* with first stage larvae of *F. occidentalis* as a host at different temperatures.

Temp	species strain	oviposition frequency total life	ovip. period	T_g	r_m	R_o
20 ^{o}C	*C. menes*					
	Brignoles-y	6.3	8.2	87.4	0.0487	69.0
	Cabrils-b	2.0	3.4	43.9	0.0848	37.9
	Brasil-i	1.5	3.2	49.2	0.0753	37.2 [1]
	Japan-y	5.5	6.6	68.2	0.0663	83.2 [1]
	C. americensis					
	Willcox	9.7	17.0	71.3	0.0719	168.2
25 ^{o}C	*C. menes*					
	Brignoles-y	10.1	12.5	36.7	0.1372	141.8
	Cabrils-b	3.4	4.9	32.2	0.1234	49.2
	Brasil-i	4.5	5.6	33.2	0.1276	60.4 [1]
	Japan-y	6.8	9.3	37.5	0.1175	74.2 [1]
	C. americensis					
	Arizona-Willcox	8.6	18.7	29.9	0.1650	129.1

[1] Data from Murai & Loomans (1995)

The maximum number of parasitised hosts was 57 for *C. americensis* and 31 for *C. menes* ('Brignoles'; 25 Brasil, 23 'Japan' and 21 'Cabrils', all at 25 ^{0}C). Because fecundity is estimated as the number of parasitoid pupae, possible egg-mortality and superparasitism may have underestimated its value in this set-up and therefore must be considered as minimum values. From behavioural experiments, we also know that, although *C .menes* can recognise and discriminate previously parasitised larvae from unparasitised ones (Banasik, 1994), at peak oviposition periods and a high encounter rate, 75 larvae might not always be a 'surplus'.

Population growth parameters, presented in table 4, show that calculated values varied largely with temperature. The intrinsic rate of population increase (r_m) of *C. americensis* was much higher at 25 ^{0}C than those for *C. menes*. Within species, the rate of increase for 'Brignoles' was larger than for 'Cabrils' at 25 ^{0}C, but much smaller at 20 ^{0}C. Values of the Japan (yellow) and the Brasil (buff) strain resemble much that of the 'Brignoles' and 'Cabrils' strain respectively. The values and differences at the lowest temperature are largely due to differences in developmental time. In general, both yellow strains had the highest net reproduction, but had the longest developmental time, thus levelling off the r_m value. The net reproduction (R_0) of *C. americensis* was not influenced by temperature, but of *C. menes* it clearly was (table 5). R_0 values of *C. menes* at 20 ^{0}C were much lower, except for the Japanese strain. Between *C. menes* colour-types, fecundity (R_0) varied largely, yellow strains ('Brignoles', 'Japan') giving higher values than the brown ('Cabrils') and intermediate ('Brasil') ones at both temperatures. Older females contributed very little to the intrinsic rate of increase as indicated by the low fecundity values. The outcome for *C. americensis* at 25 0C, however, are partly affected by experimental circumstances: at day 3-5 less host larvae were available and partly T. tabaci had to be used, from which we know (chapter 5) that they are less suitable as hosts than larvae of a similar age-group of *F. occidentalis*. This resulted in a clear decline in the fecundity curve (figure 3). At 20 ^{0}C the r_m value for both parasitoids were comparable and relatively low compared to the thrips host (table 5). Differences are largely due to the extreme long developmental period for both species at 20 ^{0}C.

Discussion

Developmental time

Life history parameters (development rate, immature mortality, sex-ratio, longevity, oviposition period, fecundity) vary largely with temperature, the host-parasitoid combination and geographical origin of the parasitoid. Intraspecific differences in qualitative and quantitative aspects of host physiology and nutrition clearly affect development in *C. menes*. In multivoltine hosts, developmental time varies with host age (Sakimura 1937a), sex of the larva on which the egg is laid (Murai, 1988), the host species attacked (Murai & Loomans, 1995) and even between geographical strains of the same host (Loomans, 1997). In general, males emerge shortly before females (*C. menes*: Sakimura, 1937a; Murai, 1990; Castineiras *et al.*, 1996). All strains we tested here, reproduced asexually: no males were produced, results of the females, however, were similar to ours.

Ceranisus menes populations varied significantly in developmental time according to colour-type (yellow versus brown) and geographical origin and latitude (north versus south), with a large variation occurring in yellow strains. Also other authors (Galazzi *et al.*, 1992; Murai & Loomans 1995) noticed a large variation in developmental time, which can even extend beyond 150 days (Murai & Loomans, 1995) in unisexual yellow strains. Murai (1990) also found this in a bisexual strain in Japan, whereas others did not (Sakimura, 1937a; Castineiras *et al.*, 1996). Daniel (1986) noted an extreme short life-cycle of 10.8 days parasitising *Zaniothrips ricini* Bhatti and 16.3 days on *Retithrips syriacus* Mayet, but these records need further confirmation of the parasitoid's identity. *C. menes* development is largely governed by host physiology, as shown when it is parasitising a univoltine host like *Kakothrips pisivorus*, producing only one generation a year (Bühl, 1937). Pupal duration of the parent had no relation to that of its offspring (Murai, 1988). With the advance of cold

temperatures Sakimura (1937a) noticed an increase of the number of specimens that did not emerge ("hibernated"). At low temperatures *C. menes* pupae probably are not in diapause, but in a quiescent state: pupae readily started hatching when transferred to higher temperatures (Murai, 1988).

Developmental time within a certain strain of *C. menes* is also affected by the thrips species which was used as a host (*Thrips tabaci, Frankliniella intonsa*, Murai 1990; *Kakothrips pisivorus* (univoltine), Bühl 1937) and even population differences within a species, can affect developmental time (Loomans, 1997). Developmental time of both parasitoid species is clearly longer than that of its major thrips hosts, *F. occidentalis* and *T. tabaci*: with about 2 and 3 weeks at 25 and 20 ^{0}C respectively (Robb 1989; Jarošík & Lapchin, 1998) developing times of the parasitoid are approximately 1.5-2 times that of the host, soon leading to asynchronous generations.

Temperature strongly mediates developmental time and seasonal synchronisation. Although able to survive cold and hot weather extremes, field temperature requirements for parasitoids are between 20-30^{0}C (Murai & Loomans, 1995; Castineiras *et al.*, 1996). In multivoltine host species, parasitoids can have more generations a year (4 in *C. menes:* Sakimura, 1937b). As we see for *C. menes*, this can vary with the geographical origin of the parasitoid and the colour-type and this has implications for which strain or species to select. Castineiras *et al.* (1996) noticed a clear difference in developmental threshold of 8^{0}C (egg-adult) for a northern (Japanese) and 13.7^{0}C for a southern (Thailand) population of *C. menes* and a thermal constant of 500 and 333 degree-days respectively. At 20^{0}C or lower, life-cycles of *C. menes* can be very long (Murai, 1990; Murai and Loomans, 1995) and be a serious limiting factor to seasonal inoculative releases in temperate greenhouses. For mass-rearing and for releasing parasitoids in a seasonal inoculative programme, a large variation in developmental time as shown by the yellow strain of *C. menes* and *C. americensis* at low temperatures has clear disadvantages. Results presented here indicate that *C. menes* (yellow strain France) and *C. americensis* (Arizona strain) showed promising potential as a biological control agent of *F. occidentalis*.

Reproductive capacity

Whereas *C. americensis* can start ovipositing from the day of emergence onwards, C. menes takes a bit more time depending on temperature. Also Sakimura (1937a) recorded a pre-oviposition period of 1 day in summer and 2 days in autumn, Daniel (1986) noted 2-3 days for *C. menes* and Rahman & Bhardway (1937) 3-5 days for *C. maculatus*. According to Sakimura (1937a) several oocytes mature within 24 hours after emergence and full grown oocytes vary from 29-48 per female with an average of 38.6 for *C. menes*. Our preliminary dissection results are in line with his findings. Maturation of eggs continues over life-time, but in all cases numbers decrease with age. At its peak, *C. menes c*an lay 20 to 30 (Murai & Loomans, 1995) eggs per day, but this varies with temperature, host species and age of the larva encountered. Parasitising *Z. ricini* and *R. syriacus*, Daniel (1986) recorded a maximum of 46±2.6 eggs per day. *C. americensis* lays 40-50 eggs/day at its peak, when supplied with a daily surplus of hosts. Its oviposition curve shows a peak after a few days, and sharply declines for *C. americensis*, whereas *C. menes* shows a gradual decline. Total fecundity (and net reproduction, R_0) is also significantly affected by temperature, and variable per host-parasitoid combination: 37-61 eggs per female at 20^{0}C and 60-170 at 25^{0}C (Murai & Loomans, 1995) for *C. menes - F. occidentalis* and *F. intonsa* respectively.

Adult longevity is relatively short and much shorter than that of most of its potential thrips hosts (Jarošík & Lapchin, 1997). Females (*C. menes, C. americensis*) live for 10-20 days days on average at 25^{0}C and one week more at 20^{0}C (Murai, 1990; Murai & Loomans, 1995), which is about half of most of its hosts. Longevity of females is positively

Table 5: Literature population growth rate parameters of *Frankliniella occidentalis* at different temperatures, using different susceptible host plants and additional food – sources.

temp.	foodsource	T_g	r_m	R_0	reference
20 ^{0}C	chrysanthemum	47.2	0.095	86.5	Robb, 1989
25 ^{0}C	cotton leaves+pollen	23.4	0.220	111.8	Trichilo & Leigh, 1988
	chrysanthemum	26.9	0.171	99.5	Robb, 1989
	cucumber	20.4	0.166	22.1	van Rijn *et al.*, 1995
	cotton leaves	21.6	0.157	30.1	Trichilo & Leigh, 1988
	bean leaves	17.9	0.139	12.2	Brødsgaard,1991
	bean leaves	25.3	0.140	34.7	Gerin *et al.*, 1994
	petunia	19.6	0.127	12.0	Wijkamp, 1995
27.2 ^{0}C	chrysanthemum	19.0	0.255	124.9	Robb, 1989

affected when fed with sugar or honey solution, but it is considerably reduced at high temperatures (figure 5; Sakimura, 1937a; Antsiferova & Timraleev, 1974).

Parasitoid species reproduce parthenogenetically, thelytokous (*C. americensis*), arrhenotokous or both (*C. menes*). *C. menes* collected and cultured in Europe, North and South America, the Near East (chapter 2; Loomans & Van Lenteren, 1994) only produce females. In several Asian countries (Ishii, 1933; Tachikawa, 1986; Saxena, 1971) and Australia (collection British Museum of Natural History) sexual populations predominate in field collected material, but non-sexual populations are present as well. In culture females mostly dominate (sex ratio 3:2, Japan: Sakimura, 1937a; India: Daniel, 1986; Indonesia: van Heurn, 1923), or ratios are equal (1:1, India: Carl, 1971; Thailand: Hirose *et al.*, 1993; Japan: Murai, 1990; Hirose *et al.*, 1992), but in occasional laboratory records males predominate (1:2, Thailand: Castineiras *et al.*, 1996). Murai & Loomans (1995) noticed a gradual change in sex ratio in the laboratory to thelytokous parthenogenesis. Temperature did not affect sex ratio (Castineiras *et al.*, 1996) in *C. menes.*

Calculations of population growth of *C. menes* for other thrips hosts are scarce and yet absent for *C. americensis*. Population growth parameters, the intrinsic rate of increase (r_m) and net reproduction rate (R_0), varied largely with temperature and host species for *C. menes* (Murai, 1990; Murai & Loomans, 1995), mainly due to differences in adult longevity and generation time. Form behavioural experiments (chapter 4 and 5), we also know that about 1 out of 10 hosts encountered and inserted, host-feeding occurs. As this extra host-kill rate is not included in our life-time fecundity, the overall effects will be larger. Murai & Loomans (1995) found a much higher R_0 (170.9) for the Japanese strain of *C. menes*, when parasitising *F. intonsa*, but the r_m values, 0.0642 and 0.1019 at 20^{0}C and 25^{0}C respectively, were not very different from the ones mentioned in table 4. Tagashira & Hirose (2001) studying another Japanese strain on *Thrips palmi* found much higher r_m values (0.169, 0.174 and 0.178) and net reproductive rate (118.6, 99.0 and 109.8) at 25 ^{0}C, which is largely due to a difference in maternal hosts, acceptance and suitability of the thrips host offered.

Population growth parameters usually are lower than or equal those of the thrips hosts (Murai, 1990; van Rijn *et al.*, 1995). *F. occidentalis* is a very polyphagous species and various authors determined demographic parameters of this species on a wide range of food sources (table 5). Their results (Jarošík & Lapchin, 1997) show that host plants largely influence the developmental rate of *F. occidentalis*. Especially when adult females have access to a pollen source, this greatly influences a female's fertility and thus her fecundity and significantly higher values of R_0 and r_m are found (Robb, 1989; Trichilo & Leigh, 1988; Katayama, 1997) (table 5). Comparison with of life-history parameters of the target pest, *F. occidentalis* shows that R_0's of yellow types ('Brignoles' and 'Shimane'-Japan) can come up to that of the host at 25^{0}C, depending on the food source. The net rates of increase of *C. americensis* and *C. menes* were at its best equal to ('Cabrils' at 20 ^{0}C, 'Brignoles' and 'Willcox' at 25 ^{0}C), but mostly they were smaller than those of the host, *F. occidentalis*. Based on its relative r_m value only, as a measure for parasite control potential, *C. menes* cannot be considered as a suitable candidate for seasonal inoculative biological control of *F. occidentalis*. Since both parasitoid species not only kill their host by oviposition and

developing in them but also by host-feeding, the overall death rate will likely be somewhat higher. If we take the reproductive capacity into account, predicting the effectiveness, *C. menes* is expected to be less effective than *C. americensis*. An investment in reproduction in the early phase of life, like *C. americensis* does, results in a larger r_m value. Both parasitoid species will perform best at relatively high temperature regimes, such as prevail in southern Europe. In Dutch glasshouse conditions, where temperature ranges between 18° and 22°C on average, temperature will be a limiting factor in seasonal inoculative releases. In a glasshouse situation, the female wasp has to search for hosts, hosts are concealed and present in low densities only, and parasitoids will not be egg-limited. Therefore, the reproductive potential realised under glasshouse conditions at low host densities, probably is only part (related to the quality of the host plant as a food source for *F. occidentalis*, see table 5) of that measured in laboratory experiments with a surplus of hosts in a confined situation.

General aspects

Life-history parameters are considered as a valuable tool for estimating the effectiveness of new biological control agents (van Lenteren, 1986; van Lenteren & Woets, 1988). As an integrated part of tritrophic systems, changes in the lower trophic levels likely affect the life-history results of hymenopteran parasitoids too. As shown by a large number of authors temperature is very important, but also agricultural practices like chemical applications (Borgemeister *et al*., 1993), host species (Brodeur *et al.*, 1998), host developmental stage and size (Sequeira & Mackauer, 1996), host plant cultivars (Stadler & Mackauer, 1996; Hare & Luck, 1991) and in particular resistant cultivars (de Kogel et al, 1997) interact and affect the performance of a parasitoid. In the case of thrips parasitoids this is not different and differences we find between strains of *C. menes* partly reflect their specific interaction and performance on western flower thrips, for our specific experimental conditions.

Life-history studies are almost all performed inside the laboratory, in small cages, using excised leaves, a continuous exposure to a surplus of host larvae and high moisture conditions. This can lead to inaccurate estimates of reproductive potential and population growth rates (Kopelman & Chabora, 1992). Very few studies take density effects into account (Kopelman & Chabora, 1992 for *Leptopilina boulardi*; Bouskila *et al.*, 1995 for *Anagrus delicatus*; Harvey *et al.*, 2001 for *Venturia canescens*; De Vis *et al.*, 2001 for *Amitus fuscipennis*). Beside these environmental factors, intrinsic effects largely affect the outcome, such as type of 'ovigeny' (Jervis *et al.*, 2001; Jervis & Kidd, 1986), life-expectancy, or maternal effects (Tagashira & Hirose, 2001) and as shown here by differences between colour types and strains of a particular parasitoid species.

Interpretation of population growth parameters is of crucial importance as well (de Kogel *et al.*, 1997; Drost *et al.*, 1998). Lewontin (1965) already showed that, when evaluating population growth models of colonising species (high r_m), difference in developmental period had the greatest impact on population growth. Caswell & Hastings (1980), on the other hand, argued that when r_m is low, changes in fecundity have a greater impact on r_m. Absolute values of population parameters, as presented in table 4, are therefore of certain, but limited value, because of two reasons. First, calculated parameters (r_m) can have similar values, but the reproductive strategy used by the parasitoid can be more relevant as shown here for *C. americensis* and *C. menes* on one hand, and for differences between strains on the other. For *Ceranisus* species, when parasitising *F .occidentalis* with a relatively low r_m, the reproductive curves - the age-specific survival rate, in combination with fecundity curves - can be very different, seem a better parameter for differentiating strains and species. Population growth parameters as calculated by Tagashira & Hirose (2001) for *C. menes* parasitising *T. palmi*, also show that, although almost similar in absolute value, survival and fecundity curves are very different: steep and short for specimens grown on *F. intonsa*, more levelled off for specimens grown on *T. palmi*. Their results are in concordance with those presented here, that the host – parasitoid combination used is of critical importance:

1) the thrips species on which the parasitoid has been cultured can have a great effect on the outcome on the level of reproduction. When bread on small hosts, adult size is

smaller and females have more difficulty to overcome host-defence behaviour than large ones (chapter 4 and 5; *T. palmi*, Tagashira & Hirose, 2001), and thus will have a lower oviposition rate (eggs / day), but live longer.

2) the influence of the thrips species to which females are exposed is also reflected in the outcome of the fecundity and survival curves, even more than in the calculated population growth parameters *sec*. As shown in chapter 5 differences exist in acceptance and suitability of a specific thrips host species for different strains of the parasitoids: 'Cabrils' and 'Brasil' performed worse than the yellow representatives 'Brignoles' and 'Japan' on *F. occidentalis*. Also in the results shown here their oviposition rate is smaller, but they live longer.

Second, differences in larval density and the presence of different combinations of age and size classes of the same and mixtures of 2 species or more, are common in the field and greenhouse: larvae occur in clusters (young buds and leaves, pollen producing flowers), but can move about freely. First stage and early second stage larvae, which are the most suitable stage for the parasitoids, usually are more concealed than less suitable second stage larvae, which are more exposed. The few studies that take density in account (Harvey *et al*., 2001) include host species that cannot move freely but either are patch-bound (yeast spots, egg-masses, oatmeal rests) or are sedentary and stuck to a particular leaf: once the parasitoid has found a patch, its density does not change as an interactive result of the searching parasitoid. Like for *Venturia canescens* (Harvey *et al*., 2001), fecundity curves will likely level off and survival is prolonged when densities of a suitable host are lower. Our results of continuous and transferred exposure experiments with *C. menes* and *C. americensis* indicate in that direction (chapter 4).

A high intrinsic rate of increase is considered as one of the attributes characteristic of effective biological control agents (van Lenteren, 1986). In conclusion, we argue that establishing life-history parameters is of a profound but also of limited value. It provides a vast amount of relevant information on the biology, development and life-history of the natural enemy, and therefore is a good starting point for any evaluation study, especially of those where little information of the natural enemy is known. But as argued above, care has to be taken, interpreting the outcome. For biological control purposes, especially in ornamental crops, a parasitoid has to be able to perform well at very low pest densities. At low host densities the full reproductive potential may not be realised and the parasitoid's searching efficiency becomes of great importance as well. In particular during the early season, when few hosts are available, searching ability and host acceptance capacity are important. If all available hosts are parasitised or killed the infection cycle may be interrupted. Therefore, it may be more effective then to select parasitoids that do not have a high reproductive potential, but do have a high host-finding capacity, in particular those that parasitise on hosts that move about freely. Release practices are, however, less sophisticated: seasonal inoculative control is less common a biocontrol application practice than a decade ago. More and more it is common practice that a greenhouse is swamped on a regular basis with large amounts of biological control agents, which do not have to reproduce and almost not to search, just to kill the pest fast. This will lead to selection of natural enemies with a high, immediate host-kill rate, and only limited by mass-production costs.

From a taxonomic point of view, this study can contribute to a proper identification and discrimination of various types within the *C. menes* species group. Walker (1839, as *Pteroptrix menes*) and Vuillet (1914, as *Thripoctenus brui*) originally described *C. menes* from a yellow holotype. Ishii (1931) described a yellow type from Japan (as *T. brui).* Later DeSantis (1961) also described a brown colour-type as *Ceranisus rosilloi* from Argentina, which recently is synonymised with *C. menes* (DeSantis, personal communication, 1991). Based on the existence of morphological colour-types (adults and pupae), behavioural differences in host acceptance, in host suitability, in developmental time and net reproduction, the present taxonomic status and species identification should be reconsidered.

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Chapter 7

Searching for hosts by *Ceranisus menes* (Walker) and *Ceranisus americensis* (Girault), parasitoids of thrips: short-range host location

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Abstract

Short-range host location by two thrips parasitoid species, *Ceranisus menes* (Walker) and *Ceranisus americensis* (Girault) (Hymenoptera: Eulophidae) is positively affected by visual and chemical stimuli. In a short-range flight test, yellow sticky traps trapped more females of *C. menes* than white, transparent or blue traps. Direct observations on the searching behaviour of both parasitoid species, showed that non-volatile larval products influenced wasps searching for hosts from a short range. Also, female parasitoids spent significantly more time in an area where thrips larvae had been allowed to feed for 24 hours, than in a clean area. Females changed their searching / walking pattern when coming into contact with larval excrements, slowing down and standing still more than on the clean part. *C. menes* remained longer on contaminated spots than *C. americensis*, but arrestment did not seem to be host specific: within a parasitoid species no difference was found between an area contaminated by either one of the thrips hosts, *Thrips tabaci* or *F. occidentalis*. Parasitoid females were not attracted to the synthetic compounds of the alarm pheromone (decylacetate plus dodecylacetate) of western flower thrips in short-range flight tests, indicating a non-volatile effect. Females of two colour-types of *C. menes* (yellow and brown) as well as *C. americensis* did not react to damage or excretion substances produced by larvae of a non-host thrips species (*Heliothrips haemorrhoidalis* Bouché), or to excretions and damage caused by the two-spotted spider mite, *Tetranichus urticae* (Koch).

Introduction

The ability to locate and reduce pest populations in a greenhouse largely influences the overall rate of parasitism of a parasitoid. A series of search characteristics have been used to predict the ability to locate loci of pest infestations in a largely empty space, like travel speed, ability to disperse, preference for certain hosts or developmental stages, handling time, interference and high intrinsic searching capacity. Recent studies, evaluating the characteristics of effective natural enemies for the control of greenhouse pests, show that foraging behaviour of insect parasitoids is of crucial importance to its success (van Roermund, 1995). The host finding and selection process has been divided in a sequential series of steps from location of the host habitat, the host community and the host itself o one side and host examination, host regulation on the other (Vinson, 1984; 1985). Volatiles produced by the host plant, produced or induced by their insect hosts are often used as long-range orientation cues or synomones (Vet & Dicke, 1992). Visual and chemical stimuli, volatiles or contact chemicals produced by the host or host plant, can play a role in short-range location of the host or host community.

Ceranisus menes (Walker) and *Ceranisus americensis* (Girault) are solitary endoparasitoids of larvae of thrips. Their host range is limited to species within the family of Thripidae. *C. menes* is known to parasitise over 20 species of thrips inhabiting a wide

range of host plants and occurring in a wide range of biotopes (Loomans & van Lenteren, 1995; Chapter 2). *C. americensis* seems to have a more narrow host range. Adults of both *Ceranisus* species have mostly been collected in association with various flowering host plants, but colour, host preferences and host-plant relationships are unclear. Whether semiochemicals are involved in host searching by thrips parasitoids, has gained little attention so far (Bazzocchi & Santi, 1994). Excretion droplets produced by larvae of *F. occidentalis,* contain two substances which act as an alarm pheromone for conspecifics (Teerling *et al.*, 1993a; Kirk *et al*., 1999). They can also act as a short-range kairomone for polyphagous predators (*Amblyseius cucumeris* (Oudemans) and *Orius tristicolor* (White)) (Teerling *et al.*, 1993b), by attracting and arresting these natural enemies to the place where these chemicals were emitted. Whether these substances are used by parasitoid species is yet unknown.

Here we report about the visual and chemical stimuli of the host and host plant that are involved in short-range location of the host habitat and of the host itself. We pay particular attention to the question whether parasitoids are attracted to certain colours or volatiles, and if chemicals produced by different thrips species (hosts as well as non-hosts) influence host location by *Ceranisus* species.

Material and Methods

We performed our experiments as flight tests (reaction to colour and volatiles prior to landing) or as tests on searching after landing (reaction to volatiles and contact chemicals).

Experiment 1

Cultures: Three strains of parasitoids were used, *C. menes* (yellow strain 'Brignoles', collected in France – Brignoles (Aire Barcelone, 1990), *C. menes* (brown strain 'Maximin', collected in France - St. Maximin, 1990) and *C. americensis* (strain 'Willcox', collected near Willcox, Arizona, 1993). *C. menes* was reared on *Thrips tabaci* Lind. using leek leaves and french beans (Chapter 2) and *C. americensis* on *F. occidentalis*, using the artificial method (Chapter 2) for about 10 and 20 generations respectively. All strains reproduce by thelytokous parthenogenesis. *F. occidentalis* and *T. tabaci* (Thripidae: Thripinae) originated from a stock colony kept on chrysanthemum and onion respectively. *Heliothrips haemorrhoidalis* (Bouché) (Thripidae: Panchaetothripinae) originated from Sintra (Portugal, collected in September 1994) and maintained on *Viburnum tinus* L. since then and *Tetranychus urticae* Koch (Prostigmata: Tetranychidae) was reared on lima bean (*Phaseolus lunatus* L.).

Set-up: Our tests on short-range volatile components and contact chemicals were carried out as choice tests for excretions of *F. occidentalis* larvae and by analysing the walking pattern to recognise attraction and arrestment behaviour as responses in searching behaviour to anal fluids and/or excretions. In a first series of experiments we verified if wasps are attracted and/or arrested to feeding sites of thrips hosts (*F. occidentalis* and *T. tabaci*). In a second series, we verified if this reaction was host-specific or could be a result of more general damage to the leaf: would damage or chemicals produced by a non-host thrips (*H. haemorrhoidalis*) or a non-host spider mite (*T. urticae*) also affect the searching behaviour by *Ceranisus* spp.?

A Tashiro cage (modified Munger-cell of 25 mm diameter, 11 mm high) was used as an experimental arena (figure 1) with a sweet pepper leaf (*Capsicum annum* cv. 'Mazurka') as a host-plant substrate. A small plastic ring was put in this Tashiro cage to conceal the larvae in the central part of the leaf (diameter 13 mm). Twenty-five first stage larvae were put in the small ring to feed for 20-22 hours on the underside of the leaf. After removing the ring and the larvae, the leaf surface could be divided into two parts: a damaged part contaminated with excrements and excretion droplets in the centre (133 mm^2 = 27% of the total surface) and the clean part on the outer side (358 mm^2 = 73% of the total surface). Webbing produced by the

spider mites was gently removed with a brush, before introduction of the parasitoid. A control treatment consisted of the same set-up without any larvae.

Test wasps of 2-3 days old were experienced with first stage larvae of *F. occidentalis* or *T. tabaci* during 1 hour, 1-4 hours prior to testing. A single wasp was put into a small cell in the glass cover (introduction cell, figure 2) for 30 minutes in a horizontal position to settle down. After the onset of observation, it was introduced into the test cell by moving the cover over the arena. During observation, the cell was put in a standard at an inclination of 135^{o} face down, above a stereomicroscope. A cold-light source was placed behind the arena, to direct the wasps towards the leaf. The behaviour of the wasp was observed from below, immediately after its introduction into the test cell for 30 minutes and the duration of different behaviourial components (walking, standing still and preening) and their location (contaminated, uncontaminated parts) was recorded using 'The Observer' vs. 2.0 (Noldus IT, Wageningen). Ten females were observed for each host-parasitoid combination. All observations were carried out in a climate cell, temperature 22 ± 1^{o}C, rh >80%.

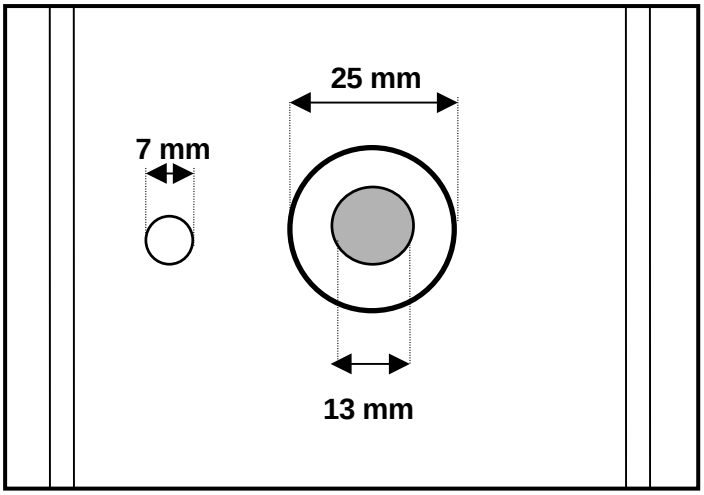

Figure 1. Tashiro test cage with a small introduction cell situated on top of it, seen from above. Left: introduction cell, right: test cell including 'contaminated' (grey) area and 'uncontaminated' (clear) area.

Experiment 2

To check whether adult wasps are attracted to the synthetic alarm pheromone of *F. occidentalis,* females of a certain parasitoid strain were released in the bottom part of a dark grey PVC cylinder, 20 cm high and 12 cm diameter (a set-up modified after the short-range flight test used for *Encarsia formosa* (Doodeman *et al.* 1994, Posthuma-Doodeman *et al.*, 1995)). In a first choice experiment, two transparent sticky (Soveurode®) plates, 3*3 cm each, were attached in the central upper part of the cylinder, 4 cm from the top (Figure 2). In the centre of one trap a paper wick (3*3 mm) impregnated with 100 μg of the synthetic alarm pheromone (decylacetate - Sigma Chemical Co., dodecylacetate - Aldrich Chemical Co., Milwaukee, USA at a molar ratio of 1.5:1, Teerling *et al.*, 1993b) solved in 2 μl pentane, was attached. In the other trap, pentane alone served as a control. 10 females each of 7 strains of *C. menes* and a single strain of *C. americensis* were released and this was repeated 6-7 times. The number of wasps caught by the trap was checked after 1, 2, 3 and 24 hours. In a second, no-choice experiment, a single trap was placed in the top centre of the cylinder and 30 females of *C. menes* (strains 'Brignoles' and 'Maximin') were released as described above.

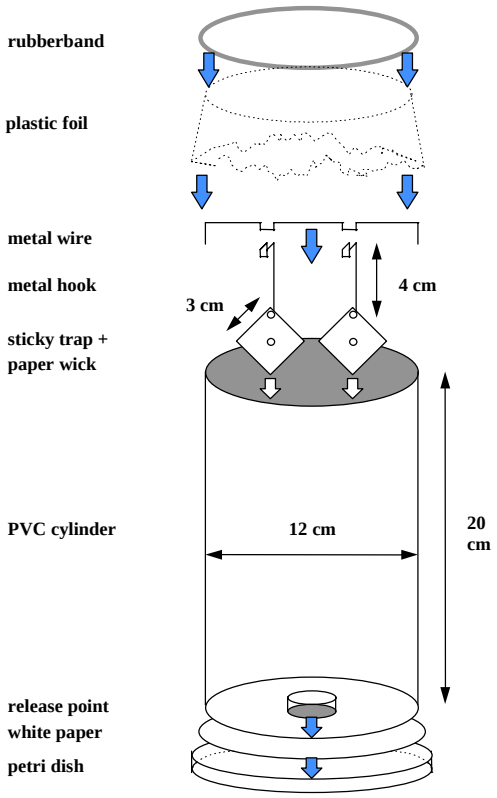

Figure 2. Experimental set-up used for a short-range flight test for testing the attractiveness of a synthetic alarm pheromone of *Frankliniella occidentalis* for the parasitoid *Ceranisus menes*.

Experiment 3

Colour-attractiveness was tested in a cage, 100 cm wide, 75 cm high and 70 cm deep. All glass walls of the cage were covered on the inside with white filter paper, except for the top glass (90 * 60 cm), to allow natural light. The cage was placed inside a greenhouse compartment at 25^0C and 60% rh. In the centre of the cage we placed a small rose plant 25 cm tall in a 15 cm tall pot. Four colour traps were tested in various combinations of yellow (Horiver®), blue (Horiver®), white and transparent. The last two types were transparent sheets, sprayed with glue (Soveurode®, Solivo-France) 24 hours before the release of the parasitoids. Every combination of traps was tried in two positions: the left and right side of the cage. Trap size was 10*20 cm and 2 plates were fixed to the top by transparent tape 40 cm apart and 25 cm from the margin. Fifty females of *C. menes*, 1-2 days old (origin Brasil, collected in Reeuwijk 1990) were released from a glass jar, placed at the bottom of the rose plant in a closed cage. After the wasps had settled for 15 minutes, 2 traps were fixed to the top, 2 colour combinations at one time. The number of specimens trapped during 24 hours was counted on the trap, as well as the number of individuals present in the cage. Sixteen combinations were tested and every combination was repeated 3 or 4 times.

Statistics: Data were analysed statistically by the Kruskall-Wallis (between and within strains) and Mann-Whitney U-test (between treatments), $p < 0.05$. Significant differences found by the Kruskall-Wallis test, were tested with a test for multiple comparison when significant. Relative time distributions of behaviour in different areas where analysed by a Willcoxon Matched Pairs Signed Ranks test ($p<0.05$).

Table 1. Latency time (± s.e.) of *Ceranisus menes* (strain 'Brignoles', strain 'Maximin') and *Ceranisus americensis* ('Willcox') upon arrival at larval feeding sites of *Frankliniella occidentalis* and at non-feeding sites (n=10 females per strain). Significant differences are indicated by different letters (multiple comparison after Kruskall-Wallis, p<0.05) (n =30 min.)

Parasitoid species strain	time to the leaf (s) control	test	time to the central site (s) control	test
Ceranisus menes				
yellow Brignoles	40.8 ^{a} ± 15.2	31.1 ^{a} ± 9.4	136.3 ^{a} ± 84.6	79.0 ^{a} ± 19.1
brown Maximin	43.9 ^{a} ± 10.6	16.7 ^{a} ± 6.1	184.0 ^{a} ± 72.4	41.6 ^{a} ± 11.0
Ceranisus americensis				
Willcox	12.9 ^{a} ± 2.7	25.0 ^{a} ± 4.7	107.8 ^{a} ± 21.8	224.0 ^{a} ± 157.1

Table 2. Residence time (seconds ± s.e.) and distribution of behaviourial components to larval feeding sites of *Frankliniella occidentalis* and *Thrips tabaci* of *Ceranisus menes* and *Ceranisus americensis* females. Differences in response time between treatments are indicated by different letters (horizontal), between parasitoids within host species (vertical) by an * (multiple comparison after Kruskall-Wallis, p<0.05) (n = 30 min. observation time / treatment)

Parasitoid strain behaviour	Control	*F. occidentalis*	*T. tabaci*
C.menes (yellow 'Brignoles')			
total time (s)	*89.1* ^{a} ± *30.4*	*837.2* ^{b**} ± 171.8	*1104.2* ^{b**} ± *156.7*
walking	82.9 ^{a} ± 28.2	357.0 ^{b**} ± 78.8	163.7 ^{b*} ± 40.7
standing still	5.5 ^{a} ± 4.9	386.4 ^{b} ± 124.1	862.0 ^{b***} ± 164.9
preening	0.7 ^{a} ± 0.7	93.8 ^{b} ± 42.5	78.5 ^{b} ± 37.1
C. menes (brown 'Maximin')			
total time (s)	*95.2* ^{a} ± *16.6*	*956.6* ^{b**} ± *137.4*	*862.1* ^{b**} ± 121.5
walking	92.2 ^{a} ± 17.1	557.6 ^{b***} ± 72.9	440.2 ^{b**} ± 88.0
standing still	1.2 ^{a} ± 1.1	371.1 ^{b} ± 127.4	370.9 ^{b**} ± 99.3
preening	1.8 ^{a} ± 1.1	27.9 ^{b} ± 12.9	51.0 ^{b} ± 20.5
C. americensis ('Willcox')			
total time (s)	*69.0* ^{a} ± *16.6*	*179.7* ^{b*} ± *26.2*	*221.9* ^{b*} ± 73.6
walking	63.6 ^{b} ± 15.0	102.0 ^{b*} ± 9.3	122.0 ^{b*} ± 37.6
standing still	1.7 ^{a} ± 1.6	56.5 ^{b} ± 19.6	58.7 ^{b*} ± 47.9
preening	3.2 ^{a} ± 3.1	21.3 ^{b} ± 7.2	41.2 ^{b} ± 17.2

Results

Host location/ Short-range orientation

1. Response to feeding sites of host species (Frankliniella occidentalis, Thrips tabaci)

Wasps were not attracted to a feeding site when within a distance of 1-2 cm: Latency time - the time between release and the time they arrived to the contaminated part of the leaf in the test and the clean centre in the control - was similar for all strains (table 1). The arena was very small, however, and the concentration of the chemicals or emitted substances could have saturated the cell content, thus not allowing us to examine attractant behaviour properly.

Table 3. Residence time and time spent per behaviourial component by *Ceranisus menes* (yellow - Brignoles), *C. menes* (brown - Maximin), *C. americensis* (Willcox) in response to feeding sites of *F. occidentalis* and *T. tabaci* and to non feeding sites. Significant differences in behaviour between treatments within an area are indicated by different letters (Kruskall-Wallis test), within a treatment between parasitoids by a * (vertical, Kruskall-Wallis test) and are underligned (only for the outer area) for the same treatment in 2 differrent areas of the arean (Willcoxon matched pairs signed ranks test) ($p<0.05$); 10 females / treatment, 30 min. observation each).

species (strain, nr.)	central area			outer area		
behaviour	control	*F. occ*	*T. tab*	control	*F. occ*	*T. tab*
C.menes (yellow)						
total time (s)	89.1 a	837.2 b	1104.2 b	804.4 a	480.1 b	315.7 b
walking	82.9 a	357.0 b	163.7 b	287.2	252.8	117.0 b*
standing still	5.5 a	386.4 b	862.0 c	474.1 a	168.3 b	179.4 b
preening	0.7 a	93.8 b	78.5 b	43.1 b	59.0 b	19.3 a*
C. menes (brown)						
total time (s)	95.2 a	956.6 b	862.1 b	631.3	531.6	553.1
walking	92.2 a	557.6 b	440.2 b	539.9	473.1	486.5 **
standing still	1.2 a	371.1 b	370.9 b	50.6	45.9	37.0
preening	1.8 a	27.9 b	51.0 b	40.8	12.6	29.6 *
C. americensis)						
total time (s)	69.0 a	179.8 b	221.9 b	603.5	538.3	671.0
walking	63.6 a	102.0 b	122.0 b	317.8	326.6	339.7 **
standing still	1.7 a	56.5 b	58.7 b	243.9	170.1	182.4
preening	3.2 a	21.3 b	41.2 b	41.8	41.6	148.9 **

Table 4. Relative time distribution of behaviourial components by *Ceranisus menes* (yellow strain - Brignoles), *C. menes* (brown strain - Maximin) and *C. americensis* (Willcox) and the percentage of total observation time (1800 sec.) spent on feeding sites and control sites. Significant differences as in table 3 (n=10 females per treatment, 30 min. observation each).

species (strain)	central area			outer area		
behaviour	control	*F.occ*	T.tab	control	*F.occ*	*T.tab*
C.menes (yellow)						
% of total time	5.0 a	46.5 b	61.3 b	44.7 a	26.7 b	17.6 b
walking	93.0 b	42.6 a	14.8 a*	35.7 *	52.7 *	37.1 *
standing still	6.2 a	46.2 b	78.1 c***	58.9 **	35.0 **	56.8 **
preening	0.8 a	11.2 b	7.1 b	5.4	12.3	6.1 *
C. menes (brown)						%
of total time	5.3 a	53.1 b	47.9 b	35.1	29.5	30.7
walking	96.8 b	58.3 a	51.1 a**	85.5 **	89.0 **	87.9 **
standing still	1.3 a	38.8 b	43.0 b**	8.0 *	8.6 *	6.7 *
preening	1.9 a	2.9 a	5.9 b	6.5	2.4	5.4 *
C. americensis						
% of total time	3.8 a	10.0 a	12.3 a	33.5	30.1	37.3
walking	93.0 b	56.8 a	55.0 a**	52.6 *	60.2 *	50.6 *
standing still	2.4 a	31.4 b	26.4 b *	40.4 **	31.9 **	27.2 **
preening	4.6 a	11.8 b	18.6 b	7.0	7.9	22.2*

Parasitoid strains or species (*C. menes* yellow, *C. menes* brown, *C. americensis*) showed a clear area restricted search after contacting contaminated sites: females of each species or strain spent significantly more time in the area were thrips larvae had been feeding compared to a clean leaf (table 2). Whereas on the clean central leaf area in the control arena, parasitoids mostly just walked across, significantly more time was spent standing still and preening in the leaf area contaminated by larvae of either one of the two host species, indicating an clear response. Females of the same species reacted in a similar way to feeding sites of *F. occidentalis* as to those of *T. tabaci,* but species differed from one another, in total time spent on the contaminated spot as well as in distribution of time amongst the 3 different components – walking, standing still and preening (table 2).

When we compare the time the individual wasps spent in different areas within the same arena (table 3), we see that *C. menes* and *C. americensis* reacted differently. When searching the clean outer circle (figure 1) of the arena, where no larvae had been feeding, all three parasitoid strains spent a similar absolute time walking, standing or preening in the control (table 3 right, down). *C. menes*, however, spent significantly more time in the part of the leaf contaminated by larvae of *F. occidentalis* and *T. tabaci* than *C. americensis* did. When we compare the time distribution in the much smaller centre (27%) to the time spent in the clean part (73% of the total surface), both *C. menes* strains spent about 70% of its searching time in the central 27% feeding site and only 30% in the much larger outer section that was not contaminated (table 3). When measured to relative surface area, *C. americensis* on the other hand, spent as much time in the centre as in the outer clean part.

When we look how parasitoids distributed their time (table 4) – walking, standing still and preening – we see that females mostly walk in the central area and rest and preen in the outer area in the control, when no hosts were present. When hosts had been feeding recently, the behaviour of each parasitoid strain was similar in the uncontaminated as in the control (table 4 right); once searching the centre, the yellow *C. menes* and *C. americensis* did not just cross, but walked less and stood still and preened more often (table 4) than in the control. Their time distribution was now similar all over the arena. The brown strain of *C. menes*, on the other hand, showed a clear change of its behaviour: where it walked most of its time when on uncontaminated leaf areas (in the control and in the test), its relative time distribution changed once in touch with larval feeding sites, regardless the host. This could indicate a different type of response of both species once being in contact with larval feeding sites and exudates: whereas *C. menes* showed a clear 'area restricted search', *C. americensis* seems aroused more than being arrested to the site itself. The difference in % of total time that parasitoids spend on feeding sites in the control and in the test (table 4 left) could also indicate that: *C. menes* spent 10 times more time in the central feeding site compared to the control (table 3), whereas *C. americensis* only doubled or tripled its time.

2. Response to feeding sites of non-host species.

The time distribution and absolute time spent by females of *C. menes* (yellow strain 'Brignoles') on larval feeding sites of non-host species like the greenhouse thrips, *Heliothrips haemorrhoidalis* or the greenhouse spider mite, *Tetranichus urticae,* did not differ from that spent on clean sites (table 5). Only in one case the time that parasitoids walked contaminated area is different between treatments. Excretion droplets produced by a non- related thrips species or by spider mites, or the damage caused to the leave tissue by the feeding larvae apparently did not cause an increase or change in behaviour of the parasitoids. The difference in time distribution shown by *C. menes* ('Brignoles') on the clean part and the part contaminated by feeding larvae of *F. occidentalis* and *T. tabaci* (table 2, table 3), did not occur when *H. haemorrhoidalis* and *T. urticae* had been present (table 5). Although more time was spent on feeding sites as well as on clean sites and less time was spent on walking ('across') in this series compared to those in the previous one (table 2), their relative time distribution did not differ.

Table 5. Residence time (in seconds) and relative distribution of behaviourial components of *Ceranisus menes* (yellow strain, 'Brignoles') to *Heliothrips haemorrhoidalis* and *Tetranichus urticae* feeding sites. Averages (± s.e.) indicated with different letters are significantly different between control and test treatments. Significant differences among treatments are indicated by different letters, (Mann - Whitney U test, $p < 0.05$).

Behaviour	*Heliothrips haemorrhoidalis*		*Tetranichus urticae*	
	test	control	test	control
total duration (s)	251.1 ± 105.4	135.2 ± 64.3	138.2 ± 60.3	287.0 ± 155.0
walking	78.8 [b] ± 16.1	18.6 [a] ± 10.2	80.1 ± 22.4	33.5 ± 12.0
standing still	143.1 ± 107.1	84.5 ± 54.7	39.8 ± 38.9	191.3 ± 128.5
preening	28.4 ± 12.3	32.0 ± 13.9	18.3 ± 9.1	62.2 ± 39.4
total duration (%)	13.9	7.5	7.7	16.0
walking	31.4	13.8	58.0	11.7
standing still	57.3	62.5	28.8	66.6
preening	11.3	23.7	13.2	21.6

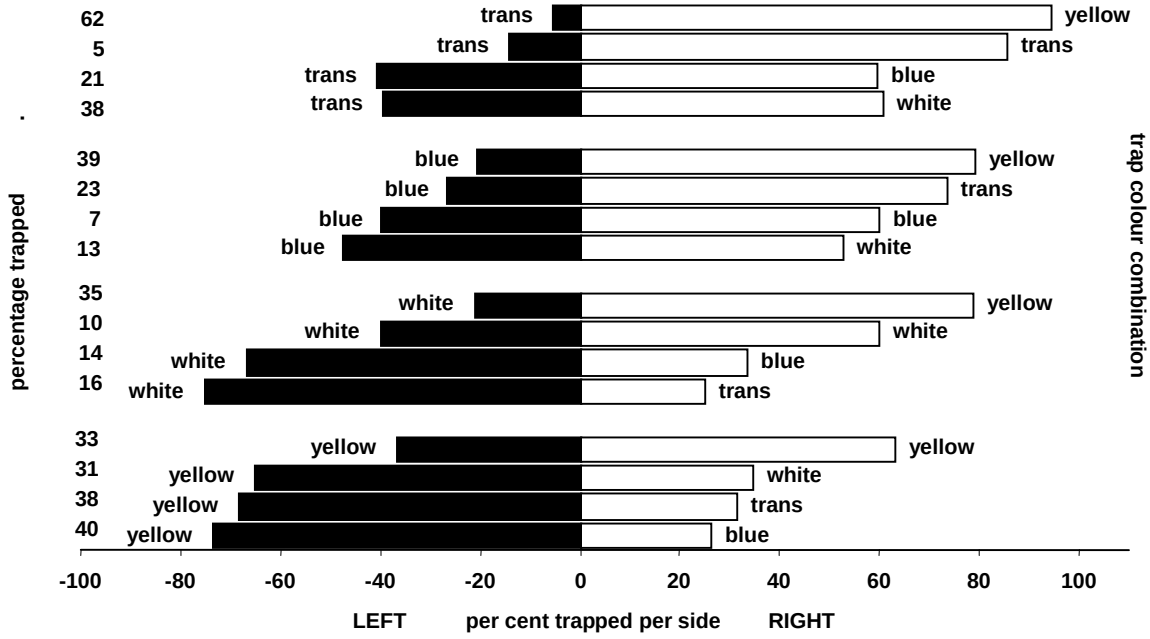

Figure 3. Percentage of *Ceranisus menes* females trapped on sticky colour traps, when offered in a combination of two trap types at a time. Vertical axis = percentage trapped on sticky plates, horizontal axis = percentage trapped on sticky plate at the left or right side of cage.

Long-range and short-range orientation

1. Colour-attractiveness.

Numbers trapped on the sticky plates, varied per combination and depended on trap colour and the place inside the cage. On the plates placed on the right side (the more bright side) of the cage, more individuals were trapped than those placed on the left (60% versus 40%). However, overall, yellow plates trapped 3 times more specimens of *C. menes* (54.5 %) than white (17.6 %), transparent (14.3%) and/or blue (13.6%) plates (figure 3).

2. Short-range chemical attraction.
The average number of trapped wasps per time interval is shown in table 1 and 2. In both the choice test (figure 4 left) and no-choice test (figure 4 right) no attraction of various strains of *C. menes* to traps holding the synthetic alarm pheromone of *F. occidentalis* was found over a distance of 3-4 cm. Although the total surface with glue was only half the size in the single trap cylinders, the average percentage of wasps trapped during the first 3 hours, was more than twice the percentage of those trapped in the double trap cylinders. One day after release this levelled of to about 60% of the wasps in both set-ups. Wasps reached the trap by flying, not by walking on the wire as they were distributed randomly over the surface of the trap.

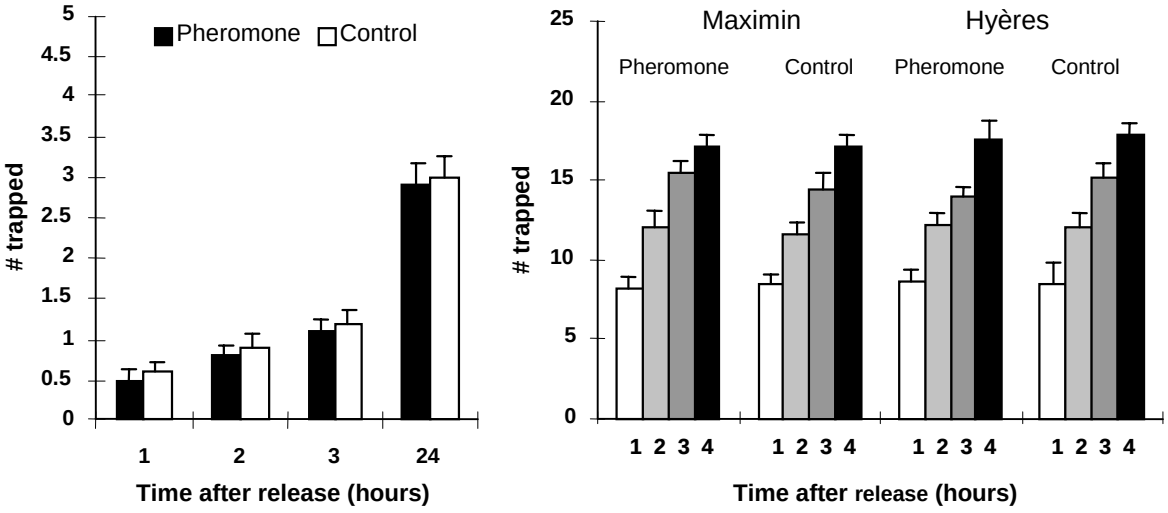

Figure 4. Average number *Ceranisus menes* females (± s.e.) trapped during short-range flight tests in a choice test using double trap cylinders (pheromone, control) (n=10 wasps / cylinder; 48 tests; left) and in a no-choice test, using single trap cylinders (n = 30 wasps/cylinder; 10 cylinders/strain; right). No significant differences found between traps per time period (t-test, p >0.05).

Discussion

In order to judge the potential usefulness of thrips parasitoids in the greenhouse or open field, it is important to know too how they search for hosts. The two thrips species we studied, show a preference for different plant parts: *F. occidentalis* usually can be found more in flowers and *T. tabaci* on the leaves (Tommasini & Maini, 1995). Many parasitoid species use visual cues in longe-range or short-range host-searching in addition to olfactory orientation (Vinson, 1985; Vet & Dicke, 1992), but which stimuli are involved in the host-searching process by thrips parasitoids is unknown. Stimuli derived from the hosts are generally the most reliable indicators of host presence, but are usually not abundantly available. Stimuli from plants are easier to detect because they are more general present, but are less reliable indicators of the actual host presence (Vet & Dicke, 1992). From a long-distance, floral scents and colour play an important role as attractants for flower-inhabiting thrips (e.g. Kirk, 1985; Teulon & Ramakers, 1990; Frey *et al.*, 1994; Imai *et al.*, 2001). Semiochemicals likely will play a major role in Thysanoptera as well as they do in other insect orders, but compared to other insect guilds, the understanding of the ecology of semiochemical use in thrips is still in its infancy (Blum, 1991; Lewis, 1997) but recently new developments have been made (Imai *et al*., 2001; MacDonald *et al*., 2002).

Pre-landing behaviour

Colours and scents are used by flower-dwelling thrips as cues for detection of and orientation to their hosts (Lewis, 1997). In Integrated Pest Management systems, sticky coloured traps are widely used as a tool for early detection and monitoring of pests. Trap efficiency is affected by various features of the insect species (age, sex) involved, climatic conditions and features of the trap itself, like colour, trap size, shape, adhesives, chemical attractants, orientation and location in the crop, spacing between traps and the background colour of the crop (e.g. Heinz *et al.*, 1992; Frey *et al.*, 1994). Colour preferences of *Ceranisus menes* reflect those of many other insects, both pests and beneficials. Many insect groups, for example aphids, whiteflies, thrips and parasitoids are attracted to yellow, although species may differ in their individual colour preference. Polyphagous thrips pests like *F. occidentalis* and *T. tabaci* that feed on a variety of host plant tissues, but with a preference for flowers and foliage respectively, have a general preference for white, yellow and blue colours (Brødsgaard, 1989; Teulon & Penman, 1992). Monopaghous species are often attracted to the colour of their host plants, whereas grass-inhabiting thrips show little preference for different colours (Kirk, 1984; Czenz, 1987).

In short-range flight tests for quality control (Doodeman *et al.*, 1994, Posthuma-Doodeman *et al.,* 1995) the percentage of *Encarsia formosa* females trapped, depend on temperature and trap size. In the slightly modified set-ups we used, the percentage of animals trapped was similar, about 60 % or more after one day. However, its usefulness as a set-up for testing short-range volatile effects might be doubtful. Problems associated with odour diffusion from a point source in a closed environment might result in an overall increase in activity, with no directed orientation, although this seems not to occur in our set-up: parasitoids were trapped in equal amounts both in the no-choice test as in the control during all intervals checked (table 7). Responses to the alarm pheromone, if any, might be weak and taking place during a short period of time: the response time to a volatile, which evaporates quickly, might be effective only within minutes after exposure and the short distance from which it might be effective could be below the minimum distance of 4 cm to be covered inside our test cylinder. Also responses (negative taxis, dropping from the host plant, reduced oviposition) of *F. occidentalis* larvae to their alarm pheromone were quite weak and the distance moved in response to it was only about 5 mm (Teerling *et al.*, 1993ab; MacDonald *et al*., 2002).

Whether semiochemicals are involved in long-range host-searching behaviour by thrips parasitoids, is not yet clear. Volatiles emitted from leaves damaged by *F. occidentalis,* attract predatory mites like *Amblyseius potentillae* (Garman) (Dicke & Groeneveld, 1986). The phytoseiid predator *Phytoseiulus persimilis* not only responds to herbivore induced synomones (HIS) emitted from leaves infested by its host *T. urticae,* but also to those infested by *F. occidentalis*, a non-host species (Lansink, 1992). Adults of *C. menes* and *C. americensis* have often been collected from flowers of a wide variety of host habitats and host-plant species (Chapter 2; Loomans & van Lenteren, 1995). *C. menes* accepts thrips larvae as a host in a wide range of host plant species, and could be considered a generalist at both the plant and the host level (Vet and Dicke, 1992). Thus we expect that this parasitoid would initially not react to specific infochemicals. This is in fact confirmed by recent work of Murai *et al*. (2000). Performing field tests in a wide range of agro-ecosystems they found that that methyl anthranilate is a potent attractant for *Ceranisus menes,* while other flower scents like p-anisaldehyde and geraniol had no effect. Methyl anthranilate is a common flower scent component in several plants (Knudsen *et al*., 1993) and attractant for a wide range of flower dwelling thrips (Imai *et al*., 2001) and other insect species (Imai *et al*, 1997). This can largely explain our findings of a close association of *Ceranisus* species with flowering plants during our field surveys and parasitoid collections (chapter2).

Post-landing behaviour

Thrips larvae of many species produce anal droplets which they deposit on the feeding sites, either actively when disturbed (by other larvae, natural enemies, etc.) or passively as frass as a result of feeding on the leaf. Larvae of a wide array of panchaetothripine species constantly keep their abdomen in an uplifted position bearing a droplet of intestinal liquid, enclosed by the anal bristles (e.g. *Retithrips*, *Caliothrips*, *Selenothrips*, *Heliothrips*, *Rhipiphorothrips*: Rivnay, 1935, 1939; Entwistle, 1972; Johansen, 1976; Chiu, 1984). Some species have a large part of their body covered with liquid excrements (*Hercinothrips:* Loomans, personal observation). Other species, belonging to Tubulifera as well as Terebrantia, excrete anal droplets at regular intervals as frass or when they are disturbed. By smearing and throwing them at the intruder upon contact, these droplets may protect larvae against predators (Lewis, 1973; McCaffrey & Horsburgh, 1982), parasitoids (Chapter 4) or conspecifics. Fungivorous phlaeothripids, inhabiting leaf-galls, produce anal exudates that can act as defensive allomones (Blum, 1989; Haga *et al.*, 1989, 1990; Howard *et al.*, 1983, 1987; Suzuki *et al.*, 1986, 1988ab, 1990, 1993, 1995). A diversity of aromatic compounds, monoterpenes, hydrocarbons, esters and acids (Blum, 1991), from either major or minor constituents of these anal discharges. Some of these secretions either work as an effective short-range repellent (Howard *et al.*, 1983; Suzuki *et al.*, 1988), a contact deterrent or as a distracting adhesive (Howard *et al.*, 1987; Blum, 1991) for ant workers (Howard *et al.*, 1983; 1987). But they can also function as an alarm pheromone (Suzuki *et al*., 1988; Teerling *et al*., 1993a; Kirk *et al*., 1999, MacDonald *et al*., 2002) or an aggregation pheromone (Haga *et al.*, 1989) for conspecifics and may also be involved in causing larvae to retreat to refuges (Venzon *et al*., 2000). Except as a defensive allomone to some predators, anal exudates can act as prey-finding kairomone to others. Semiochemicals are likely involved in short-range host-searching by the thrips egg parasitoid, *Megaphragma mymaripenne* Timberlake. Excrements (sealing fluid, faeces) of the host *(H. haemorrhoidalis)* are one of the main factors for the female to elicit probing and oviposition responses, although egg blisters without faecal material were sometimes stung too (Hessein & McMurtry, 1988).

The present study shows that the thrips parasitoids *Ceranisus menes* and *Ceranisus americensis* searching from a close distance were arrested on host larval feeding sites. More time was spent on these sites compared to clean leaf parts. This arrestment behaviour was the result of a change in overall behaviour: both *C. menes* (yellow strain as well as a brown one) and *C. americensis* were standing still more and walked less on contaminated sites. But parasitoids also walked more slowly and turned back when the edges of the feeding-area was reached and thus stayed inside the feeding site ('area restricted search'). Arrestment behaviour on the contaminated area was not thrips-host specific, we noticed a similar response to excretion products produced by larvae of *F. occidentalis* as well as of *T. tabaci*. Parasitoids did not show any reaction to patches with excretions and feeding-damage by larval *H. haemorrhoidalis*, which is not a host for both parasitoids, and of spider mite *(T. urticae*). This arrestment behaviour, therefore, seems to be the result of damage caused by, or of specific substances deposited by *F. occidentalis* and/or *T. tabaci*. Droplets of anal fluid produced by second larval stage of *F. occidentalis* physically deter predators and parasitoids but, act as a kairomone for two thrips predators (Teerling *et al.*, 1993b). Whether the alarm pheromone substances (decylacetate and dodecylacetate) are involved in the host-location process by *C. menes* remains an open question: in a study of the response of thrips larvae and the parasitoid to the synthetic alarm pheromone of *F. occidentalis*, *T. tabaci* showed a weak positive response to these substances, but arrestment behaviour could not be detected for *C. menes* (van Leeuwen, 1995).

The actual host range and reproductive success of a parasitoid depends on the probability of a host being found ('ecological host range'), host defense reactions ('behavioural host range') and host suitability ('physiological host range'). Larvae of the same thrips host species are attacked on one host plant, but not on another. Taking the hypothesis into consideration (Vet & Dicke, 1992) that the degree of specialisation

determines the relative importance of infochemical use from the first and second trophic level, one would expect that *C. menes*, a generalist species, and *C. americensis,* a specialist species, would rely more on the use of plant-derived and host-derived stimuli respectively. So the specialist species would benefit more from a reduction in search time through an effective use of infochemicals than the generalist. Parasitoid colour-types, although occurring occasionally on the same host plant, differ however in their host preference (Chapter 5): *C. menes* (brown type) prefers *T. tabaci* over *F. occidentalis,* whereas the yellow colour-type shows no difference. *C. americensis* is even more specialised and prefers *F. occidentalis* over *T. tabaci* (see Chapter 5) and spends less time searching for hosts in an empty patch than *C. menes*, but the time allocation is equal both species. Thrips larvae that move to another feeding site after an attack of a conspecific wasp, may fool larval parasitoids into searching in an empty place as they are attracted/arrested to the feeding damage of their host for a long time. Intraspecific variation in foraging behavioural response to the most suitable host, in *C. menes* colour-types and *C. americensis*, however, is not supported by our data: both colour-types react in a similar manner to feeding sites of both *F. occidentalis* and *T. tabaci*. However, rather than an attribute of the species throughout its geographical range, specialization in *C. menes* might vary not only intraspecifically (according to colour-types), but even within and among populations (Chapter 5; Vet & Dicke, 1992).

From our study, we can conclude that colour plays a role in the long-range host-searching process before landing, and host-derived odours play a role on a short-range after landing on the damaged plant, resulting in arrestment in the host patch. Parasitoids did not show attraction to volatiles emitting from larval feeding sites. Ecologically, it is curious however that polyphagous predators like *Amblyseius cucumeris* and *Orius tristicolor* are attracted to a substance, such as an alarm pheromone, which is likely to be highly specific for its emitter, whereas our specialised parasitoids are not.

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Chapter 8

Releases of parasitoids (*Ceranisus* spp.) as biological control agents of western flower thrips (*Frankliniella occidentalis*) in experimental greenhouses[1]

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Abstract

Experimental releases were performed to investigate the potential of thrips parasitoids as biological control agents of western flower thrips, *Frankliniella occidentalis* (Pergande). Strains of two larval parasitoid species (Hymenoptera: Eulophidae), *Ceranisus menes* (Walker) (a strain from France and from Brasil) and *Ceranisus americensis* (Girault) (Arizona strain), were released in different commercial greenhouse crops. In all crops only traces of parasitism were recorded. In an experimental rose crop(cv 'Frisco'), releases were made of two parasitoid species, *C. menes* (a French strain) and *C. americensis* (Girault) (Arizona strain) in two separate greenhouse compartments. An account is given on the release, dispersal, establishment, population dynamics and control capacity of both parasitoid species. Parasitoids spread readily and established themselves throughout the crops, but releases did not result in reduction of thrips during a five month period. Rates of parasitism stayed lower than 10% throughout the season, resulting in severe damage of the rose crop. The potentail of parasitoids as biological control agents of thrips pests in ornamental crops is discussed.

Introduction

Western flower thrips, *Frankliniella occidentalis* (Pergande), is an extremely polyphagous invading pest species. Two hundred and forty-four species of plants belonging to 62 different plant families, have been found to host *F. occidentalis* (Tommasini & Maini, 1995), and its number is increasing with time and its expansion to new areas. These plant species include many important crops, open-field as well as protected crops, such as ornamental, fruit, garden and agricultural crops (Yudin *et al.*, 1986; Mantel & Van de Vrie, 1988; Tommasini & Maini, 1995). In Europe, most commonly infested vegetable crops include cucumber, sweet pepper, lettuce and tomato, whereas a large range of ornamental crops are hosting *F. occidentalis* as well, the most important being Saintpaulia, chrysantehmum, gerbera and rose (Tommasini & Maini, 1995). Except vectoring a number of plant viruses (Wijkamp *et al.*, 1995), the predominant way of damage being inflicted to plants is direct and largely mechanical. Depending on the organ and growth stage attacked this can vary from discolouration and silvering to necrosis and growth damage (Brødsgaard, 1989; Kirk & Lewis, 1997).

Since *F. occidentalis* has established in Dutch greenhouses, biological control of has been most successful in vegetable crops, in particular those where pollen is available as a secondary food source (van de Meiracker & Ramakers, 1991; van Rijn *et al.*, 1995). In ornamental crops, on the other hand, biological has been mainly chemical, because the damage is inflicted largely to the end product, the flowers itself. The level of damage

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1 This article is based on Loomans, A.J.M., Tolsma, J., Van Heest, J.P.N.F. and Fransen, J.J., 1995. Releases of parasitoids (*Ceransisus* spp.) as biological control agents of western flower thrips (*Frankliniella occidentalis*) in experimentla greenhouses. Mededelingen van de Faculteit voor Landbowwetenschappen van de Rijksuniversiteit Gent, 60/3a: 869-877, with amendments.

tolerance is much lower than in vegetables, and in most crops even a zero-tolerance is the standard.

Rose is one of the most important ornamental crops in The Netherlands (898 ha, Ekkes *et al.*, 1994). Except for *Thrips tabaci* Lind., *F. occidentalis* can cause severe damage at low density levels, visible as discolouration of the flower and necrosis of the petals. Natural enemies currently used to control western flower thrips, *F. occidentalis*, belong to two predator groups, predatory mites (Phytoseiidae) like *Amblyseius cucumeris* (Oudemans) and more recently *Amblyseius degenerans* Berlese or pirate bugs (Anthocoridae) like *Orius* spp.. In vegetables, sweet pepper (van den Meiracker & Ramakers, 1991) and cucumber (Riudavets, 1995) in particular, commercial releases of either one of these groups is able to keep thrips pests outbreaks in check. In greenhouse ornamentals, experimental releases of pirate bugs (*Orius* spp.) resulted in reduction of thrips numbers in chrysanthemum and Saintpaulia (Fransen & Tolsma, 1992; Sörensson & Nedstam, 1993), but not in roses (Fransen *et al.*, 1993ab; Bertaux, 1993). *Orius insidiosus* (Say) showed a lower level of searching time (Beekman *et al.*, 1991) and reproduction (Fransen *et al.*, 1993a) on rose, compared to other ornamental crops. *Orius laevigatus* (Fieber) reproduced in rose (cv 'Sonia'), but was not able to keep *F. occidentalis* populations in check (Bertaux, 1993). Occasionally *A. cucumeris* is released in roses, but control of thrips pests is incomplete and chemical corrections are necessary (Fransen, pers. comm.). The cultivation of propagation material and container plants in particular, represents a small but significant section in the ornamental industry (Ekkes *et al.*, 1994). In these nurseries, plants are kept in the greenhouse over a relatively long period of time, and are not a finished product. Therefore, the damage threshold is relatively high compared to that used in cut-flowers, which gives more opportunity for biological measures to control thrips pests.

A group of the natural enemies currently studied for its prospects to control thrips pests are thrips parasitoids, and *Ceranisus menes* (Walker) and *Ceranisus americensis* (Girault) (Hymenoptera: Eulophidae) in particular. Both species have been found in association with *F. occidentalis* on roses and flowering plants before, in the open as well as in the greenhouse at various locations (Greene & Parella, 1993; Loomans, 1991). Based on evaluation trials in the laboratory (Loomans & Van Lenteren, 1994) strains of each parasitoid species have been selected for experimental releases in greenhouse tests. The present study reflects the results of pilot releases in commercial greenhouses, vegetable crops as well as ornamental container plants. In two experimental greenhouse compartments, we investigated the release, dispersal, establishment, population dynamics and control capacity of thrips parasitoids in a rose crop.

Material and Methods

1. Commercial greenhouses

Preceding the principal experiment, parasitoids were released in different crops and systems. During spring 1992, pilot releases were made in two commercial greenhouse crops of 1 ha each (table 1). Adult parasitoids (strain Brasil, grown on *Frankliniella schultzei,* reared on bean pods (see Chapter 3)), were released during noon in small cohorts of 25 specimens each 40-50 cm below the top of the plants, in a *Frankliniella occidentalis* infested hotspot. Both crops were 5-6 months old and were 150-200 cm high. In both greenhouses until one week before our parasitoid releases started, regular biological control measures were taken, i.c. releases of *Orius insidiosus* and *Amblyseius cucumeris* had been made. Because in sweet pepper the thrips infestation was not yet under control, additional releases were made during our program (table 1). In cucumber thrips densities were relatively low (adults/leaf = 0,18 ± 0,06, larvae / leaf = 0,61 ± 0,20). In total 500 (cucumber) and 3165 (sweet pepper) adult parasitoids were released once or at regular intervals. Samples of leaves (cucumber) and flowers and leaves (sweet pepper) were taken on a weekly basis, taken to the laboratory and larvae checked for parasitism.

Table 1. Overview of experimental releases of *Ceranisus menes* (strain Brasil) in vegetable crops in two commercial greenhouses (1 ha each) during spring 1992, under regular biological control; temperature minimum 21^{0}C during the day, 18^{0}C at night.

Location	crop	date	release parasitoids number	age	# sites	# rows
Bleiswijk 1	cucumber	27.03	500	1-4d	20	4
Pijnacker 2	sw.pepper	23.03	875	1-4d	35	5
		31.03	300	4-7d	16	3
		14.04	600	1-4d	24	4
		23.04	450	4-8d	18	6
		20.05	825	2-8d	33	7

[1,2] Two releases of pirate bugs (*Orius insidiosus,* Anthocoridae) and predatory mites (*Amblyseius cucumeris,* Phytoseiidae*)* until March 18.

During 1993, releases were made in a 0.25 ha nursery of Mediterranean and subtropical plants in Malden (Gelderland), The Netherlands. In this nursery a large variety of plants (~120 species) were grown in containers in three different compartments: a 'warm' section (minimum 18^{0}C in winter), a 'cold' section (minimum 8^{0}C in winter) and an 'open' section (minimum 0^{0}C) (Klerx, 1993). Pesticides were used only once a year, just after pruning in October and pests were controlled biologically, wherever necessary and whenever possible, but not during our release period. Small cohorts of parasitoids were released at intervals of 2 or 4 weeks and regularly distributed in space, i.c. in those tablets covering plant species that were infested with *F. occidentalis* (table 3). Release were made form May till October 1993, in the 'cold' section only. Main purpose of this experiment was to verify if *C. menes* would be able to establish, to build up a population and overwinter. Samples of different plant species were taken of flowers (table 3) by picking or by shaking the head, just prior to a new parasitoid release. Samples were taken to the laboratory and larvae were reared to maturity on pollen and checked for parasitism.

2. Experimental greenhouses

Experimental design:
Experiments were carried out in two greenhouse compartments of 100 m^2 each (G1 and G2) at the Research Station for Floriculture in Aalsmeer, The Netherlands from March until August 1994. Both compartments had an open ventilation system. 672 and 700 rose plants of a yellow variety (cv 'Frisco') were planted October 1993 in the respective greenhouse compartments G1 and G2 (see figure 1). Rose plants were cultivated on rockwool at an average constant temperature of 20 ^{o}C and 16 h. light, including assimilation light in spring. Crop maintenance and harvest of the rose crops was carried out conform common practice. Pests and diseases were controlled biologically or by use of selective chemicals with minimum side effects for the thrips parasitoids (see table 2).

Hosts and parasitoids
C. menes, originating from France (yellow strain 'Brignoles'; Loomans, 1991) was reared on *Frankliniella schultzei* (Trybom) in the laboratory since 1990 and *C. americensis* ('Willcox'-Arizona) on *F. occidentalis* since 1993 (Loomans & van Lenteren, 1994). Thrips and parasitoids were reared on bean pods and additional bee pollen at 25^{0}C and 16L:8D. Freshly emerged adult wasps were stored at 15^{0}C until the time of release (Loomans *et al.*, 1995). The age of the wasps at the moment of release varied from 1 to 6 days.

Dispersal capacity

Dispersal experiments started in March 1994, when no thrips was present in the crop. For studies on dispersal capacity, trap plants were placed at five sites in both crops (see figure 1). Each trap site consisted of 3 jars with 2 rose flowers on water, each about 1 m apart. Each flower was infested with 10 freshly emerged *F. occidentalis* larvae in the first experiment and 20 in the second experiment. Five cm below the flower bud, a square piece of transparent sticky plate of 150 cm² was placed horizontally circumventing the stem and attached to the stem with 'Tanglefoot' (figure 2d). In that way we hoped to prevent thrips larvae and parasitoids to walk up or down and to estimate parasitisation by parasitoids which had landed on the flower. A number of 300 adult female parasitoids of *C. menes* and *C. americensis* were released in compartment G1 and G2 respectively. In the first experiment they were released in the centre, (see figure 1, left) and in the second experiment on five sites: one in the centre and one close to each corner (figure 1, right). All trap flowers and host larvae were replaced by new ones and checked 1, 4 and 7 days after release in experiment 1 and after 7 days in experiment 2. Thrips larvae present in the flowers were checked for parasitism by dissecting the larvae under a stereo microscope, looking for parasitoid eggs and or larvae. Other flowering roses were present during the experiment. They were harvested at regular intervals and checked for the presence of adult parasitoids as well. In each compartment 8 yellow sticky plates were placed, about 4 m (right side) and 6 m (left side) from the centre and 2 m from the walls, and checked for parasitoids following the same schedule.

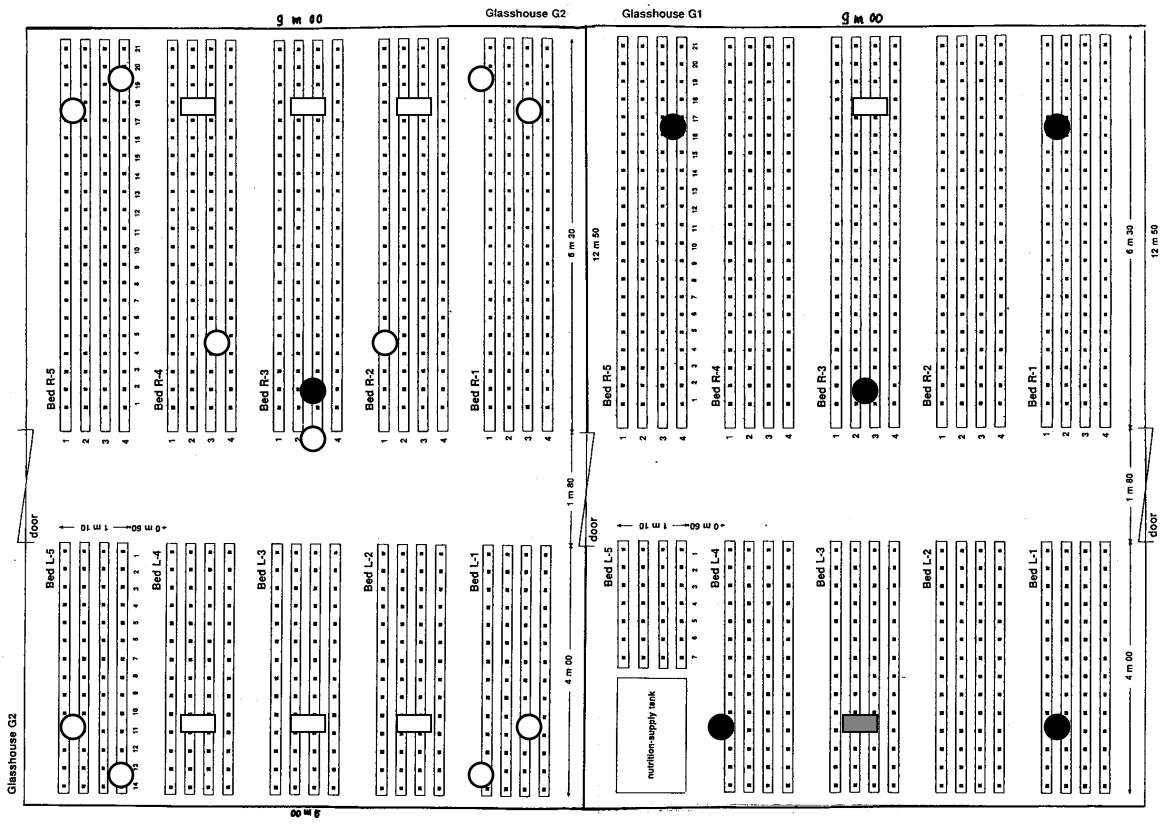

Figure 1. The experimental design of test plots G1 and G2, planted with roses on rock-wool; the thrips parasitoid release sites are indicated by solid circles (●), the trap flowers by open circles (◯) and sticky traps by squares (▪); the situation for the dispersal experiment is indicated for compartment G2 (left), that for the control experiment is indicated for G1 (right).

Figure 2. Different growing stages of rose flowers (cv ' Frisco'): a) 'bud', b) 'harvest' and c) 'ripe'; d) rose flower used as a trap plant in the dispersal experiment showing a transparent sticky plate (150 cm^2) to isolate the flower from the stem. Different parts of the flower – sepals and petals - are indicated; thrips damage on petals in (a).

Table 2. Application of control measures in experimental greenhouses G1 and G2, planted with roses on rockwool; a: release rates and timing of thrips parasitoids (*C. menes* in G1, *C. americensis* in G2), b: release rates and timing for both biological agents and chemicals for pest control; * *T. tabaci* also present.

Week #	Pest species	Control measure G1/G2	# *Ceranisus*	Other
a) thrips parasitoids				
16	*F. occidentalis*	*C.menes / C. americensis*	300 / 300	-
17	*F. occidentalis*	*C.menes / C. americensis*	150 / 150	-
18	*F. occidentalis*	*C.menes / C. americensis*	165 / 300	-
19	*F. occidentalis*	*C.menes / C. americensis*	150 / 165	-
20	*F. occidentalis*	*C.menes / C. americensis*	280 / 300	-
28	*F. occidentalis**	*C.menes / C. americensis*	635 / 150	-
29	*F. occidentalis**	*C.menes / C. americensis*	310 / 180	-
33	*F. occidentalis**	*C.menes / C. americensis*	- / 260	-
b) biological / chemical				
5, 19	whitefly	*Encarsia formosa*		Enstrip®
24	whitefly	Savona 1%		80 liter
6,7, 23,27	aphids	*Aphidius colemani*		Aphipar®
7, 23	aphids	*Aphidoletes aphidimyza*		Aphidend®
12,13,14	aphids	Savona 1%		80 liter
13, 23	*M. euphorbiae*	*Aphilinus abdominalis*		
10,11,19	powdery mildew	Baycor 0.1-0.15 %		40-60 liter
35	powdery mildew	Fungaflor 0.15 %		60 liter
29	spider mite	Torque 0.05 %		100 liter

Control capacity
Population development experiments of both thrips and parasitoids were started from half of April onwards. For population studies, rose plants in each greenhouse compartment were infested with 600 (5 females :1 male) *F. occidentalis* adults once, on April 13th. In compartment G2 a natural infestation of *Thrips tabaci* occurred from April onwards. Parasitoids were released on a weekly bases in two periods (April-May and August) from glass jars placed on the rock-wool at the base of the plants, numbers equally divided over space (table 2, figure 1).

Immediately before their harvest, all rose flowers (200-450 per week) were checked twice (March, April and May 1994) or three (June, July and August 1994) times a week for thrips damage. Damage was scored for 'raw' (closed bud, first petal colour visible), 'harvest' (sepals still vertical, yellow petals : green sepals as 1 : 1) and 'ripe' (sepals and flower leaves open) flowers, and checked if either the sepals or petal were damaged or both (figure 2). Damage symptoms mainly concern necrotic spots on the sepals, and fainting colours and necrotic spots on the flower leaves. To follow population developments, insect numbers were monitored indirectly by blue and yellow sticky trap (Horiver®) counts and directly by sampling flowers. In each compartment two sticky traps (one blue, one yellow) were placed about 10 cm above the top level of the crop (figure 1). From each compartment a sample of 50 flowers was taken once a week and after a short period of cold storage at 2-3 ^{o}C, each single rose flower was immersed in 50% alcohol. Flower parts were removed and insects washed and collected in a 80 mesh sieve. Numbers of parasitoids, thrips adults and larvae were counted and the latter were checked for parasitism by dissection under a stereo microscope. Identification of thrips adults on the sticky plates was done by a stereo microscope, verifying characteristics of antennae and pronotum of the thrips specimens.

Results

1. Commercial greenhouse releases

Vegetable crops
In the first pilot releases in commercial greenhouse crops, parasitisation levels by *C. menes* were very low. In cucumber 250 larvae were collected from leaves 4, 8 and 40 days after the single release. After dissection in the laboratory no parasitism was found. In sweet pepper only 10 and 2 parasitised larvae were found 4 and 8 days respectively after the first release, representing levels of less than 2 % parasitism (figure 3). Since that moment, no parasitoid adults or parasitised larvae were found. Within 2 months after the commercial release of *Orius indidiosus* this predator kept *F. occidentalis* populations under control, From April onwards, very low levels of thrips larvae were found (figure 3). This experiment shows that *C. menes* either lacks the capacity to control thrips in vegetable crops or that it's releases are incompatible with other biocontrol measures. I also shows that pirate bugs controlled thrips populations within two months after release and establishment in the crop.

Container nursery
In 1993, during a second release experiment, we saw a similar picture develop in the nursery of container plants. In spite of the release of 3230 adult wasps at regular intervals during the summer and fall of 1993, hardly any parasitism was found. Of the more than 2800 larvae that reached maturity (67 % of those collected) only 3 larvae were found parasitised in total (table 3): 2 from the Brasilian strain and 1 from the French (P-yellow) strain, both in flowers of *Anisodonthea capensis*. In spite of the numbers released and a moderate thrips infestation, *C. menes* did not spread and establish in this nursery. Also an additional sample of 500 larvae taken in March 1994 and at inspections of sticky traps, no parasitised larvae or adult parasitoids were found, thus confirming the inabilty to establish and overwinter under semi-natural conditions.

Table 3. Release and sampling program of *Ceranisus menes* (strains France-Perpignan and Brasil released in mixed batches; numbers in ***italics-bold***) and *Frankliniella occidentalis* larvae (standard font) in a nursery of Mediterranean plants (Malden-Netherlands) during summer and fall of 1993; temperature minimum 8^0C, maximum 43^0C.

Plant species	Tablet	Action	Date (day.month) 30.05	11.06	17.06	30.06	23.07	29.07	03.08	07.08	11.08	01.10	07.10		# wasps # larvae	Sample #flowers
Alyogyne huegueli	k2-T1	**release**	**50**	**50**						1				**100**		
		collect		56	65	112	2								236	30
Anisodontea capensis	k2-T1	**release**	**50**			**125**	**225**							**400**		pick
		collect		56	20	75	275	41	8						475	100
Anisodontea capensis	k2-T2	**release**							**165**	**200**				**365**		pick
		collect								31	48	17	11		107	290
Anisodontea capensis	k2-T7	**release**					**140**	**95**	**100**	**200**				**535**		pick
		collect					800	230	91	60	235	60	23		1499	380
Mimulus puniceus	k2-T7	**release**												**0**		pick
		collect			130	85	80	83	38	33		68	54		571	285
Fuchsia	k2-T4	**release**										**100**		**100**		pick
		collect											19		19	50
Solanum nierembergia	k2-G8	**release**	**100**											**100**		pick
		collect		47											47	25
Oxypetalum ceruleus	k2-T11	**release**	**100**											**100**		shake
		collect		43											43	25
Cassia australis	k2-T10	**release**		**75**										**75**		shake
		collect			29										29	25
Lotus berteloti	k2-G9	**release**	**100**	**50**			**100**			**100**				**350**		shake
		collect		235	300	65	70								670	100
Solanum bonariense	k2-T8	**release**	**225**	**150**		**200**	**100**			0				**675**		shake
		collect		55	80	130	40	8							313	150
Solanum rantoneti	k2-T9	**release**						**55**		**75**		**100**		**230**		shake
		collect							0		0		14		14	75
Lantana sp.	k2-T5	**release**										**100**		**100**		shake
		collect											77		77	25
Lantana sp.	k2-T8	**release**										**100**		**100**		shake
		collect											68		68	25
																shake
Wasps released		**release**	**625**	**325**		**325**	**565**	**150**	**265**	**575**		**400**		**3230**		
Strain France (Pb)			175				140	55	80	175				625		
Strain France (Py)			450	75			150		125					800		
Strain Brasil				250		325	275	95	60	400		400		1805		
Total number of larvae		collect		492	624	467	1267	362	137	125	283	145	266		4168	
		matured		358	386	304	775	230	92	109	240	114	203		2811	
		parasitised		0	0	0	2	0	0	0	1	0	0		3	

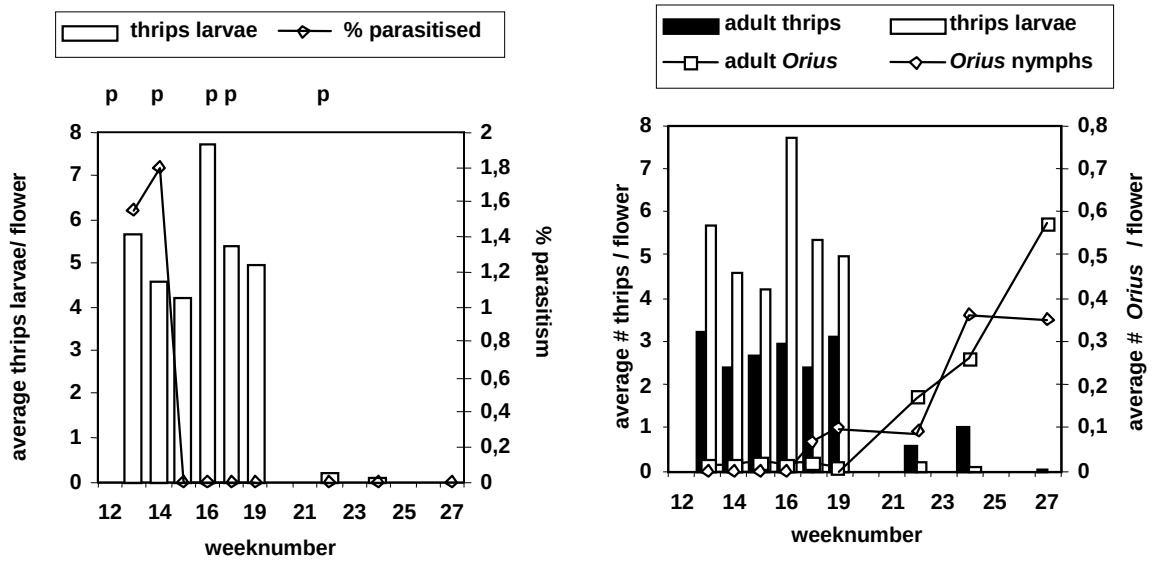

Figure 3. Development of thrips infestations and natural enemies – *Ceranisus menes* (strain Brasil; left) and *Orius insidiosus* (right) – in a commercial sweet pepper greenhouse, spring 1993; release *Orius* 3x < 18.03, 10.04 (wk 15), 10.05 (wk 20); p = parasitoid releases.

2. Experimental greenhouse tests

Dispersal capacity

Adults of both *C. menes* and *C. americensis* spread immediately after release. Some females could be followed flying onto the rose plants near the release site, but could be traced during a few minutes only. Tests on the capacity to disperse in the two experimental rose plots, showed that adults of both species spread horizontally in the rose crop and remained there for almost two weeks (table 4). Adult parasitoids were found inside cut rose flowers and on yellow sticky traps up to 6 meters from the release point within 4 days and the corners were reached within 7 days after release. Numbers recaptured however were low (2% - 5 %) (table 4). Although in compartment G2, two wasps of *C. americensis* were found on the transparant sticky plate placed just below the trap plants, no wasps were found inside the flowers and none of the thrips larvae in the trap plants had been parasitised (table 4). Yellow flowering roses were available during the experiment, the trap plants represented 5-10 % of the total number of flowers present.

Control capacity

Thrips infestations in both compartments developed in a similar way (figure 4 and 5) and consisted mainly of *F. occidentalis* (table 5). In compartment G2, almost half the trap catches consisted of other species, predominantly *T. tabaci*, which had established spontaneously early March, and gradually built up during the sampling period. In compartment G1, *T. tabaci* started to build up from June onwards. Except for the 'Savona' treatment against whitefly in week 24 (figure 4), measures to control other pests did not interfere with thrips population build-up. During the summer period, other thrips species which had entered from outside, regularly occurred on the sticky traps (4-5%) and in the washed samples (table 5). It mainly concerned *Thrips fuscipennis* Haliday, which can be harmful to roses as well (Tommasini & Maini, 1995), and occasionally *Frankliniella intonsa* (Trybom), *Thrips major* Uzel, *Limothrips cerealium* Haliday and *Frankliniella tenuicornis* Uzel, common air dwellers.

Table 4. Location and numbers of parasitoids trapped 1, 4 and 7 days after release in rose; greenhouse G1, *C. americensis*, n = 300; greenhouse G2, *C. menes*, n = 300; distance is indicated by 'Left' (L) or 'Right' (R) orientation and the respective distance in meters.

Greenhouse number	day	larvae introduced	found	% parasitism	parasitoids traps	flowers	distance trap	flowers
G1-1	1	220	120	0	0	2	-	R2-R4
	4	220	94	0	7	2	L6	L4-L6
	7	220	103	0	0	0	-	-
	13	-	-	-	1	0	R4	-
G2-1	1	220	116	0	1	1	R4	R3
	4	220	106	0	1	0	R4	-
	7	220	99	0	0	1	-	L6
	13	-	-	-	2	0	R4	-
G1-2	1	600	-	-	2	-	R2L2	-
	4	-	-	-	4	2	R2L2	R1-R2-L2
	7	-	23	0	1	*6	R2	R1-R2
G2-2	1	600	-	-	1	-	R2	-
	4	-	-	-	3	2	R2	R3-R4
	7	-	60	0	1	3	R2	R1-R2

*: two parasitoids trapped on sticky plate below trap plant

Development of both parasitoid - *C. menes* and *C. americensis* - populations in their respective compartments remained very low. In order to cover the estimated developmental time of 4-5 weeks for both wasp species at 20 ^{o}C (Loomans & van Lenteren, 1994), 150-300 adult wasps of each species were released during five weeks. At an estimated host/parasitoid ratio of 0.5-2 for *C. menes* and 2-6 for *C. americensis* (table 5, releases resulted in the establishment and maintenance of the parasitoid population, but parasitism rates stayed at a very low level: less than 7 % parasitism occurred during the following five month period (figure 3). Parasitoids did not show any density response, parasitism rates were the same either at low or at high host densities (figure 4 and 6). Throughout the experimental period 5 adults were captured of *C. menes* and 25 adults of *C. americensis* on both trap types. Of a total of 2557 larvae sampled in G1, only 24 (0.93%) were parasitised by *C. menes*, and of 3146 larvae in G2, 48 (1.52 %) were parasitised by *C. americensis*.

The mean percentage of damaged flowers (figure 6; 'harvest + ripe', 100-300 per week), increased in both plots up to 100% in week 30, coinciding with the increase in number of thrips (figure 4 and 5). During the first period damage symptoms mainly concerned necrotic spots on the sepals, from week 27 onwards the percentage of damaged petals increased, causing severe damage to the crop (figure 6). The decrease in adult thrips numbers after week 33 is probably temperature related. During summer, end of July and August, due to a heat wave, temperatures increased during the day up to 35^{0}C and sometimes 40^{0}C or more.

Table 5. Comparison of total adult thrips numbers (♀/♂) in trap catches and flower samples

Greenhouse number	trap-type	trap catches *F.occidentalis* total	%♂	other total	%♂	flower samples *F.occidentalis* total	%♂	other total	%♂
G1	yellow	1123	69.2	210	15.8	2640	40.7	149	5.4
G1	blue	1061	69.7	243	18.6				
G2	yellow	856	74.6	518	37.7	1825	46.1	673	27.1
G2	blue	845	76.2	809	48.9				

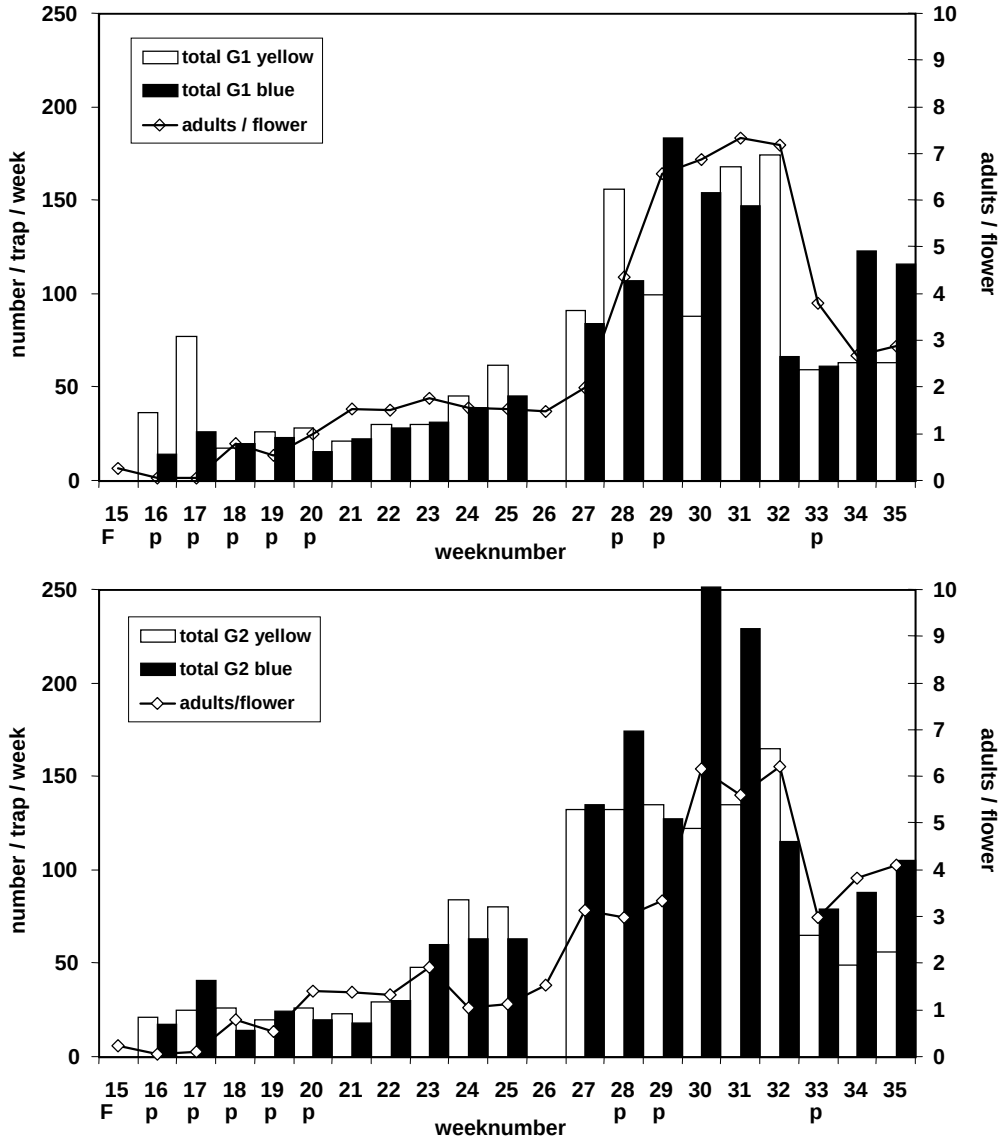

Figure 4. Mean number of thrips adults (*F. occidentalis*, *T. tabaci*, others) found per week in 50 rose flowers and on a blue an yellow sticky trap for two rose compartments (*C. menes* top, *C. americensis*, below); releases of thrips (F) and parasitoids (p) are indicated by letters.

Discussion

Results of parasitoid releases (*C. menes* and / or *C. americensis*) in commercial and experimental greenhouses indicate that these species played only a very minor role in thrips control. In commercial cucumber and sweet pepper crops, *C. menes* was recovered after releases in very low densities. Later in the season thrips populations were controlled by releases of *Orius insidiosus*, and the parasitoid played no role. Theoretically the low performance could, in part, be explained by negative interactions (intra-guild predation) between *Orius* and *C. menes* in the commercial greenhouses, preying on parasitised larvae, But our results in both ornamental crops do not support this explains its overall low preformance. Parasitoids could establish themselves in the experimental greenhouse on rose, and were able to produce new generations. However, hey were unable to reduce thrips populations to sufficiently low levels. Small scale pilot studies performed with *C. menes* a few years later in Florida (Castineiras, pers. comm.) and Australia (Steiner, pers. comm) lead to the same conclusion: only traces of parasitism were found and an incapability to control thrips pests. The prospects of larval parasitoids seem very low for thrips control in commercial vegetable and ornamental crops.

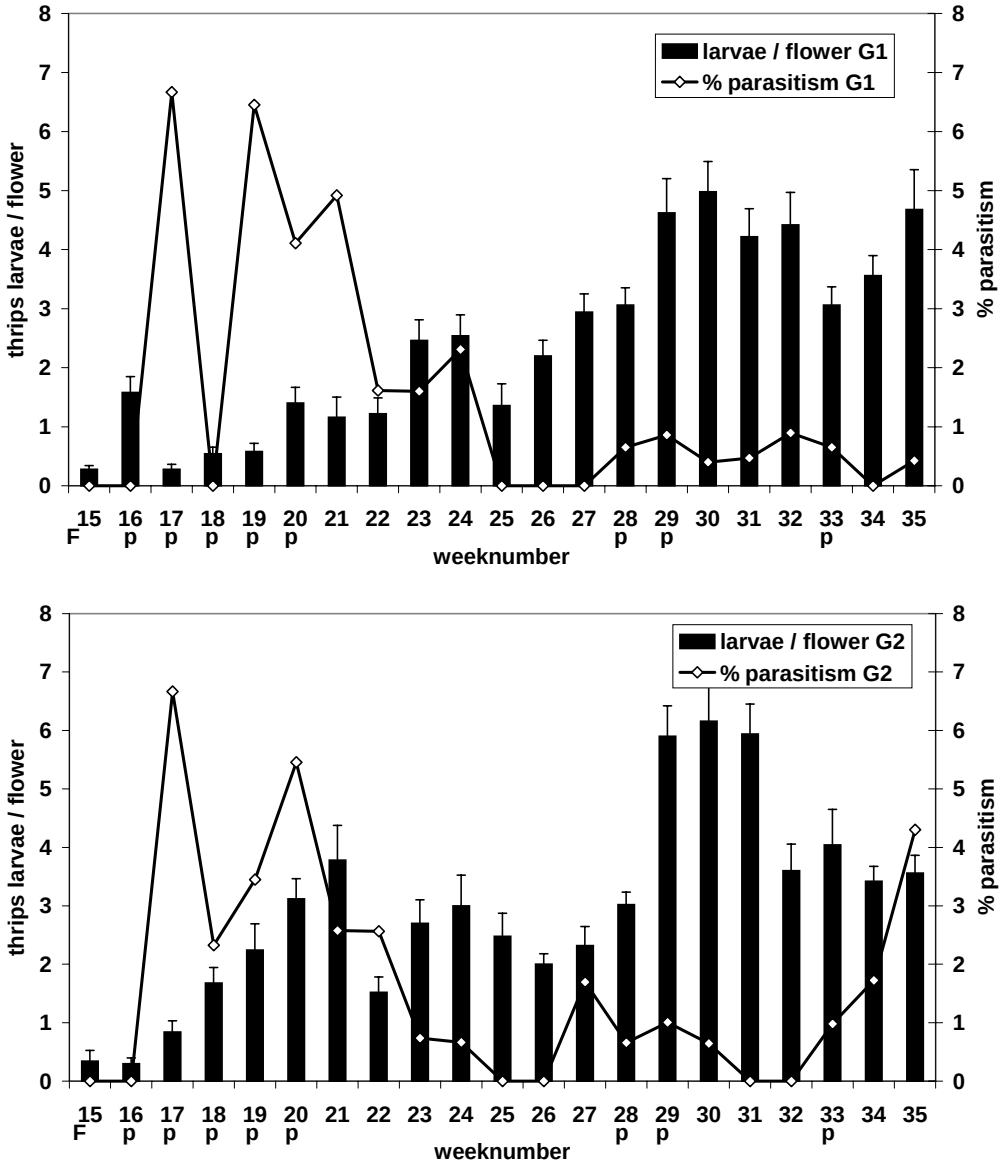

Figure 5. Mean number (± s.e.) of thrips larvae (L1-L2) found per week in 50 flowers and percentage of parasitism after release of *C. menes* (top) and *C. americensis* (below) in two rose compartments; releases of thrips (F) and parasitoids (p) are indicated by letters.

Roses are attacked by a wide range of pests (Baas *et al.*, 1993). Against some pests correction measures were necessary to allow the crop to develop (table 3). A wide range of thrips species are known to attack roses in greenhouses (Sauer, 1997ab), but in temperate areas, *F.occidentalis*, *T. tabaci* and occasionally *Thrips fuscipennis* are the most relevant pests. Large differences exist in attractiveness (Park *et al.*, 2001), suitability (Dash & Naik, 1998) and host plant resistance to feeding damage (Gaum *et al.*, 1994; Sütterlin, 1999) to western flower thrips between different rose cultivars. Yellow cultivars, like 'Frisco', are more attractive for adult *F. occidentalis* than for instance red cultivars (Park *et al.*, 2001) and although *F. occidentalis* prefers flower-leaves (sepals) for oviposition, the petal tissue of yellow and white flowers is preferred over red and orange petal tissue (Dash & Naik, 1998). Developmental time is generally shortest on white- and yellow-flowered cultivars than on red or orange (Dash & Naik, 1998).

In rose high numbers of thrips developed in both greenhouse compartments, up to 15-20 individuals per flower in July. For rose a threshold level for control measures is advised if 10 or more thrips adults, not separated for sex, are monitored per trap per week or when

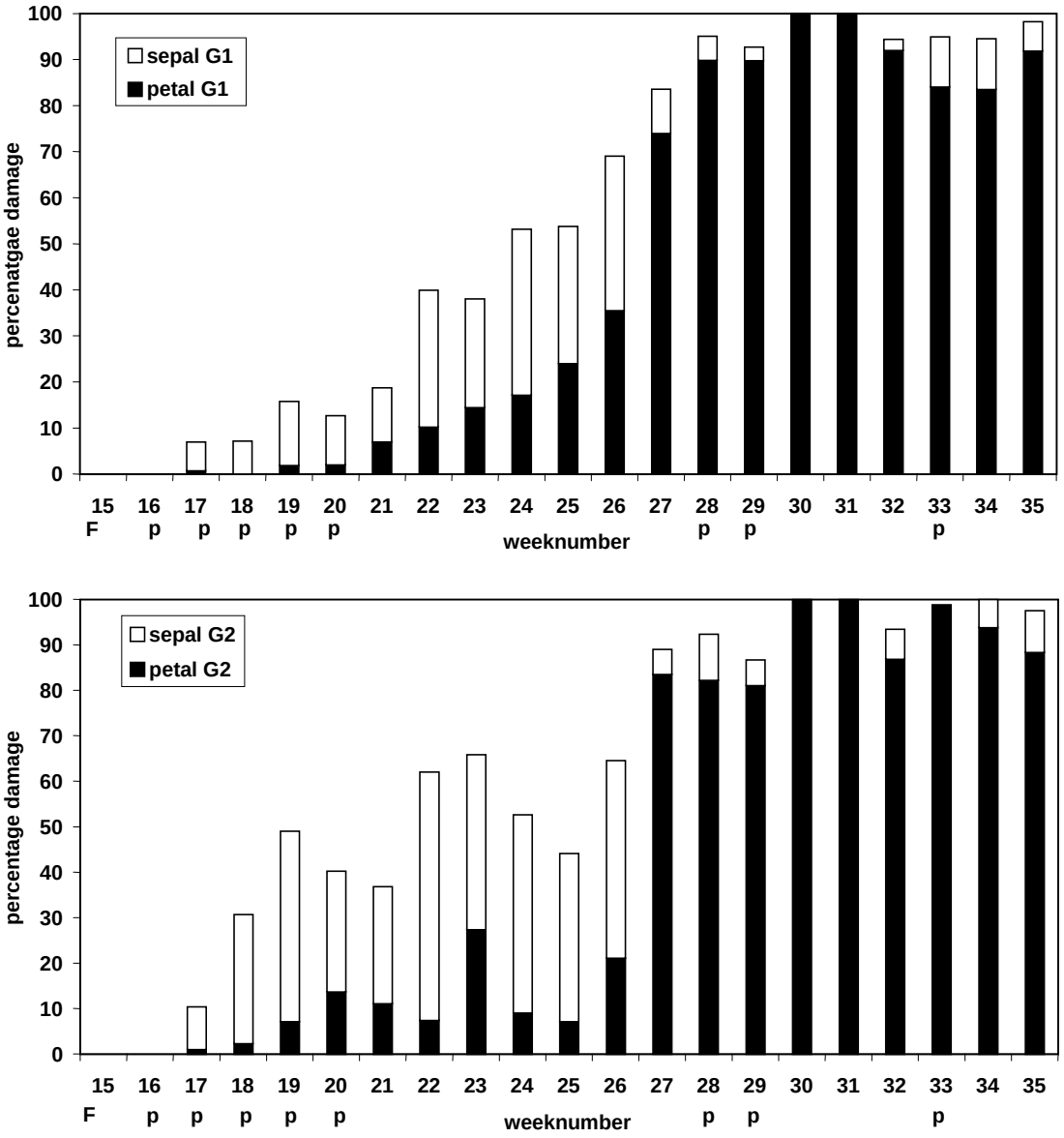

Figure 6. The mean percentage of rose flowers ('harvest'+ 'ripe') showing thrips damage over time, separated for damage to flowers on the sepals and petals) in two experimental rose compartments (*C. menes*, top; *C. americensis*, below); releases of thrips (F) and parasitoids (p) are indicated by letters.

Table 6. Estimated release ratio's of thrips larvae / parasitoid (t / p) and of pupal parasitoid offspring after release, based on thrips and parasitoid numbers, % parasitism in the weekly sample and the total number of flowers present in the crop.

Week #	Greenhouse 1 (*C. menes*)			Greenhouse 2 (*C. americensis*)		
	total larvae (#)	ratio (t/p)	parasitoid pupae (sum)	total larvae (#)	ratio (t/p)	parasitoid pupae (sum)
17	150	0.49	10.0	960	3.20	64.1
18	272	0.81	0.0	872	5.80	20.3
19	184	1.12	11.9	878	2.93	30.3
20	275	1.84	10.7	637	3.86	34.7
21	206	0.74	4.4	647	2.15	16.6

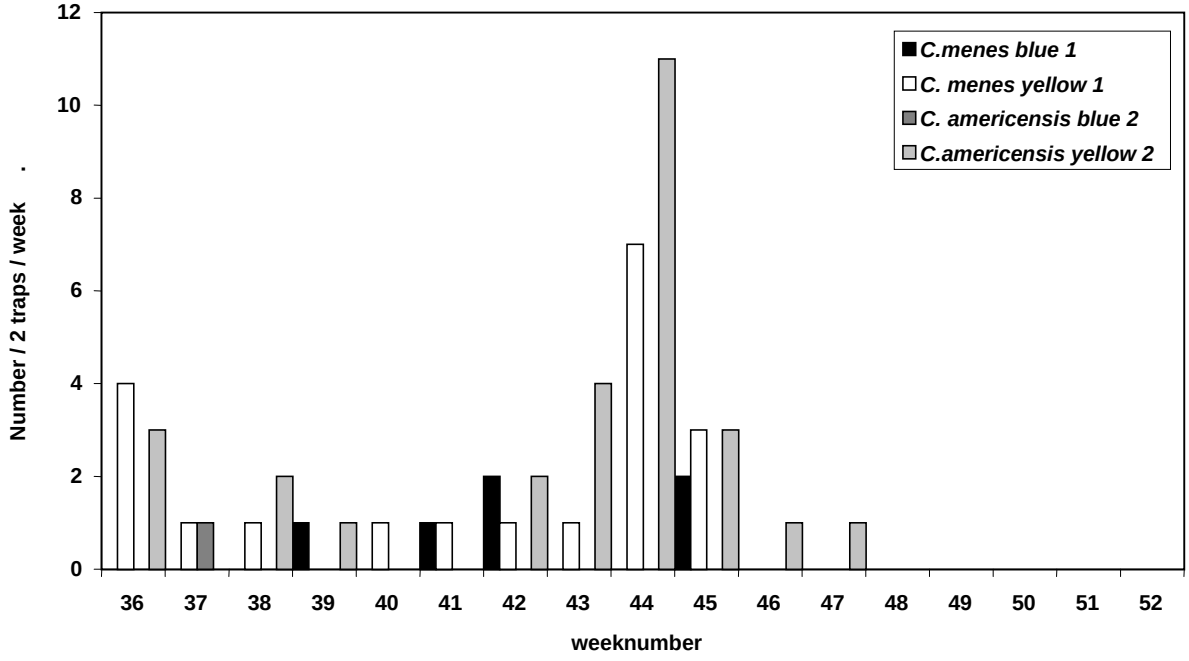

Figure 7. Trap catches of *Ceranisus menes* (Greenhouse 1) and *Ceranisus americensis* (Greenhouse 2) on blue and yellow sticky traps, in rose from September till December 1994.

damage symptoms increase with 10 % a week for cv 'Frisco' (Fransen *et al.*, 1993), or within 20-30 adults trapped weekly for other cultivars (Frey, 1993; Schmidt & Frey, 1995). In our crops, the threshold level was passed and damage symptoms occurred from the beginning onwards, in May and June first on the sepals and from July onwards, mainly on the petals too. A spray with insecticidal soap (Savona 1%) against whitefly caused a temporary decline in thrips numbers (figure 4 and 5) and damage (figure 6), but populations soon recovered. From week 25 onwards when more than 10 western flower thrips (WFT) females were trapped and the average number per flower was 2 or more, the 80 % of the harvested flowers was damaged. A good correlation was found between thrips numbers in the flower samples and on sticky traps (Pearson's r >0.76 yellow traps, r >0.80 blue traps), but overall more WFT males were trapped on the yellow and blue sticky traps than females (table 5). Because males are more active, swarming in the coloured reproductive parts (Terry, 1990), in the top layer of the rose crop, they are more likely to be trapped. In general, during May and early June more WFT males were washed from the flowers than females (52-84 %), but later in the season there was a shift in sex ratio towards females (52-67%). This shift in sex ratio is probably density related (Higgins & Myers, 1992): in greenhouse vegetable crops, 80-100 % of *F. occidentalis* adults on traps were males at low densities and 60-90 % females when thrips infestations were high.

Releases of adult thrips parasitoids during the period that numbers reached threshold levels or higher (week 17-21, table 6), did not result in any control of the thrips population. Keeping thrips populations at a low level will depend on the searching efficiency of the parasitoid as well as the capacity to build up a population. At the moment of release the estimated thrips larvae/parasitoid ratios varied from 0.5 to 2 (*C. menes)* and from 2 to 6 (*C. americensis*) (table 6). The parasitoid's reproductive capacity will not have been a limiting factor (Loomans & van Lenteren, 1994), but could not be realised under glasshouse conditions at low host densities. The low level of parasitism might be due to a limited searching efficiency and / or accessibility of the infested young rose buds and searching time on the flowers. *C. menes* females exposed in the laboratory to caged rose buds infested with 10 first instar larvae of *F.occidentalis* introduced 24 hours before, were able to locate and

parasitise about 50% (4.8 ± 1.3, n=12) of them. However, it is unknown whether larvae behaved similar in confinement to those in flowers in the greenhouse, because some of the larvae were found outside the buds at the breakdown of the experiment after 24 hours.

C. menes and *C. americensis* were found on traps as well as in rose flowers throughout the greenhouse during and after the release, but in very low numbers. These could be explained by three different factors: difference in attraction, accessibility and availability, and thus synchronisation, for thrips and their parasitoids. Both thrips and parasitoids are attracted to certain colours. However, parasitoids are more attracted to yellow than to blue, and the exact role of visual and chemical stimuli in host location is yet unknown. In roses, thrips infestations mainly occur in the top layer of the crop. Thrips adults lay their eggs and damage the rose bud in a very early stage of growth (Park *et al.*, 2001), when the buds are still 'raw' (sepals completely closed until the first yellow petals become visible, figure 2a), but first and second instar larvae are then already present. Parasitoids can have difficulty entering these young rose buds. Shortly before the flowers are harvested (figure 2b), when the sepals are still erect and petals start to open, they become more accessible, but damage has already been inflicted upon the bud (Park *et al.*, 2001). The stage which is most accessible, rose flowers that are ‘ripe’ (figure 2c), rarely occur in a commercial greenhouse: flowers are harvested before that, leaving a period of about 2 weeks in which roses are available for both thrips and parasitoids. This is long enough for *F. occidentalis* to reach the pupal stage, but too short for the parasitoid to reach its pupal phase. If parasitisation is successful, and because parasitised larvae continue to feed and develop unlike when being eaten by a predator, most of these larvae will be taken out at harvest. In addition. *C. menes* is able to parasitise only young larvae of *T. tabaci* and *F. occidentalis*. *C. americensis* prefers *F. occidentalis* over *T. tabaci*, which is only parasitised to a very low extent (chapter 4 and 5). By the time that rose flowers are easily accessible, the larval population has developed so far that few young thrips larvae are available.

Parasitoids maintained themselves during the season, but were not able to build up a population. In May and early June ripening of flowers is faster than development from egg till pupa of thrips (two weeks at 25^0C, three weeks at 20^0C: Fransen *et al.*, 1993b), and most of the parasitised and unparasitised thrips larvae (estimated totals, table 6) are removed from the greenhouse. Developmental times of *C. menes* and *C. americensis* are much longer and show a large variation (Loomans & Van Lenteren, 1995; chapter 6) compared to those of *F. occidentalis* or *T. tabaci*, in particular at 20 ^{0}C, the normal temperature during the first weeks. During late June, early July (week 22-27), only a few adults from a next parasitoid generation were trapped and the rate of parasitism was very low. At higher temperatures thrips infestations can develop quickly and the few parasitoids of a next generation (table 6) hatching in June and early July, are not able to keep pace with the pest. After the parasitoid release experiment had ended, August 31st, the predatory mite *Amblyseius degenerans w*as introduced in both greenhouse compartments. During these trials, adults of *Ceranisus menes* (in G1) and *Ceranisus americensis* (in G2) were still found when sampling and washing flowers (1* *C. menes* in week 42, 1* *C. americensis* week 44) and monitoring sticky traps (figure 7). This indicates that both species were able to establish and maintain itself in the rose crop.

No other dataset is available of releases of parasitoids to control thrips pests in any greenhouse crops. The low rate of parasitism can, in part be explained by a reduced searching ability on flowers of rose, sweet pepper and various potted plants, and leaves of sweet pepper or cucumber. It might also be partly explained by a difference in encounter probability with hosts of different sizes (see chapter 4), in particular when the vulnerable host stage is concealed in buds (rose) and flowers and thus unavailable for the parasitoid. In other crops, with a different crop structure, host larvae could be more accessible for parasitoids. A single count in 'ripe' (wide open, figure 1c) roses of various cultivars in a greenhouse in Hyères (France) in September 1990, showed 14% parasitism by *C. menes* (brown colour-type) which had entered the greenhouse from the outside (Loomans, 1991). Occasionally natural parasitism levels by *C. menes* are quite high on vegetative plant

structures in the field. In Japan, on onion infested by *T. tabaci*, parasitism levels by *C. menes* reached as high as 79% and showed a clear positive density dependent response (Loomans & van Lenteren, 1995). A high level of natural parasitism (40-60 %) by *C. menes* of *Thrips palmi* infesting leaves of eggplant was found in Thailand and Japan (ibid.). Development of a biological control programme for thrips pests in greenhouse crops, and in roses in particular, were infestations largely occur in the marketable reproductive parts, will depend on the ability to bring and keep thrips densities at a very low level in an early growth stage of the crop. Our results indicate that parasitoids may not be suitable candidates for biological control of thrips in roses. The question remains which factors can explain the failure of parasitoids to keep thrips infestations down. Biological control in ornamentals remains problematic and chemical control is still the predominant practice. Prophylactic use of predatory mites, including combinations of crop-dwellers (*Amblyseius cucumeris*) and soil-dwellers (*Stratiolelaps miles*) has shown prospects in some systems of cut roses (Linnamaki *et al.*, 1998) as has the use of fungal pathogens (Murphy *et al.*, 1998; Ekesi & Maniania, 2003). Biological control of thrips in roses has a very narrow 'activity window" - from the moment that the flower is accessible till the infliction of damage and harvest - during which a natural enemy has to find and diminish the pest. In the case of parasitoids the juvenile thrips stages have almost completed their development and damage has already been done, before they are prone to attack. Predators seem to have somewhat better prospects for thrips control in ornamentals than larval parasitoids. The period during which larvae are available for predation is less relevant for these groups, because of their ability to kill their prey or host directly. However, the lack of alternative food sources in non-pollen producing ornamentals is a serious constraint for a reliable biological control solution.

Our results of parasitoid releases (*C. menes* as well as *C. americensis*) in commercial and experimental greenhouses indicate that these species can only play a very minor role in thrips control. At best parasitoids can maintain themselves in some (ornamental) greenhouses, and are able to produce new generations, but are unable to reduce thrips to sufficiently low populations. Control of thrips pests with *Ceranisus* spp. seems insufficient under northern European greenhouse conditions.

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Chapter 9

Biological Control of Thrips Pests: Summarising discussion

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Introduction

The thesis presented here is the result of a joint European EC-CAMAR research project "Biological Control of Thrips Pests", performed between March 1st, 1991 and February 28th, 1995. Other participants were the Univeristità degli Studi di Bologna, Istituto Entomología 'Guido Grandi', Bologna – Italy and Institut de Recerca i Tecnología Agroalimentáries, Centre de Cabrils, Entomología Aplicada, Cabrils, Spain. All partners focussed on different aspects of the biological control of thrips pests. Researchers in Italy and Spain evaluated various aspects of selected generalist predators, whereas my research focussed itself on the evaluation of thrips parasitoids as potential biocontrol agents of thrips pests with particular emphasis on western flower thrips, *Frankliniella occidentalis* (Pergande).

Specific aims of the project were to collect, evaluate, mass produce and commercially apply natural enemies of thrips species. Experiments were conducted in various phases. First, an evaluation was made of literature information on thrips pests and the control capacity of natural enemies already known. Second, surveys were made of natural enemies, predators and parasitoids in Europe and collections of parasitoids were made worldwide. Next, selection criteria were applied, developed previously (van Lenteren, 1986; Minkenberg, 1990), using biological and behavioural characteristics of the natural enemies, in order to investigate the potentials of the newly collected beneficial insects. After that, rearing methods for thrips and its enemies were developed and evaluation experiments were performed - first in the laboratory, followed by tests in experimental glasshouses and finally in commercial glasshouses and in the field - to test whether the selected natural enemies were sufficiently effective in controlling thrips pests. Finally, a mass production and release system was developed for the best natural enemy, together with information material for extension services and farmers.

Since its accidental introduction in The Netherlands in 1983, western flower thrips (*Frankliniella occidentalis* (Pergande) became the number one key pest in European glasshouses. In the late eighties it invaded vegetables and ornamentals grown in plastic tunnels and the field as well as fruit trees in the Mediterranean area of Europe. As chemical control of thrips was difficult or impossible and did not fit into the applied Integrated Pest Management (IPM) programmes in greenhouses, a biological control method had to be developed. The international scientific community put most efforts into developing programmes using generalist predators, established and proven ones such as *Amblyseius cucumeris* (Oudemans) (Acari: Phytoseiidae) and new ones, such as *Orius insidiosus* (Say) (Hemiptera: Anthocoridae). Since parasitoids (Hymenoptera) had not been considered till then, their potential as biological control agents of thrips pests needed further evaluation.

Here I summarise, discuss and integrate the results of my parasitoid research, based on and evaluated according to the application of specified selection criteria and discuss the prospects of parasitoids for the biological control of western flower thrips.

Criteria used for the evaluation of natural enemies of thrips

The most critical phase in development of any biological control programme is that where the selection of natural enemies takes place. Originally, selection of natural enemies had been an empirical procedure, and most natural enemies had been found through ' trial-and-error', by releasing candidates in the greenhouse and evaluate the results by monitoring pests and natural enemy populations. Because of the large number of natural enemies per pest species, it is impossible to evaluate all of them. Therefore, many researchers developed and optimised pre-introductory selection procedures, to come from a large array of natural enemies to a few selected ones and so to increase the predictability of success before introductions are made (van Lenteren, 1993). In the eighties, a set of selection criteria was developed at Entomology in Wageningen for the evaluation of natural enemies (van Lenteren, 1986; Minkenberg, 1990), which had proven its efficiency in biocontrol progammes for leafminers, whiteflies and aphids. Van Lenteren (1986) selected the following criteria:

1. Seasonal synchronisation with the host;
2. Internal synchronisation with the host (development on the host);
3. Climatic adaptation (develop, reproduce and disperse under greenhouse conditions);
4. No negative effects (no attack of beneficial organisms);
5. Good culture method (ability to mass-produce);
6. Host specificity (host range including the pest organism);
7. Great reproductive potential (population growth rate to cause substantial mortality);
8. Good density responsiveness.

A pre-introduction procedure should select, on the basis of these proposed criteria, the best candidates for greenhouse trials by making comparisons between parasitoids. Depending on the type of biological control programme - inoculative (classical), seasonal inoculative or inundative - some of these criteria were considered more important than others. For greenhouse seasonal inoculative biocontrol programmes, criteria 2-3-4-5 and 7-8 are considered important, whereas for inundative releases 3-4 and 5 were most critical. In my specific evaluation programme on thrips parasitoids, the criteria mentioned above were considered. Bioassays were included to identify how parasitoids search and locate hosts at a long and short distance (host location, host acceptance), how they complete the different phases of the host selection process (Vinson, 1976), and use the results of the host selection process as a tool for evaluation and selection of the parasitoids themselves.

Review and collection of parasitoids

Before the project started thrips parasitoids had gained very little interest as potential biocontrol agents for thrips pests in greenhouse vegetables and ornamentals. Our literature review (**chapter1**) data showed that at the start no parasitoids were known to attack and develop on *F. occidentalis* in specific, but that a number of parasitoid species had been recorded from closely related thrips pest species belonging to the genera *Frankliniella* (e.g. *Frankliniella intonsa*, *Frankliniella schultzei*) and *Thrips*, (*Thrips tabaci*, *Thrips palmi*) within the same subfamily (Thripidae: Thripinae) (Loomans et al., 1995). Literature information further pointed out that thrips parasitoids are specific to genera within the same (sub)family of Thysanoptera and no side effects, such as parasitizing beneficials (e.g. predatory thrips) or hyperparasitism, had been found.

In our search for parasitoid candidates, we concentrated our sampling programme on *F. occidentalis* populations in its original area of distribution (USA) and newly invaded areas (South of Europe), and on closely related species, distributed worldwide, preferrably in areas with climatically conditions similar to northwest European glasshouses (climatic adaptation). Based on the host and geographic distribution records in the literature, my interest was first

concentrated on species within the genus *Ceranisus* (Walker), solitary larval endoparasitoids of thrips species closely related to *F. occidentalis.* A thorough and systematic exploration of *F. occidentalis* populations for natural enemies in newly invaded areas and its country of origin was never been performed properly, but could be initiated in the South of Europe and Western USA, during the course of our project. Out of the potential group of candidates, we were able to collect (**chapter 2**) and evaluate a limited number of parasitoid species. *Ceranisus menes* was found to be the most common parasitoid of thrips. It occurs worldwide and is widely distributed in Europe. In Italy, Spain, France and The Netherlands it was found regularly on natural vegetation infested by a wide variety of thrips species, belonging to the genera *Frankliniella*, *Thrips* and *Taeniothrips* (Thysanoptera: Thripidae: Thripinae), including important pest species like *Frankliniella occidentalis* and *Thrips tabaci*. It rarely invaded cultivated crops, either in glasshouses or open field. In 1993 it was first recorded from California-USA. *C. menes* is known to attack a wide range of hosts within the genera *Frankliniella, Thrips*, etc. and was the first thrips parasitoid which actually attacked and developed on *F. occidentalis*. *C. americensis* is the second thrips parasitoid which is known to attack this host. It was collected in California and Arizona - USA from roadside vegetation, May 1993. It was found earlier in association with *F. occidentalis* in Canada, but no biological data were available.

The collection and selection of thrips parasitoids however, could not fully be exploited during the relatively short period of time that was available during the course of the project and the characterisation and existence of biotypes (geographical races) still needs to be properly evaluated, before a final conclusion can be drawn about the use of parasitoids as agents for the biological control of thrips pests. It also shows that not only thrips pests enter The Netherlands accidentally, but their natural enemies (including thrips parasitoids) are imported by accident as well.

Development of a rearing method for thrips and parasitoids

In **chapter 3** we present part of our research developing a rearing method for western flower thrips and their parasitoids. It illustrates that for the evaluation of natural enemies as biocontrol agents, the availability of reliable methods for performing bioassays is a conditional but essential element, sometimes a pleasure and sometimes a pain. For rearing thrips hosts (*F. occidentalis*, *Thrips tabaci* Lindeman *Frankliniella schultzei* (Trybom)*, Frankliniella intonsa* (Trybom)) and parasitoids, two rearing methods were used: the bean pod method, using fresh beans (*Phaseolus vulgaris*) and additional bee-pollen (Loomans & Murai, 1997) and the artficial method, using 10%honey-solution and plant – pollen described in **chapter 3**. Both methods were used for stock as well as experimental rearing of thrips hosts and parasitoids, applying different devices respectively. In general each method consisted of four parts: an oviposition unit were adult females were allowed to lay eggs during a fixed amount of time, a rearing unit for parasitised and unparasitised larvae, an incubation unit for parasitoid pupae and a storage unit for adult parasitoids. Both methods allow us to synchronise host larvae to age (per day). Although the artificial method is more labourious and less productive (amount of parasitoids / unit of working-time), it is more consistent than the bean pod method, where secondary infections with other (predatory!) insects or mites introduced with the bean tissue occasionally contaminated our cultures. This method also allows us to check a wide variety of larvae of thrips species feeding on pollen for parasitism (chapter 2), originating from various host plants, which is more difficult using bean pods. Both culture methods, however, had its serious drawbacks, with respect to rearing thrips as host for natural enemies: because they are very labour intensive, they are not designed for mass-rearing procedures when 100,000s of wasps need to be reared per week. On the other hand, the methods described, and also others described in literature (Loomans & Murai, 1997) are often not very suitable for the individual rearing of larvae, as indicated in **chapters 4** and **chapter 5**, where cultures of individual larvae were lost or suffered from

high mortality rates because of humidity problems and thus partly hampered a full and adequate interpretation of our results. It was only till after this project finished that a reliable method was developed for the rearing of individual larvae, using leaf disks on agar in tightly sealed 24 cell multi-well plates.

Host selection

Determination of host-specificity of parasitoids was used for a proper evaluation and pre-selection of our candidate species. In order to evaluate host specificity and the parasitoid's effectiveness, behavioural (host selection) and biological (development) characteristics were used as criteria.

Host age selection (chapter 4)
Detailed analysis of behavioural characteristics showed that acceptance of *F. occidentalis* larvae by both colour-types of *C. menes* was related to size and thus to age and stage of *F. occidentalis* larvae: the attack-ratio, insertion-ratio and acceptance-ratio (ratio of inserted hosts per encounter) decreased significantly with increasing size (age) of host larvae for both colour-types, yellow parasitoid strains being somewhat more effective than brown strains. Behavioural defensive reactions of *F. occidentalis* larva (movements of the abdomen, excretion of anal exudates, escape by walking away) when attacked, largely explained this gradual decrease in host acceptance: large size, second stage larvae were less prone to attacks and more able to escape from parasitisation. Observations on *C. americensis* parasitisation behaviour showed a similar trend, but this parasitoid was able to attack and parasitise older and larger-sized larvae more successfully. The apparent preference for small and young host larvae is valuable for developing a mass-production system for thrips parasitoids (**chapter 3**) and for the timing of future releases as a biological control agent in the greenhouse. Their actual parasitism in the greenhouse will depend on the searching abilities (**chapter 7**) in different crops and thrips infested host plant.

Host species selection (chapter 5)
C. menes, known to attack a wide range of hosts within the genera *Frankliniella, Thrips*, etc., was the first thrips parasitoid which was actually found to attack and develop on *F. occidentalis* (**chapter 2**). *C. americensis* was the second parasitoid species which attacked and developed on this host. It was found earlier in association with *F. occidentalis*, but no biological data were available. Our results showed that *C. americensis* preformed best on its original co-evolved host *F. occidentalis*. *C. menes*, on the other hand, consists of a large complex of regional populations that differ in their mode or reproduction, and that differed morphologically, geographically, behaviourally and physiologically in their response to different geographical populations of thrips species, each of them having its unique characteristics. Our results indicate, however, that intra-specific variation in host-specificity by various strains of parasitoids can be of great importance to possible failure or success in biological control.

Development
One of the main problems in the biological control of thrips is the synchronisation of the pest and predators or parasitoids, particularly for releases during winter and early spring. Whereas in predators preferably species and strains are selected with no reproductive diapause (Tommasini, 2003), the reaction to changing daylight conditions in parasitoids is still unknown. In **chapter 5** and **chapter 6**, however, we showed that developmental time is significantly affected by temperature and can severely hamper seasonal ánd internal synchronisation with the target pest *F. occidentalis.* At both temperatures tested (20 ^{0}C and 25 ^{0}C) developmental times differed between parasitoid species and between strains of *C. menes.* The difference is mainly caused by a large variation in parasite emergence over time for the yellow strains of *C. menes* and is related to the climatic / geographical origin (North

versus South) of the strain (climatic adaptation criterion). In particular at low temperatures this is very pronounced. American strains of *C. menes* show developmental times comparable to the Mediterranean European strains at 25 ^{0}C. Variation in developmental was independent from the host species. *C. americensis* did not show a large variation per se, but developed very slowly at 20 ^{0}C. Developmental time of both parasitoid species is much longer than that of their host *F. occidentalis*, in particular at 20 ^{0}C. Extreme developmental times as shown for both parasitoid species, could severely hamper seasonal synchronisation and inoculative control applications, especially in temperate greenhouse areas and early spring cultures. Because thrips generations in glasshouse conditions will not be discrete, parasitoids will be able to find suitable host larvae at any time. Synchronisation in development between host and parasitoids therefore is not necessarily a prerequisite as a critical selection criterion for thrips parasitoids. The large variation in developmental time, however, could be a serious constraint for mass-production, where the production of synchronised cohorts of parasitoids is essential.

Life – history studies

Establishing life-history parameters provides a vast amount of relevant information on the biology, development and life-history of the natural enemy, and therefore is a good starting point for any evaluation study, especially of those where little information of the natural enemy is known. A high intrinsic rate of increase is considered as one of the attributes characteristic of effective biological control agents (Van Lenteren, 1986). In **chapter 6** we saw that the life-history parameters of both *C. menes* and *C. americensis* were lower or at its best equal to that of its host, *F. occidentalis*. The net reproduction (R_0) values were higher at 25 ^{0}C than at 20 ^{0}C and varied largely between *C. menes* strains, yellow strains giving higher values than the others at both temperatures. The intrinsic rate of population increase (r_m) of the 4 strains of *C. menes*, increased with temperature. The r_m value for *C. americensis* was comparable to that of its host and much higher than those for *C. menes*. If we take the reproductive capacity to predict the effectiveness, *C. menes* is expected to be less effective than *C. americensis.* However, as we argue in **chapter 6** care has to be taken, interpreting the outcome: an r_m larger than the r_m of the host is not by itself sufficient predicting parasitoid efficiency. First, because in our calculations we did not include the additional hosts killed through host-feeding, so the overall host-kill rate is likely higher. Second, parameters may have similar absolute values, but are the overall result of the survival and fecundity curves. Life-history studies are almost all performed inside the laboratory, in small cages, using excised leaves, a continuous exposure to a surplus of host larvae and high moisture conditions. This can lead to inaccurate estimates of reproductive potential and population growth rates. The shape of the fecundity curve can be of more value predicting the effectiveness of a particular parasitoid in a field situation than the absolute value. Fecundity and survival curves are the reflection of various factors: environmental factors like pest density (Kopelman & Chabora, 1992; Harvey et al, 2001) and intrinsic effects such as the type of 'ovigeny' (Jervis et al., 2001), life- expectancy, or maternal effects (Tagashira & Hirose, 2001) and as shown in **chapter 6** by differences between colour types and strains of a particular parasitoid species. For intance, the type of 'ovigeny' of a parasitoid can give an indication of how fast it can react to a sudden increase in the density of the host, either because of encountering patches of high densities or a population increase. In *C. americensis* the fecundity curve was steep and short, whereas *C. menes* strains all had a curve that levelled off gradually. We expect that *C. americensis* is able to react faster to changes in patch densities when foraging in a crop, than *C. menes.* For biological control purposes, especially in ornamental crops, a parasitoid has to be able to perform well at very low pest densities. At low host densities the full reproductive potential will not be realised and the parasitoid's searching efficiency becomes of great importance. In particular during the early season, when few hosts are available, searching ability and

host acceptance capacity will be important. Therefore, it may be more effective to select parasitoids that do not have a high reproductive potential, but do have a high host-finding capacity, in particular those that parasitise on hosts that move about freely.

Searching behaviour

Behavioural experiments on the searching behaviour of *C. amercensis* and *C. menes* indicate that chemical and visual stimuli are involved in host habitat location and host location. Results of the behavioural studies presented in **chapter 7** show that visual stimuli (colour) positively affected short-range flight, and that both species use chemical stimuli for short-range host location after landing: female parasitoids spent significantly more time in an area where thrips larvae had been feeding shortly before. This arrestment response, however, did not seem to be host specific: within a parasitoid species no difference was found between an area contaminated by either one of the thrips hosts, *T. tabaci* or *F. occidentalis*. Parasitoid females were not attracted to the synthetic compounds of the alarm pheromone (decylacetate plus dodecylacetate) of western flower thrips in short-range flight tests, indicating a non-volatile effect. Did our results still give a fragmentary picture, recent developments allow us to get a better understanding. *C. menes,* parasitising thrips larvae on a wide range of host plant species, can be considered a generalist at both the plant and on the host level and reaction to specific info-chemicals would be not expected (Vet & Dicke, 1992). This is in fact confirmed by recent work of Murai *et al*. (2000), who found that methyl anthranilate - a common flower scent component in several plants and an attractant for a wide range of flower dwelling thrips and other insect species - is a potent attractant for *C. menes* as well. Whether this holds for *C. americensis* too, remains to be sorted out. It still can largely explain our findings of the close association of *Ceranisus* species with flowering plants during our field surveys and parasitoid collections (**chapter 2**).

Releases of *C. menes* and *C. americensis* in experimental and commercial greenhouses (**chapter 8**), showed very poor results. Searching efficiency and ability to disperse in a crop were very low and parasitoids performed poorly under (temperate) greenhouse conditions. Both parasitoid species could maintain themselves, dispersed and reproduced at Dutch glasshouse conditions, but they were unable to reduce thrips populations to sufficiently low levels. Partly this can be explained by a reduced searching ability on different substrates, such as flowers of rose, sweet pepper and various potted plants, or leaves of sweet pepper or cucumber. It might also be partly explained by a difference in encounter probability with hosts of different sizes (**chapter 4**), in particular when the preferred hosts are concealed in buds (rose) and flowers, thus making the vulnerable stages unavailable for the parasitoid. The presence of mixed infestations of *T. tabaci* and *F. occidentalis*, like occurred in the rose crops, can have had its consequences as well, because species (and strains) largely differ in their preference for the host species (**chapter 5**).

In conclusion: why thrips parasitoids?

As a result of field collection, and laboratory and field evaluations, several candidates for biological control of thrips were discovered. Of these candidates, *C. americensis* and *C. menes* (yellow strain) seemed to have some prospects for application in greenhouses, but still did not prove to be suitable candidates for commercial exploitation. Although a number of the pre-introduction criteria were met, evaluation experiments performed in laboratory experiments using behavioural (host selection and searching efficiency), and biological (development and reproduction capacity) characteristics as selection criteria, indicated that thrips parasitoids tested show limited potential for greenhouse biological control:

1. *No negative effects*. Thrips parasitoids are specific for certain genera and species of thrips and have no negative side effects, i.c. hyperparasitism does not occur and other beneficials (like predatory thrips) are not attacked;
2. *Seasonal synchronisation and internal synchronisation with the host.* Developmental studies on *C. menes* and *C. americensis* show that developmental time of both parasitoid species is relatively long compared to the thrips pest species, *F. occidentalis* and *T. tabaci*, especially at temperature ranges prevalent in North European greenhouses. Both parasitoid species could perform better at relatively high temperature regimes, such as prevail in southern Europe. In Dutch glasshouse conditions, where temperature ranges between 18° and 22°C on average, temperature will be a limiting factor in seasonal inoculative releases, making repetitive releases necessary;
3. *Climatic adaptation.* Although we expected that parasitoids would be adapted to greenhouse conditions, their ability to complete development, to reproduce and to disperse under greenhouse conditions was very poor;
4. *Host specificity.* Acceptance of host larvae belonging to the subfamily Thripinae (Thysanoptera: Thripidae) (*F. occidentalis*, *F. schultzei*, *T. tabaci*) is related to age and size of the host larvae. First and early second stage, small sized host larvae are preferred for oviposition and successful development, by both parasitoid species. In a crop, host stages preferred are mostly concealed within flowers and buds compared to than older, second stage larvae. The differences in host species preference between morphological colour-types and between various geographic populations of the parasitoid on one hand and the variability between populations of certain host species on the other, brings about that a tailor made solution by *Ceranisus* can only be made for a local situation or crop, when all other prerequisites are met. Mixed populations often occur and this has consequences for the biocontrol strategy to use. The occurrence of mixed populations of two or more thrips pests in one crop makes the commercial use of these specialised larval parasitoids unlikely, and the option of a more general approach and a generalist predator, specialised in thrips, more feasible
5. *Great reproductive potential.* Of the *Ceranisus* species tested, only the reproductive capacity (R_o) of *C. americensis* was equal to that of *F. occidentalis*; the net rate of increase (r_m) of *C. americensis* was higher at 25 ^oC than at 20 ^oC, and about equal to *F. occidentalis*. Rates of increase of all *C. menes* strains tested, however, were smaller than those of the thrips host, *F. occidentalis*, or were at its best equal to it. If we take the reproductive capacity to predict the effectiveness, *C. menes* is expected to be less effective than *C. americensis*. An r_m larger than the r_m of the host is not by itself sufficient to predict parasitoid efficiency.
6. *Density responsiveness.* Although we did not check this directly, searching efficiency decreased drastically when the size of the experimental arena increased from a Mungercell to a greenhouse. Preliminary experiments on the functional response of *C. menes* in encaged leaves infested with larval densities ranging from 1-40 showed a maximum of 3.5 and 8 parasitised larvae during 8 and 24 hours respectively.
7. *Good culture method.* Would the above criteria exclude seasonal inoculative releases, for inundative release programmes, thrips parasitoids have their limitations as well. First, because a large variation in developmental time makes it difficult to synchronise cultures. Second, for mass-producing obligate parasitoids of thrips, one needs a mass-production system for thrips as hosts. Current methods are not appropriate for mass-rearing 100,000s of wasps or more per week and is very labour-intensive.

In conclusion: evaluation of the parasitoids I investigated show that they have very limited potential for both seasonal inoculative and inundative release programmes in temperate and Mediterranean greenhouses. They simply are not the “best”.

In addition, spin – off and what we did more

Working with a new group of natural enemies has its charm ('everything can be exploited') and its drawback ('everything is unexploited'). In spite of the criteria used, a certain trial-and-error element was still involved, when starting research on a fully new group. In particular the necessity to develop bioassay methods, as modifications to standard methods or new ones, tailored to these certain species. Although I had to stay working within the practical constraints of the project, it allowed me to take some interesting sideways as well, sometime dead – end streets, sometimes open horizons, but beyond the scope of the project for full evaluation. To mention a few which were touched upon:

- Presence of host discrimination in *Ceranisus menes* colour-types (not included in the thesis) and *Ceranisus americensis*;
- Effects of differences in parasitoid fitness when parasitising male and female *F. occidentalis* larvae;
- Existence of alarm-pheromones produced by thrips species (*Heliothrips haemorrhoidalis*, *Frankliniella occidentalis*) and their effects on natural enemies;
- Effects of disturbance by natural enemies on the life-history of western flower thrips;
- Functional response studies on the plant (not included in the thesis).

From a taxonomic point of view, this study hopefully can contribute to a proper identification and separation of various types within the *C. menes* species complex. *C. menes* was originally described from a yellow holotype. Later a brown colour-type was described from Argentina. Up till now brown as well as yellow colour-types of *C. menes* have been considered taxonomically as one species. Based on the existence of morphological colour-types (**chapter 2**), behavioural differences in host acceptance (**chapter 4** and **chapter 5**), in developmental time and net reproduction (**chapter 6**), there is now evidence that two different (sub)species might be involved, and the present taxonomic status and species identification should be reconsidered. Results of standardised biochemical techniques during the present study support the above differences between both colour-types. Because both types co-occur at the same time on the same host plant, further elaboration on the niche differentiation (width and degree of niche overlap) between the two colour-types might be worthwhile studying as well.

Current trends in biocontrol

Since the end of my evaluation experiments eight years have passed, and biological control programmes have developed along new lines. At the start of the first successful applications of natural enemies in seasonal inoculative biocontrol programmes in the 1970s and 1980s, all attention was focused on the selection of a 'best' natural enemy and technical improvements to increase of their efficiency, fine-tuning the releases programme in numbers, time and space. Science and practice worked hand-in-hand to develop the best solution to a particular pest problem, based on the biology of the agent. Meanwhile, the biological control industry has grown, scientific evaluation is done more and more by the industry at the production facilities itself, products become available to professionals and to the general public. This however, has important consequences and creates new responsibilities. Where biological processes brought all parties together, ecology and economy seem to drift partners apart and 'go their own way'. Currently, two major trends in biological control practice come forward. Although we share a common motto "out of the laboratory and into the field", the motivation for it is quite different, because largely based on economical and ecological principles respectively:

1. technical and economical solutions to improve efficiency a trend to 'simple and cheap solutions' on the one hand: practice (producers) tend to choose / select and release natural enemies that are easy and cheap to rear. Often these are generalist natural enemies, with a wide host range and habitat choice. Consequently, more and more

natural enemies are released in inundative programmes, where natural enemies are released repeatedly in large amounts over time and in space. Criteria like searching efficiency, development on the host and population growth rate seem to be overtaken largely by direct host kill rate,

2. ecological solutions to improve efficiency and safety on the other hand: understanding the basic biology (which is largely included in the selection criteria involved) and which still is a prerequisite for a proper first step evaluation of a natural enemy. Science more and more brings in ecological aspects and development of tailor-made solutions: extending host-parasitoid interactions to a multi-trophic context and fine-tuning the biocontrol instrument (music) by bringing in the ecological setting (acoustics):
   - development of biocontrol programmes, using 'push-pull' techniques (Pickett & Bugg, 1998, Bennison et al., 1999), in particular for those pests which have a hidden life-style, like thrips; including the use of info-chemicals and resistance breeding, making biocontrol agents more efficient by understanding and fine-tuning with the plant-host interactions;
   - taking non-target effects into account (Howarth, 1991), securing that natural enemies are not only efficient on the target pest, but at the same time safe for those insect species we do not want to control or populations we want to preserve (Hokkanen & Lynch, 1995; Wajnberg et al., 2001; Follett & Duan, 1999)

   At the same time it is necessary to orchestrate the variety of natural enemies (intra-guild predation aspects: Rosenheim et al., 1995) and technical measures into an efficient, yet safe and affordable, biological control programme.

How do we bring the economical and ecological approach together, again? For a proper selection of natural enemies of the future we need, in addition to the biological criteria we developed before, ecological-based criteria for evaluation of their safety (van Lenteren et al., 2003). In my opinion, economy and ecology will mutually benefit by taking into account the biodiversity of natural ecosystems in a certain eco-region as a source for new natural enemies (Nicoli & Burgio, 1997) and incorporate elements of these into biological control programmes. All this requires a better understanding of the ecology of a natural enemy to incorporate and translate this into efficient, economic sound and ecological safe biological control programmes. This is an attractive challenge for the years to come. Better understanding of the ecology will ricochet back to facilitating production processes and release programmes and improving the quality of biological control agents. A quick fusion between economy and ecology is in the interest of industry and science, and is crucial for an environmentally safe, yet economically feasible, food production.

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Summary

The thesis presented here is the result of a joint European Research project “Biological Control of Thrips Pests”. Specific aims of the project were to collect, evaluate, mass produce and commercially apply natural enemies of thrips species. To evaluate natural enemies we applied specified selection criteria, which had proven its value in previous pre-introduction selection of natural enemies of several other greenhouse pests. In my part of the evaluation programme, I studied what prospects hymenopterous parasitoids might have as biological control agents of thrips, in particular the western flower thrips, *Frankliniella occidentalis* (Pergande).

First (**Chapter 1**) I summarised available information on the thrips pests which currently play a key role in protected cultivation in Europe. In particular I looked into *F. occidentalis, Thrips tabaci* Lindeman and two other species that I studied: *Frankliniella schultzei* Trybom and *Frankliniella intonsa* (Trybom) and reviewed their geographical distribution, economic impact, followed by additional information on thrips biology, ecology and ways of control. Then the state of the art is discussed of the most important groups of natural enemies that are currently evaluated and/or applied as biological control agents: predatory mites, pirate bugs, entomopathogenic fungi and entomophilic nematodes. Specific emphasis is put on the current status of hymenopterous parasitoids attacking thrips, their biology, ecology and life-history and the prospects they might have for thrips control in European greenhouses. Finally, I present the aim of my research project and the outline of this thesis.

When the research project started, no parasitoid of western flower thrips was known. In our search for parasitoid candidates, presented in **Chapter 2**, a sampling programme was developed, surveying *F. occidentalis* populations in its original area of distribution (USA) and newly invaded areas (South of Europe). Parasitoids of closely related thrips species, distributed worldwide, preferably from areas with climatically conditions similar to northwest European glasshouses were collected as well . Based on the host and geographic distribution records in the literature, mainly species were collected within the genus *Ceranisus* (Walker), solitary larval endoparasitoids of thrips species closely related to *F. occidentalis.* Our collection efforts resulted in a number of parasitoid species and various geographical strains, the most important being *Ceranisus menes* (Walker) and *Ceranisus americensis* (Girault) (Hymenoptera: Eulophidae). Both are solitary koinobiont endoparasitoids of thrips larvae that reproduce asexually.

A critical phase in any evaluation programme, is the development of an adequate and reliable rearing procedure, allowing a standardised supply of insects of a constant quality and large enough quantities. For laboratory bioassays on thrips and parasitoids, and eventually mass-production, it is essential that large cohorts of even aged groups of larvae are available. In **Chapter 3** we describe and evaluate laboratory methods for rearing various species of thrips, such as *Frankliniella occidentalis*, *F. intonsa, Thrips palmi* (Karny) and *Thrips tabaci* Lind. (Thysanoptera: Thripidae) and their parasitoids. When using a method based on honey-solution and pine pollen, large numbers could be produced of high quality, with relatively little time investment. For rearing parasitoids the method proved adequate as well, but less efficient in yield and time.

A number of basic evaluation criteria for pre-introduction selection of useful natural enemies, is based on the outcome of behavioural and developmental interactions with their target host in laboratory experiments. Specific aspects of the parasitoid's host selection process are evaluated in **Chapter 4** (host age selection) and **chapter 5** (host species selection). Results presented in **Chapter 4** show that host acceptance by *C. menes* and *C. americensis* was negatively correlated with size, age and stage of the larval host. Observations on the parasitoid’s behaviour showed that the extent to which a wasp could complete and attack and oviposit significantly decreased with increasing size (age) of host larvae. The apparent preference for small sizes of larvae is largely caused by defensive

reactions (walking away, wagging the abdomen, anal exudate production) upon an encounter to vehement resistance (wriggling, dragging) of the larvae when attacked and stung. In larvae smaller or equal to her own size, a wasp could manage its victim, whereas larvae larger than herself managed to escape prior or during an attack. The apparent preference for small and young host larvae is valuable for developing a mass-production system for thrips parasitoids, for the timing of releases in the greenhouse and, because only a small part of the population is prone to attack, has consequences for the population dynamics of the host and the parasitoid.

Although in a greenhouse grown crop *F. occidentalis* often is the major, but not the only thrips species around it is important to know the host preference of the parasitoids with respect to different species. No-choice tests, presented in **Chapter 5** show that differences in the behaviour and biology of both the host and the parasitoid species strongly influenced their development and fitness. On the species level as well as on the population level parasitoids differed in host acceptance behaviour, parasitoid developmental time and size of their offspring. *C. americensis* preformed best on its original co-evolved host *F. occidentalis*. *C. menes* consists of a large complex of regional populations, that either reproduce sexually or asexually. They differ morphologically, geographically, behaviourally and physiologically in their response to different geographical populations of thrips species, each of them having its unique characteristics.

Life-history studies performed on *C. menes* and *C. americensis* in the laboratory (**Chapter 6**) shows that developmental and reproductive biology were significantly affected by temperature and characteristic for each species / strain. It was found that immature developmental time took much longer when temperature decreased, in particular for *C. americensis*. Pupal development times in *C. menes* varied greatly at both temperatures for certain types (yellow) but not for others (brown). Both species have different reproduction strategies: *C. americensis* has a higher daily reproduction, but a shorter reproduction period, compared to various strains of *C. menes,* that reproduce less during a longer period. The population growth rates differed per species / strain and temperature, but where in almost all cases lower than (literature) data of *F. occidentalis*.

In **Chapter 7** it is shown that short-range host location by *C. menes* and *C. americensis* is positively affected by visual and chemical stimuli. Both species are attracted to yellow colours and were arrested on sites were larvae had been feeding. Wasps did react to the presence or damage inflicted by feeding of non-hosts, but arrestment did not seem to be very host specific: within a parasitoid species no difference was found in reaction to feeding spots of one host species, *Thrips tabaci* or another *F. occidentalis*. Parasitoid females were not attracted to the synthetic compounds of the alarm pheromone (decylacetate plus dodecylacetate) of western flower thrips in short-range flight tests, indicating a non-volatile effect.

In **Chapter 8** evaluation studies were performed on a larger scale: experimental and commercial greenhouses. In spite of repeated introductions in infested crops, either vegetables like sweet pepper and cucumber, or ornamentals like rose and potted plants, very low levels of parasitism were found. Searching efficiency and dispersal ability in a greenhouse crop were very low and parasitoids performed poorly under (temperate) greenhouse conditions. Both parasitoid species could maintain themselves, dispersed and reproduced at Dutch glasshouse conditions, but they were unable to reduce thrips populations to sufficiently low levels.

Finally, in **Chapter 9,** I summarise and discuss the main results of my research, placed in perspective of the pre-introduction criteria we used. It is concluded that, based on behavioural (host selection and searching efficiency), biological (climatic adaptation, development and reproduction capacity) and practical (mass-production) characteristics, thrips parasitoids have very limited prospects for greenhouse biological control for both seasonal inoculative and inundative release programmes in temperate and in Mediterranean greenhouses.

Samenvatting

Het voor u liggend proefschrift is het resultaat van een gezamenlijk Europees Onderzoeksproject “Biologische Bestrijding van Tripsplagen”. Dit project had als specifieke doelstelling het verzamelen, beoordelen, het in kweek brengen en commercieel toepassen van natuurlijke vijanden als biologische bestrijders van trips. Bij de beoordeling van natuurlijke vijanden zijn specifieke selectiecriteria toegepast, die in een eerder stadium van onderzoek naar biologische bestrijders van kasplagen reeds hun waarde hadden bewezen. Zelf heb ik gekeken óf en wélke mogelijkheden sluipwespen zouden kunnen bieden als biologische bestrijders van tripsplagen, en de Californische trips - *Frankliniella occidentalis* (Pergande) - in het bijzonder.

In **Hoofdstuk 1** geef ik een overzicht van de stand van zaken van onderzoek naar trips als plaagorganisme in kassen in Europa. In het bijzonder heb ik gekeken naar enkele belangrijke plaagsoorten zoals *F. occidentalis,* de tabakstrips - *Thrips tabaci* Lindeman - en twee andere soorten die ik heb onderzocht: *Frankliniella schultzei* Trybom en *Frankliniella intonsa* (Trybom). In dit overzicht zijn aspecten nader uitgewerkt zoals de geografische verspreiding en schade, de biologie, ecologie en bestrijdingsmogelijkheden van deze soorten. Vervolgens wordt de stand van zaken besproken wat betreft de meest mogelijkheden van een aantal belangrijke groepen biologische bestrijders: roofmijten, roofwantsen, entomopathogene schimmels en aaltjes. Vooral heb ik gekeken naar informatie die beschikbaar was over sluipwespen van trips, hun biologie, ecologie, parameters die de populatiegroei bepalen en hun vooruitzichten als potentiële bestrijders van tripsplagen in Europese kassen. Tot slot presenteer ik het doel van mijn onderzoek en opzet van dit proefschrift.

Bij aanvang van mijn onderzoek was geen enkele sluipwesp bekend van Californische trips. Mijn zoektocht naar sluipwespen van Californische trips, gepresenteerd in **Hoofdstuk 2**, begon met het verzamelen van parasieten in het oorsprongsgebied van Californische trips (VS) en in recent gekoloniseerde gebieden (Zuid-Europa). Ook sluipwespen van nauw verwante trips soorten, afkomstig van over de hele wereld, heb ik verzameld, met voorkeur uit streken met een klimaat dat vergelijkbaar is met dat in kassen van Noordwest Europa. Op basis van informatie over de gastheren en klimaatsfactoren, bleken vooral soorten die behoren tot het geslacht *Ceranisus* (Walker) perspectief te bieden. Deze soorten zijn bekend als solitaire parasieten van larven van trips soorten die nauw verwant zijn aan Californische trips. De belangrijkste soorten zijn *Ceranisus menes* (Walker) en *Ceranisus americensis* (Girault) (Hymenoptera: Eulophidae). Beide soorten zijn zogenaamde solitaire koinobionte endoparasieten van larven van trips, d.w.z. de sluipwesp ontwikkelt zich in het lichaam van de gastheer (larve), die door blijft groeien zonder dat het zichtbaar is dat ze is geparasiteerd totdat het popstadium is bereikt en uit een larve komt slechts een sluipwesp. Beide soorten planten zich ongeslachtelijk voort: alleen vrouwelijke nakomelingen worden geproduceerd.

Een belangrijke randvoorwaarde van een succesvol evaluatieprogramma, en uiteindelijk het opzetten van een massakweek, is de beschikbaarheid van een betrouwbare kweekmethode. Deze moet de bevoorrading met insecten van constante kwaliteit en kwantiteit garanderen. Essentieel is daarbij tevens dat larven in grote groepen van gelijke leeftijd beschikbaar zijn. In **Hoofdstuk 3** beschrijven en evalueren we methoden voor het kweken van verschillende soorten trips, zoals *F. occidentalis*, *F. intonsa, Thrips palmi* (Karny) en *T. tabaci*. (Thysanoptera: Thripidae) en parasitaire wespen. Met deze door ons ontwikkelde en verfijnde methode is het mogelijk met behulp van honingwater en stuifmeel, grote hoeveelheden larven te produceren van goede kwaliteit, met een relatief geringe investering wat betreft tijd. Deze methode blijkt ook zeer bruikbaar voor de kweek van sluipwespen, al is de opbrengst geringer en meer tijdrovend dan deze van trips.

Waarnemingen aan het gedrag en de ontwikkelingsbiologie van sluipwespen in het laboratorium vormen een belangrijk onderdeel in de evaluatie en selectie van nieuwe en betrouwbare biologische bestrijders. Specifieke aspecten van het gastheerselectieproces zijn beschreven in **Hoofdstuk 4** (invloed van de leeftijd van de gastheer) en in **Hoofdstuk 5** (invloed van de gastheersoort). Resultaten zoals gepresenteerd in **Hoofdstuk 4** laten zien dat gastheer-acceptatie door *C. menes* en *C. americensis* omgekeerd evenredig is met de grootte, leeftijd and stadium van de larve. Waarnemingen aan het gedrag van sluipwespen geven aan dat de mate waarin een wesp een eenmaal ingezette aanval met succes kan afronden met eileg, afneemt naarmate de larven groter (en ouder) zijn. Deze klaarblijkelijke voorkeur voor kleine larven is vooral het gevolg van afweerreacties (weglopen, heftig bewegen van het achterlijf, produceren van anale druppels) na een

ontmoeting met een larve en heftig verweer (kronkelen, zich wegsleuren) wanneer een larve wordt aangevallen. Als larven kleiner zijn dan de wesp of van gelijke grootte, kunnen deze gemakkelijk door haar worden overmeesterd, terwijl larven die groter zijn dan de wesp makkelijker vooraf of tijdens een aanval kunnen ontsnappen. Kennis van de voorkeur voor een bepaalde leeftijd of stadium van de larven is van belang voor het ontwikkelen van een goede massakweek methode, voor de timing van het uitzetten van sluipwespen in kassen, en heeft, omdat slechts een klein deel van de trips populatie aangevallen kan worden, belangrijke consequenties voor het verloop in populatieopbouw van de gastheer en de sluipwesp.

In kassen is *F. occidentalis* meestal de belangrijkste, maar vaak niet de enige plaag. Daarom is het belangrijk de weten of sluipwespen een voorkeur hebben voor een bepaalde gastheersoort of niet. Uit niet-keuze proeven blijkt (**Hoofdstuk 5**) dat verschillen in gedrag en biologie van zowel de gastheer als de sluipwesp de ontwikkeling en reproductief succes sterk beïnvloeden. Op soortniveau én op populatieniveau verschilden sluipwespen in gastheer acceptatie gedrag, ontwikkelingstijd en grootte van hun nakomelingen. *C. americensis* was meer succesvol op *F. occidentalis* dan op andere gastheersoorten. *C. menes* bestaat uit een complex van een groot aantal regionale populaties, die verschillen in morfologie, biologie en gedrag. De combinatie van verschillende geografische populaties van *C. menes* met verschillende geografische populaties van haar gastheren, resulteert in specifieke interacties, ieder met haar eigen unieke kenmerken.

In het laboratorium verrichte *life-history* studies aan *C. menes* en *C. americensis* (**Hoofdstuk 6**) tonen aan dat ontwikkeling en voortplanting karakteristiek zijn voor iedere soort en stam en in sterke mate beïnvloed worden door temperatuur. Bij lage temperatuur werd de ontwikkelingstijd van de jeugdstadia in sterke mate verlengd, vooral bij *C. americensis* was dit het geval. De ontwikkelingsduur van het popstadium van *C. menes* varieerde sterk afhankelijk van het kleurtype (geel of bruin) van de stam. Beide sluipwespsoorten hebben een andere voortplantingsstrategie: *C. americensis* heeft een hoger aantal nakomelingen per dag, maar haar voortplantingsperiode is korter dan van *C. menes.* Beide stammen van de laatstgenoemde soort planten zich langzamer voort, maar doen dit over een langere periode. De populatiegroeisnelheden verschilden per soort en per stam én temperatuur, maar was bijna altijd lager dan die van *F. occidentalis*.

Uit **Hoofdstuk 7** blijkt dat het zoekgedrag van *C. menes* en *C. americensis* over korte afstand positief beïnvloed wordt door visuele en chemische prikkels. Beide soorten worden vooral aangetrokken door een gele kleur en blijven langer zoeken op plaatsen op het blad waar larven hebben gegeten. Wespen reageerden op de aanwezigheid van vraatschade door gastheersoorten, maar deze reactie bleek niet soortspecifiek: een sluipwesp soort reageerde hetzelfde op vraatschade van *T. tabaci* als van *F. occidentalis*. Sluipwespvrouwtjes werden over korte afstand niet aangetrokken door de synthetische bestanddelen van het alarmferomoon (decylacetate en dodecylacetate) van Californische trips.

In **Hoofdstuk 8** heb ik de evaluatie op wat grotere schaal uitgevoerd, in experimentele en commerciële kassen. Ondanks herhaald uitzetten van sluipwespen in met trips besmette gewassen - groentegewassen zoals paprika en komkommer, siergewassen zoals roos en potplanten - bleef het niveau van parasitering laag. Beide sluipwespsoorten konden zich in de kas handhaven, verspreiden zich en vermeerderden, maar waren niet in staat tripspopulaties voldoende omlaag te brengen of te houden. Vooral de zoekefficiëntie en het vermogen zich in het kasgewas te verspreiden waren erg laag en sluipwespen presteerden zeer matig onder de onze (gematigde) klimaatsomstandigheden.

Tot slot vat ik in **Hoofdstuk 9** de belangrijkste resultaten van mijn onderzoek nog eens samen en bespreek deze aan de hand van de pre-introductie criteria die we hebben toegepast. Op basis van mijn onderzoek aan het gedrag (gastheerselectie en zoekefficiëntie), de biologie (aanpassing aan een gematigd kasklimaat, ontwikkelingssnelheid en reproductiecapaciteit) en praktische (massaproductie) eigenschappen, kom ik tot de conclusie dat sluipwespen slechts zeer beperkte vooruitzichten bieden als biologische bestrijders in seizoensinoculatieve en in inundatieve bestrijdingsprogramma's van tripsplagen in gematigde en in mediterrane kassen.

Riassunto

Questa tesi è il risultato di un progetto di ricerca europeo dal titolo 'Biological Control of Thrips Pests'. Gli scopi specifici del progetto sono consistiti nel raccogliere, valutare, riprodurre massivamente e impiegare commercialmente nemici naturali dei tripidi. Al fine di valutare i nemici naturali dei tripidi sono stati applicati specifici criteri di selezione. Tali criteri hanno dimostrato la loro validità in precedenti selezioni pre-introduttive di nemici naturali di molti altri fitofagi di colture protette. La mia parte nel programma di valutazione è stata inerente lo studio di parassitoidi imenotteri quali agenti di controllo biologico dei tripidi ed in particolare di *Frankliniella occidentalis* (Pergande) (Western Flower Thrips).

Nel **Capitolo 1** ho riassunto le informazioni disponibili sui tripidi fitofagi che comunemente hanno un ruolo chiave nelle colture protette in Europa. In particolare le osservazioni sono state dirette su *F. occidentalis*, *Thrips tabaci* Lindeman ed altre due specie *Frankliniella schultzei* Trybom e *Frankliniella intonsa* (Trybom). L'analisi è stata indirizzata alla loro distribuzione geografica e all'impatto economico, oltre a informazioni più generali sui tripidi relative alla biologia, all'ecologia ed ai metodi di controllo. Di seguito è discusso lo stato dell'arte dei più importanti gruppi di nemici naturali che sono attualmente valutati e/o impiegati come agenti biologici di controllo, ossia: acari predatori, antocoridi, microrganismi entomopatogeni e nematodi entomofilici. Particolare enfasi è stata data allo stato dell'arte degli imenotteri parassitoidi che attaccano i tripidi, sulla loro biologia, ecologia e ciclo biologico e sul ruolo che potrebbero avere nel controllo dei tripidi nelle serre europee. Infine ho presentato lo scopo del mio progetto di ricerca e la struttura di questa tesi.

Quando il progetto di ricerca ha avuto inizio, non si conosceva nessun parassitoide di *F. occidentalis*. Nella nostra ricerca di parassitoidi candidati, descritti nel **Capitolo 2**, è stato sviluppato un programma di monitoraggio che ha previsto rilevamenti su popolazioni di *F. occidentalis* nelle sue aree di distribuzione originali (USA) ed in nuove aree di invasione (Sud Europa). Durante i sopralluoghi sono stati raccolti parassitoidi connessi ai tripidi distribuiti in tutto il mondo, ma preferibilmente presenti nelle aree con condizioni climatiche simili a quelle delle serre del Nord-Est Europa. Sulla base degli ospiti e della distribuzione geografica rilevata in letteratura, sono state raccolte specie appartenenti principalmente al genere *Ceranisus* (Walzer), endoparassitoidi larvali di specie di tripidi simili a *F. occidentalis*. La collezione di campioni ha permesso di raccogliere alcune specie di parassitoidi e vari ceppi geografici, di cui le principali specie sono state *Ceranisus menes* (Walker) e *Ceranisus americensis* (Girault) (Hymenoptera: Eulophidae). Sono entrambi endoparassitoidi coinobionti solitari di larve di tripidi a riproduzione partenogenetica.

Una fase critica in ogni programma di valutazione, è lo sviluppo di un adeguato e idoneo sistema di allevamento, che permetta una standardizzazione nella produzione di quantità sufficienti di insetti di qualità costante. Per l'esecuzione di test di laboratorio sui tripidi e sui parassitoidi, ed infine per la loro produzione commerciale, è infatti essenziale la disponibilità di grandi quantità di larve coetanee. Nel **Capitolo 3** sono descritti e valutati metodi di laboratorio per l'allevamento di diverse specie di tripidi quali, *Frankliniella occidentalis, F. intonsa, Thrips palmi* (Karny) e *Thrips tabaci* Lind. (Thysanoptera: Thripidae) e dei loro parassitoidi. Il metodo basato sull'impiego di soluzioni di miele e polline di pino, permette di ottenere grandi numeri di tripidi di buona qualità, con un investimento di tempo relativamente basso. Questo metodo è risultato adeguato anche per l'allevamento dei parassitoidi, sebbene sia apparso meno efficiente in termini di resa e di tempo speso.

Alcuni criteri di base per la selezione pre-introduttiva di organismi utili, sono basati sul risultato del comportamento e lo sviluppo di interazioni con i loro ospiti bersaglio in esperimenti di laboratorio. Nei **Capitoli 4 e 5** sono valutati specifici aspetti legati al processo di selezione dell'ospite di un parassitoide: selezione dell'età dell'ospite (**Capitolo 4**) e selezione della specie ospite (**Capitolo 5**). I risultati presentati nel **Capitolo 4** relativi ai due parassitoidi *C. menes* e *C. americensis*, mostrano una correlazione negativa nell'accettazione dell'ospite per la taglia, l'età e lo stadio di sviluppo dalla larva ospite. Le osservazioni sul comportamento dei parassitoidi hanno mostrato che la capacità dell'imenottero di attaccare, ovideporre e completare lo sviluppo, diminuisce significativamente con l'aumento della taglia (età) della larva ospite. L'evidente preferenza del parassitoide per larve di tripide di piccola taglia è causata in larga misura dalle reazioni difensive (fuga, dondolamento dell'addome, produzione di essudati anali), durante incontri

in cui si manifesta una forte reazione di difesa (contorcimento, trascinamento) delle larve di tripidi quando sono attaccate e ferite. Con larve di taglia inferiore o uguale a quella dell'imenottero, il parassitoide può gestire la sua vittima, mentre larve di taglia maggiore riescono a scappare prima o durante un attacco. La forte preferenza del parassitoide per larve ospiti giovani e quindi piccole, è però onerosa per lo sviluppo di un sistema di produzione massale, oltre a rendere più complesso il sincronismo nel lancio dei parassitoidi in serra, a causa del fatto che solo una piccola parte della popolazione è incline all'attacco, comportando quindi conseguenze sulla dinamica di popolazione dell'ospite e del parassitoide. Sebbene *F. occidentalis* sia spesso la specie più abbondante sulle colture in serra, non è la sola specie di tripide presente, quindi è importante conoscere la preferenza del parassitoide verso diverse specie di tripidi. Il no-choice test descritto nel **Capitolo 5** mostra che le differenze nel comportamento e nella biologia sia dell'ospite che del parassitoide influenzano fortemente il loro sviluppo e la loro salute. Il comportamento del parassitoide nell'accettazione dell'ospite, così come il suo tempo di sviluppo e la taglia della progenie è differente sia in relazione alla specie che alle popolazioni degli imenotteri. Ad esempio *C. americensis* ha mostrato migliori risultati su *F. occidentalis,* ospite su cui si è coevoluto*. C. menes* risulta come una specie rappresentata da un insieme complesso di popolazioni regionali, che si possono riprodurre sia sessualmente che parteno-geneticamente. Queste differiscono fra loro morfologicamente, geograficamente, sul comportamento e sulla fisiologia, oltre che sulla risposta a diverse popolazioni geografiche delle specie di tripidi, ciascuna di esse mostra quindi caratteristiche specifiche e uniche.

Gli studi condotti in laboratorio sulla life-history di *C. menes* e *C. americensis* (**Capitolo 6**) mostrano che la temperatura e le caratteristiche di ciascuna specie/ceppo influenzano significativamente lo sviluppo e la riproduzione dei due parassitoidi. In particolare si è visto come i tempi di sviluppo del parassitoide siano molto più lunghi quando le temperature diminuiscono e ciò risulta più evidente per *C. americensis*. Lo sviluppo pupale di *C. menes* invece, varia grandemente alle temperature studiate per alcuni tipi/ceppi (gialli), ma non in altri (bruni). Le due specie di parassitoidi hanno diverse strategie riproduttive: *C. americensis* ha una elevata attività riproduttiva giornaliera, ma un breve periodo riproduttivo rispetto a vari ceppi di *C. menes,* i quali invece si riproducono di meno ma durante un periodo più lungo. Il tasso di crescita delle popolazioni dei parassitoidi è diverso per specie/ceppo e temperatura di allevamento, ma in generale è risultato inferiore rispetto ai dati di letteratura relativi al tasso di crescita di *F. occidentalis*.

Nel **Capitolo 7** si evidenzia come la localizzazione dell'ospite in un breve raggio da parte di *C. menes* e *C. americensis* è influenzata positivamente da stimoli visivi e chimici. Entrambe le specie sono attratte dai colori gialli e si fermano laddove le larve di tripidi stanno mangiando. Gli imenotteri reagiscono quindi alla presenza del danno sulla pianta causato dalle punture di alimentazione dei tripidi, ma la risposta di fermarsi non è specifica per l'ospite: non si rilevano differenze intraspecifiche nei parassitoidi in relazione a punture di alimentazione di *F. occidentalis* o di *T. tabaci*. In prove di volo a breve raggio, le femmine dei parassitoidi non hanno mostrato alcuna attrazione verso i componenti sintetici del feromone di allarme (decylacetato e dodecylacetato) di *F. occidentalis*, indicando quindi che non vi è nessun effetto volatile. Studi di valutazione svolti su larga scala, ossia in serre sperimentali e commerciali, sono presentati nel **Capitolo 8**. Nonostante le introduzioni ripetute dei parassitoidi in colture infestate dai tripidi, sia orticole come peperone e cetriolo, che ornamentali, quali rosa e piante in vaso, sono stati rilevati bassi livelli di parassitizzazione. Entrambe le specie di parassitoidi hanno mostrato scarsa capacità di ricerca dell'ospite e scarsa abilità di disperdersi nella coltura in serra; i parassitoidi sono risultati poco efficienti nelle condizioni (temperate) di serra. Entrambe le specie dei parassitoidi sono comunque in grado di mantenersi, disperdersi e riprodursi nelle condizioni di serra olandesi, ma non sono risultati idonei a contenere le infestazioni di tripidi a livelli sufficientemente bassi.

Nel **Capitolo 9**, infine, ho riassunto e discusso i principali risultati della ricerca, visti in relazione ai criteri di valutazione pre-introduttivi usati. Si conclude che, sulla base delle caratteristiche del comportamento (selezione e capacità di ricerca dell'ospite), della biologia (adattamento climatico, capacità di sviluppo e riproduzione) e della praticità (produzione massale), i parassitoidi di tripidi hanno limitate prospettive per un loro impiego nel controllo biologico dei tripidi in serra, sia con lanci inoculativi stagionali che con programmi di lanci innondativi, nelle zone temperate così come in quelle Mediterranee.

Nawoord

Spannend was het tot op het laatst. Uiteindelijk ligt het proefschrift er dan toch en zetten we de laatste punt onder het '!'. De laatste letters, eens waren ze van lood, nu vederlicht. Hoe langer het duurt, hoe langer ook de lijst van mensen, die op directe of indirecte wijze, in meer of in mindere mate, aan de totstandkoming van dit proefschrift hebben bijgedragen. Een aantal van hen heb ik in de afzonderlijke hoofdstukken reeds vermeld, hier wil ik graag vooral degenen bedanken, die als vele kleine tandwielen het hele raderwerk in beweging hebben gehouden. In 1990 ben ik voor het eerst begonnen bij Entomologie, vervolgens aan een ander project gewerkt en weer teruggekomen. Een aantal mensen zijn dan ook inmiddels van baan veranderd, genieten van hun pensioen of vut, of hebben anderszins hun draai gevonden.

Allereerst wil ik mijn promotor, Joop van Lenteren, bedanken: zonder hem zou het project niet zijn begonnen en misschien ook niet met een proefschrift zijn afgerond. Zijn enthousiasme, kennis, inzet en leessnelheid waren een onmisbare schakel in het geheel. Joop, bedankt voor je vertrouwen.

Koppert Biological Systems wil ik bedanken voor het in gang zetten en mede financieren van het oriënterend onderzoek dat aan het eigenlijke project is voorafgegaan. Ook tijdens de vervolgfase heb ik meermaals een beroep op de ervaring en deskundigheid van Willem Ravensberg, Jeroen van Schelt en Sandra Mulder mogen doen.

Most of the work presented here, is the result of a joint collaboration with partners from Spain and Italy. Cristina Castañé and Jordi Riudvets (IRTA – Cabrils) I thank for helping me with sending field samples, discussing the project results and sharing their experience. Special thanks go to Maria Grazia Tommasini (BioLab, now CRPV - Crop Production Research Centre, Cesena - Italy), for sharing the ins and outs on *Orius*, and her inspiration during the finishing of my thesis, sharing its pitfalls and making the 'riassunto'. A special acknowledgment goes to the late Giorgio Nicoli (Bologna – Italy), to whom I also dedicate this thesis: I miss his friendship, inspiration, his hand around my shoulder, his laugh when sitting on the balcony of the oldest pizzeria in Naples.

Riding the waves of an invasive species like western flower thrips, I was part of a scientific boost of research on thrips, soon becoming an 'expert'. It also allowed me to travel and visit various countries and to present and discuss my results and meet many fellow researchers. Some contacts were short, others were more intense. Because mentioning all would result in a long list of colleagues that helped me out in some respect completing my research work, most of them I have acknowledged in the specific chapters in the thesis itself. Some I like to call into the light again here. Tamotsu Murai (Research Institute for Bioresources, Okayama University, Japan) I greatly thank for putting me on the right track, for the exchange of insect material, ideas and results: it was a great pleasure working and discussing thrips and parasitoid work with you. Serguei Trjapitsyn (UC Riverside, California) I like to thank for the identification of *Ceranisus* species, en op mijn collega Bert Vierbergen (Plantenziektenkundige Dienst, Wageningen) deed ik nooit een vergeefs beroep om door mij verzamelde tripsen tot op soort te laten identificeren. Dick Peters (Leerstoelgroep Virologie, Wageningen Universiteit) ben ik dankbaar voor de vele discussies en zijn kritische blik (nee, tripsen worden niet kleiner wanneer ze op bonen worden gekweekt). Dank zij Joke Fransen kon ik mijn experimentele kasproeven in Aalsmeer uitvoeren en werd daarbij met enthousiasme geholpen door Jan Tolsma. Ook na afloop van de experimenten heeft hij nog de nodige follow-up waarnemingen gedaan. Chris Mollema en Greet Steenhuis (CPRO) hebben me meer dan eens uit de brand geholpen wanneer de kweek van Californische trips volledig op haar gat lag.

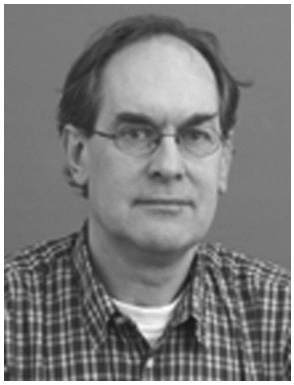
Mijn speciale dank gaat ook uit naar Hanneke van Heest, die met veel inzet de duizenden tripsen en sluipwespen heeft verzorgd en opgeleverd. Ofschoon we niet altijd op dezelfde golflengte zaten, ben ik zeer tevreden met ons uiteindelijk resultaat! Leo Koopman zorgde vaak voor praktische 'last-minute' oplossingen en de levering van schone planten en Wim den Dunnen en Henk Smid (Unifarm) voor de opkweek daarvan. Ofschoon de administratie van Entomologie inmiddels geheel is veranderd wil ik de 'oude garde' - Ans Klunder, Ineke Kok en Truus de Vries – alsnog bedanken voor allerlei administratieve wissewasjes die moesten worden geregeld ten behoeve van het project. Yde Jongema kon ik met zekere regelmaat lastig vallen met vragen over sluipwespen, en Dick Rozeboom sprong vaak te hulp wanneer er kooien en kooitjes van de meest verschillende afmetingen gemaakt moesten worden. Ik zou bijna Sinterklaas vergeten…. voor de bijna jaarlijkse stokjes zoethout!

Wie promotiewerk doet, parasiteert voor een belangrijk deel op het enthousiasme en inzet van een bonte mengeling van studenten van diverse herkomst: in chronologische volgorde hebben Anne Paris, Isabel Silva, Jeroen Sytsma, Kaska Banasik, Mila Mazáková, Lenka Korousova, Wim Veldhuis, Ronald Driessen, Anita Pákozdi, Gerard van Leeuwen en Merchi Reboredo-Prol in belangrijke mate aan verschillende onderdelen bijgedragen. Hun aanwezigheid illustreert ook de bijzondere omstandigheden en de gemeenschap waarin op het Laboratorium voor Entomologie wordt gewerkt: een internationaal mekka van kennis, creativiteit en enthousiasme. Van mijn medepromovendi van weleer heb ik genoten van hun scherpte en inzet tijdens aio-oio-wittevlieg-trips-lunches, met name Susanne Sütterlin, Herman van Roermund, Ellis Meekes, Yu Tong Qiu en Isabel Silva wil ik bedanken voor hun bijdragen. Van de mensen van de nieuwe generatie promovendi wil ik Tréfi bedanken voor haar hulp bij allerlei zaken die bij de afronding van mijn proefschrift komen kijken en Tibor Bukovinszky voor zijn hulp bij het vervaardigen van de omslag van dit proefschrift. Ongetwijfeld vergeet ik iemand…

Tot slot.. Lois, Romi, Oskar, Viktor en Sofia, - allemaal geboren tussen de start van het project en de afronding daarvan met dit proefschrift - jullie weten inmiddels (of over een tijdje) wat tripsen en sluipwespen en andere insecten zijn, maar jullie weten ook wat het schrijven van een proefschrift veel extra werk betekent. Het meest blij ben ik met jullie. Jeannette, bedankt voor je onverzettelijkheid en je groot talent voor organisatie.

Wageningen, juli 2003
Antoon Loomans

Curriculum Vitae



Born on the 16th of July 1954 in Geldrop - Noord-Brabant as Antonius Johannes Maria Loomans, I grew up in Lierop in the midst of fields, forests and farms. Nature and agriculture were my knife and fork. Almost first child of the 'Mammoetwet' I graduated from Carolus Borromeus College in Helmond in 1973 and moved to the Landbouwuniversiteit in Wageningen. My interest in a biological, yet practical, approach of nature and agriculture, was translated into a choice for "Plantenziektenkunde" (Plant Protection) with emphasis on Entomology. During my masters I studied spider phenology and ecology of e.g. *Lepthyphantes*, parasitoid behaviour of *Leptopilina* and field ecology of *Leptinotarsa* from which I graduated in 1988. In 1989 I started working on biological control of thrips, first as a guest scientist of Koppert Biological Systems at the Laboratory of Entomology of Wageningen Agricultural University, form 1991 onwards as a PhD student with Prof. dr. Joop van Lenteren. The research studies described in this thesis on the evaluation of parasitoids as biological control agents of thrips pests were initiated and performed under his supervision. From 1996 till 1998 - and a nose for "always selecting the wrong organism and topic" (as stated by a producer) - I was appointed as a guest scientist at the Entomology section of the Plant Protection Service, Wageningen. There I have been working in a project on *Thrips palmi*, evaluating its host specificity, fytosanitary risks and biological control options. In 1998, I again followed my nose, as mentioned before, and turned back to the Laboratory of Entomology of Wageningen University, where I worked on the evaluation of environmental risks of introducing biological control agents into Europe. Since November 2002, I am employed as a (temporary) senior scientist at the Plant Protection Service, Wageningen, continuing the work on ecological risk assessment of biological control agents.

Op 16 juli 1954 werd ik als Antonius Johannes Maria Loomans geboren in Geldrop, Noord-Brabant. Gedurende mijn jeugd in Lierop te midden van de natuur, bossen en boerderijen is de kiem voor mijn latere interesse ontsproten. Na het behalen van het VWO diploma aan het Carolus Borromeus College in Helmond vertrok ik in 1973 naar de Landbouwuniversiteit in Wageningen. Mijn interesse voor de biologie en praktische benadering daarvan zag ik het best vertaald in de Plantenziektenkunde met af en toe een uitstapje naar de ecologie. Het zwaartepunt kwam te liggen op de Entomologie, met een sterk accent op de biologische bestrijding van plagen, ziekten en onkruiden. Na vele jaren rondde ik mijn studie af, en begon in 1989 als tijdelijk onderzoeker voor Koppert Biological Systems mijn werk aan het Laboratorium voor Entomologie, toen nog Landbouwuniversiteit Wageningen. Van 1991 tot en met 1995 heb ik onder begeleiding van Prof. dr. Joop van Lenteren in internationaal verband gewerkt aan biologische bestrijding van trips. Ook van 1996 tot en met 1998 heb ik met veel plezier bij de Plantenziektenkundige Dienst te Wageningen, onder leiding van Dr. Berend Aukema, gewerkt aan toetsing van de waardplantspecificiteit, risico's en biologische bestrijding van *Thrips palmi*. Mijn neus voor maatschappelijk controversiële organismen en onderwerpen achterna, keerde ik in 1998 terug naar het Laboratorium voor Entomologie, inmiddels Wageningen Universiteit. Gedurende ruim 4 jaar heb ik daar in Europees verband gewerkt aan de evaluatie van de ecologische risico's van uitheemse biologische bestrijders. Sinds november 2002 ben ik ook op dit terrein werkzaam, als senior onderzoeker, opnieuw bij de Plantenziektenkundige Dienst.

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Ceranisus menes female attacking a thrips larva & male *C. menes* (front)
Ceranisus menes females, yellow colour-type bottom left and brown colour-type upper right (back).