

**Evaluation of *Orius* species for biological control of
Frankliniella occidentalis (Pergande)
(Thysanoptera: Thripidae)**

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**Evaluation of *Orius* species for biological control of
Frankliniella occidentalis (Pergande)
(Thysanoptera: Thripidae)**

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Proefschrift

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M.Grazia Tommasini

Chapter 1. INTRODUCTION

¹

Abstract

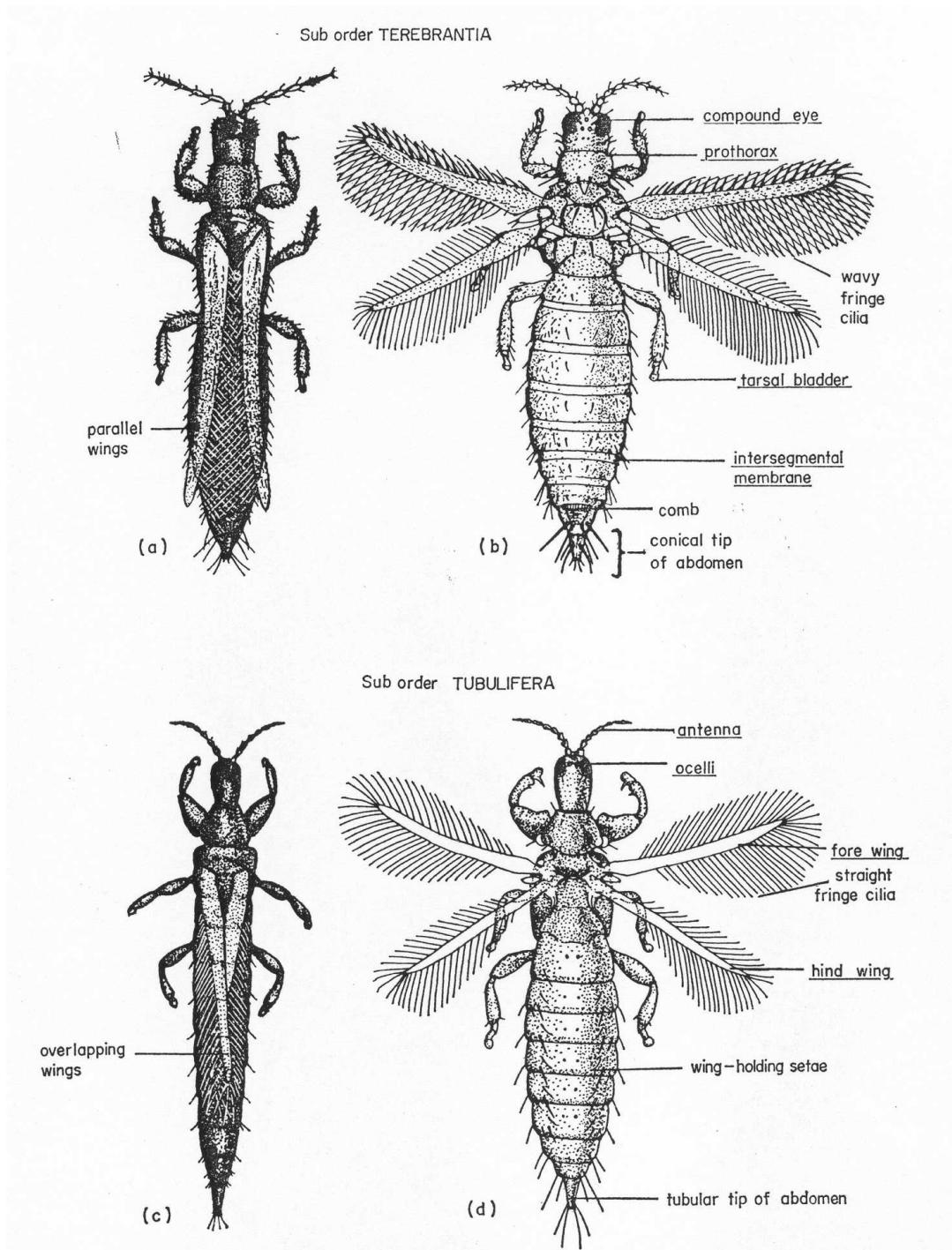
In this introduction the status of the thrips pest species in Europe and in particular of *Frankliniella occidentalis* (Western Flower Thrips), the most important pest thrips in Europe nowadays, is presented based on literature information up to 2000. Different thrips genera are mentioned amongst the Terebrantia suborder and of the Thripidae family: *Thrips*, *Taeniothrips*, *Heliothrips*, *Parthenothrips*, *Hercinothrips* and two genera of the sub-order Tubulifera, family Phlaeothripidae: *Liothrips* and *Haplothrips*. Information regarding the biology, distribution and host plants of thrips are summarized. The damage induced by thrips, in relation to the different parts of the plant attacked, is discussed. The indirect damage as well as transmission of viruses, bacteria and fungi is described. Regarding *F. occidentalis* (Western Flower Thrips), also systematic notes and a detailed description of its biology, its distribution in Europe, of the plants damaged world-wide and in Europe in particular, is provided. The typical injuries inflicted by *F. occidentalis* on different crops are discussed. Methods of sampling are shortly described. The different methods to control *F. occidentalis* are summarized. *F. occidentalis* is difficult to control chemically and treatments have to be repeated frequently, causing residue problems on food and disruption of Integrated Pest Management programs against others pests. A biological control system can reduce both the pest population and virus incidence. The main candidates as natural enemies for control of thrips emerging from this literature study and from an evaluation of all present data, are Phytoseidae and Anthocoridae.

1.1. Introduction

Thrips is the common name given to insects of the order of Thysanoptera (*thusanos* (Greek), a fringe; *pteron* (Greek), a wing). The order includes over 5,000 species, most of which are small in dimension and slender in body (in temperate regions the length generally ranges from 1-2.5 mm) with a distinct head (Palmer *et al.*, 1989). Morphology of the mouth parts differs from one family to another but feeding behaviour is generally similar, being characterized by rasping, puncturing and sucking (Borden, 1915). One oddity of the behaviour of some thrips species is that occasionally they can attack man by piercing the skin (Bailey, 1936). The front and hind wings are very slender, featuring a wide fringe of hairs and only a few veins or none at all. Wing length varies according to group, species and sex. Macropterous, brachypterous and sometimes apterous adults can all be encountered. In the sub-order of Terebrantia the wings lie parallel to each other while in the Tubulifera sub-order they are overlapping so that only one is completely visible (Figure 1). The mouth parts of these insects are typically asymmetrical, presenting maxillary and labial palps (Mound, 1971). The antennae are short and usually comprise from six to nine segments. The eyes are compound and three ocelli are present on the top of the head. The legs feature single- or double-segmented tarsi ending in a vesicle (or bladder).

¹ This introduction is largely based on the following paper: Tommasini M.G. and Maini S., 1995. *Frankliniella occidentalis* and other thrips harmful to vegetable and ornamental crops in Europe. Agricultural University Wageningen Papers 95 (1): 1-42.

Figure 1: Living (left-hand side) and mounted (right-hand side) thrips of the two sub-orders compared (from Lewis, 1973).



The abdomen is divided into eleven segments but only ten are visible. The end segments of Terebrantia usually taper to a cone in females and are bluntly rounded-off in males, whereas in both sexes of Tubulifera the tenth segment forms a tube ending in a terminal whorl of setae.

Details of the structure of external genitalia have been described by Melis (1935), Doeksen (1941), Jones (1954) and Priesner (1964). Terebrantia feature a more marked sexual dimorphism than Tubulifera, with males being smaller and of paler colour.

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Thrips reproduction is either partially or totally parthenogenetic. Either way, the various species are all either arrhenotokous or thelytokous and, according to most authors, females are always diploid and males haploid (Lewis, 1973). As in all typically bisexual thrips species, adults usually mate within two or three days after the last pupal moult, each male being capable of fertilizing more than one female. The sexes locate each other by means of a sensory cone situated at the top of the antennae. Most thrips are oviparous. The white or yellowish coloured eggs are cylindrical and bean shaped and large with respect to the size of the female body. The eggs of *Tubulifera* are larger than those of *Terebrantia*, each sub-order also featuring a different egg-laying behaviour. Both, zoophagous and phytophagous *Terebrantia* species, insert isolated eggs into the plant tissue by means of an ovipositor. The *Tubulifera* species, that have no saw-like ovipositor generally attach the eggs onto plant surfaces by means of gelatinous substances. Egg mortality is usually greater in *Tubulifera* than in *Terebrantia*.

There are four or five instars between egg and adult; generally four in *Terebrantia* and five in *Tubulifera*, as shown in figure 2. Usually, the first two feeding instars are called larvae and the subsequent, non-feeding ones, pupae. There are various objections to the use of this terminology to describe the growth of these insects, as some aspects of the development of thrips resemble more that of hemimetabolous insects (*i.e.* exopterygote), whose young are called nymphs, rather than that of holometabolous ones, (*i.e.* endopterygote), whose young are called larvae. Nevertheless, the term larvae is generally used and has therefore become well established, so adoption of a new term runs the risk of generating more confusion (Lewis, 1973). The subsequent stages of development are: egg, larvae I, larvae II, prepupa, pupa I, pupa II (only for *Tubulifera*) and adult. It should be noted that in French the developmental instars are indicated as *I stade larvaire*, *II stade larvaire*, *pronymph*, *nymph* and *adulte* (Bournier, 1983), in Italian: *neanide I*, *neanide II*, *prepupa* or *preninfa*, *pupa* or *ninfa*, *adulto* (Grandi, 1951), in Spanish: *larva I*, *larva II*, *proninfa*, *ninfa* and *adulto* (Lacasa, 1990b).

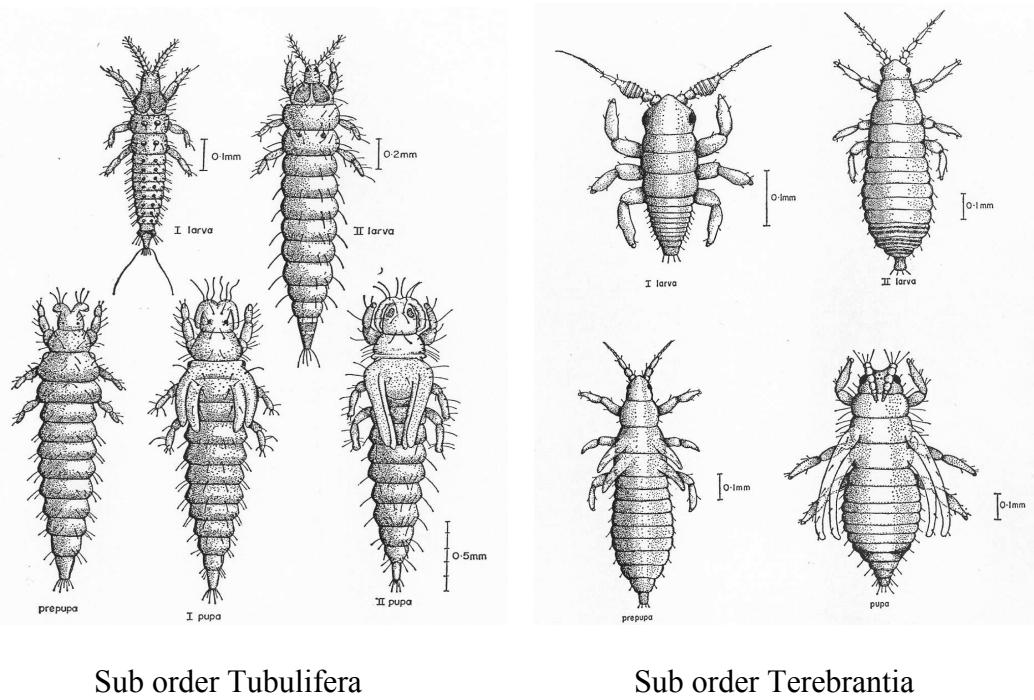
Pupation normally takes place in the soil or under fallen and decayed plant tissues near host plants, within which the insect usually builds a pupal cell, while several *Terebrantia* species dwell in leaves.

The detailed life history of several thrips pest species is summarized in section 1.3.2.

1.2. Methodology

We have used a computerized bibliographical search to find what has been published on Thysanoptera and their natural enemies, using the key words: Thysanoptera, *F. occidentalis* and *T. tabaci* combined with predator, biological control and natural enemies. Additional references not directly related to these key words are not expected to be exhaustive. The computerized information was obtained mostly from the databases: CAB abstracts (on line) 1972-1983; CAB abstracts CD ROM, 1984-00; BIOSIS 1969-91/may; PASCAL 1983-91/june; SCI 1980-90; AGRIS 1975-90; LIFE-SCI 1982-90; AGRICOLA 1970-91/april; CRIS/ICAR 1991/March; Review of Applied Entomology, Series A, Vol. 67-77 (1979-89); Review of Agricultural Entomology, Vol. 78-79(7) (1990-91).

Figure 2: Immature stages of *Haplothrips leucanthemi* (Schrink) = *niger* (Osborne), a typical Tubulifera on the left side, immature stages of the bean thrips (*Caliothrips fasciatus* Perg.), a typical Terebrantia on the right side (from Lewis, 1973).



As I concentrated my research on biological control of thrips with predators, the literature study was extensive for predators as well. The main attributes which I summarized for each natural enemy are:

(1) Geographic distribution, prey insects upon which they fed, and plant species on which they have been found.

(2) Life history which includes:

- field studies on natural control,
- their biology and behaviour,
- results of practical application of biological control programs where those species were applied,
- natural enemies of the predators,
- possibilities for rearing the natural enemy

1.3. Thrips pests species in Europe

As stated above, the Thysanoptera order includes over 5,000 species. The order is subdivided into two sub-orders, namely Tubulifera, which only includes a single family (Phlaeothripidae) and Terebrantia, which comprises four families (Aeolothripidae, Thripidae, Merothripidae and Heterothripidae) (see Table 1) (Lewis, 1973).

Most crop damaging Thysanoptera belong to the family Thripidae of the sub-order Terebrantia. These include, for example, *Frankliniella occidentalis* (Pergande), *Thrips tabaci* Lind., *Heliothrips haemorrhoidalis* (Bouché), *Parthenothrips dracaenae* (Heeger), *Thrips*

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simplex Morison, *Thrips meridionalis* Pr., *Taeniothrips dianthi* Pr., *Thrips fuscipennis* Haliday, *Hercinothrips femoralis* (Reuter) and *Thrips palmi* Karny. Amongst the most common phytophagous thrips harmful to vegetable and ornamental crops, only *Haplothrips cottei* (Vuillet) and *Liothrips vaneeckeai* Pr. belong to the Phlaeothripidae family of the Tubulifera sub-order. In particular, with regards ornamental crops, *Thrips calcaratus* Uzel, *Dendrothrips ornatus* (Jabl.), *Gynaikothrips ficorum* (Marchal) and *Thrips laricivorus* (Kratochvil and Farsky) should be noted for the damage they cause to lime, laurel, *Ficus microcarpa* L. and larch, respectively.

1.3.1 *Frankliniella occidentalis* (Pergande) (Terebrantia, Thripidae, Thripinae)

1.3.1.1 Systematic notes

The literature about *F. occidentalis* (Western Flower Thrips = WFT) was reviewed by Mantel (1989) and covers all the references, supplied with keywords, until September 1st, 1988. Here, Mantel's (1989) information is integrated with that of Brødsgaard (1989a) and new information.

The *Frankliniella* genus was described by Karny in 1910. It had initially been classified as *Thrips* by Linnaeus in 1758. In 1881, Targioni-Tozzetti introduced the name *Euthrips* and in 1895 Uzel called the genus *Physopus*, until its current name, which is still generally accepted (Bryan and Smith, 1956), was established by Karny (1912). Synonyms which have been employed over the years for *Frankliniella occidentalis* include, as reported by Oliver and Baker (1987):

- Euthrips occidentalis* Pergande, 1895
- Euthrips tritici* Crawford, 1909
- Euthrips tritici* var. *californicus* Moulton, 1911
- Euthrips helianthi* Karny, 1912
- Frankliniella helianthi* Karny, 1912
- Frankliniella tritici* var. *moultoni* Hood, 1914
- Frankliniella tritici occidentalis* Watson, 1919
- Frankliniella tritici californica* Watson, 1923
- Frankliniella moultoni* Morgan, 1925
- Frankliniella claripennis* Morgan, 1925
- Frankliniella canadensis* Morgan, 1925
- Frankliniella trehernei* Morgan, 1925
- Frankliniella californicus* Moulton, 1929
- Frankliniella californica* Moulton, 1931
- Frankliniella venusta* Moulton, 1936
- Frankliniella obscura* Moulton, 1936
- Frankliniella chrysanthemy* Kurosawa, 1941
- Frankliniella californica* f. *trehernei* Moulton, 1948
- Frankliniella dahliae* Moulton, 1948

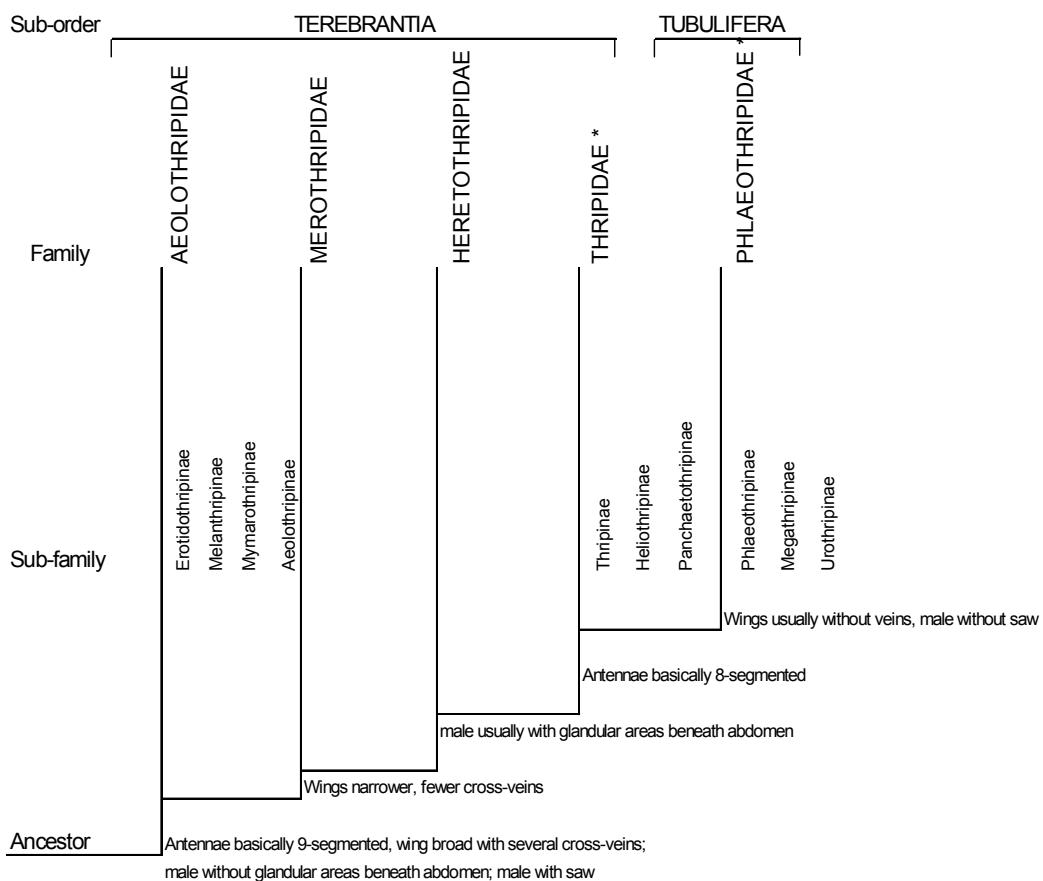
In the U.S.A., *F. occidentalis* is commonly called "Western Flower Thrips" (WFT) and "alfalfa thrips", but the latter name was not approved by the Entomological Society of America.

1.3.1.2 Origin and Distribution

F. occidentalis is a species of nearctic origin, first reported by Pergande (1895) in California on apricot and potato leaves, on orange flowers and various weeds. It was

subsequently reported in Florida on mango and bean crops (Morgan, 1913; Watson, 1918) and on citrus flowers (Childers and Beshear, 1992), in Canada (Treherne, 1923), in Utah (Pack, 1930; Maddock, 1949), in Alaska (Bryan and Smith, 1956), on Hawaii (Sakimura, 1972) and in Texas (Stewart, 1985) and can currently be found throughout the United States (Beshear, 1983; Frantz and Mellinger, 1990). In North America WFT was found from sea level to sub-alpine altitude (Bryan and Smith, 1956).

Table 1: Summarised classification of the order Thysanoptera based on Priesner (1964), with the main characteristics of families and affinities of sub-families (modified from Lewis, 1973; Palmer *et al.*, 1898). *: Family which include some thrips species encountered in protected crops.



Elsewhere, it has been encountered in New Zealand (Zur Strassen, 1973; Mound and Walker, 1982), Korea (Woo, 1974), Peru (Ortiz, 1977), Colombia and Costa Rica (Baker, 1988), South Africa (Giliomee, 1989), Kenya (Palmer *et al.*, 1989), Japan (Barletta, 1986; Anonymous, 1989b) as well as Israel and Canarian islands, where it has been detected since mid-1987 (Argaman *et al.*, 1989; Gokkes, 1991; Peña, 1990). In 1993 it was found in Australia too (Malipatil *et al.*, 1993).

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In Europe its first appearance dates back to 1983, when it was found in *Saintpaulia ionantha* Wendl. nurseries in the Netherlands (Van de Vrie, 1987; Mantel and Van de Vrie, 1988; Vierbergen and Ulenberg, 1988). Since its initial detection in Europe, it has spread rapidly to protected crops throughout the continent (Figure 3). It has been found in Sweden (Pettersson, 1986; Nedstam, 1987; Nedstam, 1989), in Norway (Taerum, 1988), in Finland in August 1987 (Brax and Lindqvist, 1989; Tiitanen and Markkula, 1989; Kurppa, 1989), in Germany in 1985 (Zur Strassen, 1986) and in the United Kingdom (Anonymous, 1986). In the United Kingdom it is no longer considered as a new pest to be absolutely eradicated, as it has definitely established itself in protected agroecosystems (Bartlett, 1991). Other European countries in which *F. occidentalis* is found, include Ireland (Dunne and O'Connor, 1989), France (Bournier and Bournier, 1987), where it has also been detected in open fields by Fougeroux (1988), as well as Belgium since 1987 (De Clercq, 1991), Czech Republic (Pelikan, 1989) and Poland since 1987 (Labanowski, 1991; Baranowski *et al.*, 1991; Nawrocka, 1991), Denmark since 1985 (Brødsgaard, 1989a), Spain (Lacasa, 1988a; Lacasa *et al.*, 1988; Lacasa, 1990a), Portugal since 1989 (Leite, 1990; Mateus, 1993) Switzerland since mid-1987 (Anonymous, 1989b; Ebener *et al.*, 1989), Hungary since 1989 (Jenser and Tusnadi, 1989; Szabo and Ceglarska-Hodi, 1991), in Greece in 1991 (Poditakis, pers. comm.) and in Crete (Poditakis *et al.*, 1993). Finally, it has also been reported by Postolovski (pers. comm.) in ex-Yugoslavia in 1991 and in Cyprus (Anonymous, 1992).

It was first reported in Italy by Rampinini in 1987, when it was detected in nursery-grown *Saintpaulia* in northern Italy. In 1988, some specimens of *F. occidentalis* were also found in Sicily, Sardinia, Calabria, Apulia, Latum and Campania on several nursery and field-grown vegetable crops as well as on protected ornamental crops (Ciampolini *et al.*, 1990). Reports have also come in from Tuscany, Liguria and South Italy where the pest has been detected on nursery and open field chrysanthemum, carnation and strawberry crops (Arzone *et al.*, 1989; Del Bene and Gargani, 1989; Viggiani and Jesu, 1989; Marullo, 1991), and from Sardinia (Luciano and Piga, 1988-92). *F. occidentalis* can currently be found in the Venetia, Lombardia and Emilia-Romagna regions as well, so that it can be considered to be present Italy-wide (Eordegħ, 1992; Ivancich Gambaro, 1995). Although it preferentially attacks protected crops, the pest can also be found on open field vegetable and ornamental crops.

1.3.1.3 Morphology and biology

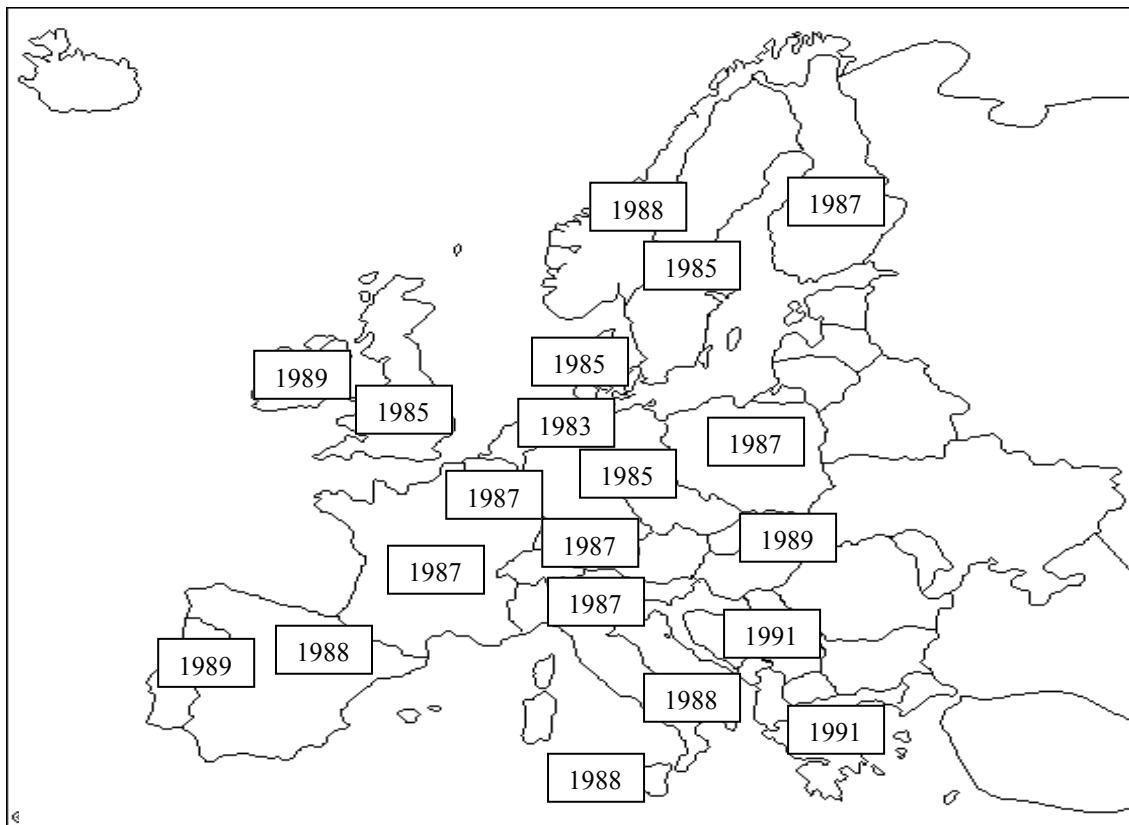
Identification of *F. occidentalis* can be done by using the following morphological keys developed by Moulton (1948), Mound and Walker (1982), Zur Strassen (1986), Bournier and Bournier (1987), Palmer *et al.* (1989) and Brødsgaard (1989a).

Lengthwise, the macropterous adult of *F. occidentalis* is characterized by the following measurements: 0.9-1.1 mm from the tip of the antennae to the tip of the abdomen in the male and 1.3-1.4 mm in the female. Both the young instars and the adult possess piercing and sucking mouthparts. The thrips feed by piercing leaf cells with the mandible and ingesting cell contents through the feeding tube formed by the maxillary stylets.

As in all Terebrantia thrips, the female of *F. occidentalis* features a saw-like ovipositor with which it drills holes into the parenchymal tissues of leaves, flowers and fruits, where it deposits a kidney-shaped opaque egg of 0.25 x 0.50 mm in size (Brødsgaard, 1989a). Three different colour forms of the polymorphic species *F. occidentalis* can be found in California (Bryan and Smith, 1956; Sakimura, 1962), one being black, one being pale and the other featuring an intermediate colour. The first two forms have a homozygous genotype while the third form has a heterozygous genotype. Only the females, which are diploid, feature all three of the possible chromatic phenotypes while the males, which are haploid, feature only the pale

colour. Bryan and Smith (1956) have demonstrated that this colour diversification is independent of host-plant variety but it is rather related to seasonal factors. Most of the darker varieties were found in California in spring, while the paler ones were found in summer and autumn. The third type, featuring an intermediate colour, was found throughout the whole year. The authors concluded that perhaps the darker variety was more resistant to low temperatures while the paler one to high temperatures. In northern Europe (Germany and The Netherlands) and in Italy, only the pale and intermediate colour types have been found except for a single case of the darker variety discovered in Denmark (Brødsgaard, 1989a).

Figure 3. Distribution of *Frankliniella occidentalis* in Europe.



F. occidentalis post-embryonic development involves two larval instars, as well as prepupa and pupa stages before the adult stage. The newly moulted larva is characterized by a glassy white colour and starts feeding immediately, becoming yellowish. As with all exopterigotes, the young instar is similar to the adult one in appearance except for the fact that it is wingless, has reddish eyes and antennae with fewer segments. Second instar larvae are more active than first instar larvae and feed more abundantly; up to three times more than during the first instar. The young second instar larvae is smaller than first instar but develop into adult size upon reaching maturity. During this stage, they take on a yellowish-waxy colour.

Upon maturity, the larvae display positive geotaxis together with negative phototaxis, moving away from the flower or the plant towards the soil (Arzone *et al.*, 1989). At a depth of between 1.5-2.0 cm, the larvae then develop into the prepupal stage (Arzone *et al.*, 1989).

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However, only a small percentage of the total *F. occidentalis* population in a greenhouse crop will be in the soil as pupae. The prepupa already features wing buds and antennae which, however, are shorter than in the adult and unsegmented. Prepupae have a whitish colour and are immobile unless disturbed. Upon developing into a pupa, the insect still remains under the soil surface, and features longer antennae which face backwards towards the abdomen. Initial segmentation of the antennae is already evident at this stage and the wing buds have also developed further. Pupae continue to remain immobile and do not feed. Adult dimensions are achieved by the end of the pupal stage.

The adult emerges upon the last moult and features a whitish colour which becomes progressively darker within 48 hours of moulting (Brødsgaard, 1989a; Del Bene and Gargani, 1989). Shortly after having emerged, the insect begins feeding voraciously. Adults start flying only 24 hours after emergence (Del Bene and Gargani, 1989). In the laboratory, WFT shows a sex ratio of 1:1, while in the open field the sex ratio is usually strongly female biased (Del Bene and Gargani, 1989). On average, just after three days from emergence, the females start to lay eggs at 20-25°C (Marullo and Tremblay, 1993).

The duration of development from egg to adult is closely related to environmental conditions, especially temperature. Table 2a presents the data concerning this relationship collected by several authors under different conditions. Recently a similar review was arranged by Jarosík and Lapchin (1998). In particular, the table shows findings as to insect development time as well as female fertility, which also seems to differ depending on climatic conditions and host-plant variety. The development time of WFT on cucumber at 25°C is longer (13.4 and 14.7 days, from egg to adult) (Mollema *et al.*, 1990; Gaum *et al.*, 1994) than on chrysanthemum at the same temperature (12.2 days) (Del Bene and Gargani, 1989). According to Jarosík *et al.* (1997), the lower developmental threshold for the pre-imaginal development of WFT on cucumber is 10.7°C. Photoperiod influence was investigated by Brødsgaard (1991). Little differences in the development time, in longevity and fertility of WFT were detected at constant temperature of 25°C and high air humidity (near 100%), as showed in table 2b. According to Lublinkhof and Foster (1977), fertility is more affected by temperature than by host-plant variety. Life-span is seen to diminish with increase in temperature. Although in 1936 Watts had found no difference in fecundity between mated and unmated *Frankliniella tritici* (Fitch) females, according to Robb and Parrella (1987) mated females seem to be more fecund than unmated ones. Pollen is so important from a nutritional and reproduction point of view that females fed on pollen have a net reproductive rate (R_o) four times as high as that of females fed solely on cotton leaves (Trichilo and Leigh, 1988). A positive pollen-effect on fecundity and larval growth of WFT was also found by Jager and Butôt (1993); in this case Chrysanthemum pollen was used. Life-span, however, does not seem to be affected by feeding behaviour (Brødsgaard, 1989a). Recently, life table data for *F. occidentalis* at different temperatures, were studied by Gaum *et al.* (1994) (Tab.2c), while a comparison of life-fertility tables between *F. occidentalis* and *F. fusca* at different temperature was done by Lowry *et al.* (1992). Reproduction of *F. occidentalis* occurs by facultative parthenogenesis, *i.e.* partly bisexual and partly parthenogenetic. Parthenogenetic reproduction is always arrhenotokous, unfertilized females laying eggs all of which develop into males, while most of the eggs laid by fertilized females develop into females (Brødsgaard, 1989a).

Both the adults and the young instars are thigmotactic and therefore particularly attracted to buds and complex flowers such as those of chrysanthemum, which offer protection and allow the insect to go deep into the plant. In Texas, both *F. occidentalis* and *T. tabaci*, overwinter in a dormant condition in protected locations such as under leaves or tree bark (Chambers and Sites, 1989). In Italy, adults overwinter in a state of quiescence protected under dry vegetable remains or immediately under the upper surface of the soil, even in open fields (Del Bene and

Gargani, 1989). In South Italy, South Spain and probably in other Mediterranean areas of infestation, WFT can have continuous generations in the greenhouse and outdoors. In a field situations with a temperature not below 5-6°C, it can overwinter on wild plants as *Amaranthus* L., *Chenopodium* L., *Solanum nigrum* L. and *Heliotropium europeum* L. (Marullo, 1991; Mateus, 1993). Unlike *T. tabaci*, *F. occidentalis* females have already mature eggs at the end of the winter.

Table 2b: Development time, preoviposition period, longevity and fertility of unmated *F. occidentalis* reared on bean leaves at three photoperiods, high air humidity and at constant temperature of 25°C (from Brødsgaard, 1991).

Parameter	Photoperiod (L:D hours)		
	4:20	8:16	16:8
Stage			
egg	3.55	3.59	3.50
1st instar	1.12	1.05	1.06
2nd instar	6.02	5.52	4.94
prepupa	1.18	1.15	1.05
pupa	2.88	2.61	2.59
egg to imago	14.75	13.92	13.15
egg to egg	16.65	15.45	14.80
Adult			
preoviposition period	1.90	1.53	1.65
longevity	13.32	9.63	10.80
fertility (offspring)	22.00	24.95	10.80

Table 2c: Life-table data for *F. occidentalis* at different temperatures on cucumber (from Gaum *et al.*, 1994)

Temperature (°C)	Σ_{mx}	R_0	r_m	T (days)	Sex ratio (% females)	day degrees for developm. (egg to adult)
15	2.24	1.02	0.002	12.69	55	274
18	2.64	2.54	0.11	8.79	58	253
20	5.24	5.00	0.21	8.06	61	242
23	6.68	5.77	0.30	6.15	69	228
25	5.20	6.04	0.30	4.58	64	245
30	9.48	8.48	0.51	4.32	86	257

R_0 = net reproductive rate; r_m = intrinsic rate of natural increase; T = mean generation time; Σ_{mx} = sum of average number of female offspring.

Table 2a: Biological traits of *F. occidentalis* at different temperatures and on different host plants.

Temper- ature (°C)	Host plant	Eggs (days)	1st instar (days)	2nd instar (days)	Prepupa (days)	Pupal stage (days)	Youth stages total (days)	Imago (days)	Preovi- position (days)	Ovipo- sition (days)	Fecundity no. eggs offspring	Source
12	Pepper	2-14	1-4	4-8	1-5	1-4	20	-	-	-	-	Lacasa, 1990b
15	Radish	13	7	12	4.2	8	44	90	3	30	40	Bryan and Smith, 1956
15	Bean	11.2	4.9	9.1	2.99	5.6	33.7	70.8	10.4	60	24.2	Lublinkhof and Foster, 1977
15	Chrysanthemum	10	5.6	11.5	3.6	8.6	39.	46	6.4	-	50	Robb, 1989
15	Cucumber	-	-	-	-	-	48	-	-	-	-	Gaum <i>et al.</i> , 1994
16.7	Chrysanthemum	3	2	4	2	3	14	45	-	-	300	Robb and Parrella, 1987
18	Cucumber	-	-	-	-	-	28.2	-	-	-	-	Jarosik <i>et al.</i> , 1997
18	Cucumber	-	-	-	-	-	28.4	-	-	-	-	Gaum <i>et al.</i> , 1994
20	Radish	6	3.3	5.7	2	4.8	21.8	40	3	0	65	Bryan and Smith, 1956
20	Bean	6.4	2.3	5.2	2.2	2.9	19	56.8	2.4	54	95.5	Lublinkhof and Foster, 1977
20	Chrysanthemum	6.6	2.9	9.5	2.2	5.1	26.1	75	2.1	-	26	Robb, 1989
20	Cucumber	-	-	-	-	-	21.9	-	-	-	-	Gaum <i>et al.</i> , 1994
20	Peanuts	-	-	-	-	-	18.7	-	-	-	-	Lowry <i>et al.</i> , 1992
21	Cucumber	-	-	-	-	-	27.3	-	-	-	-	Jarosik <i>et al.</i> , 1997
25	Chrysanthemum	3.2	1.7	4.8	1.1	2.7	12.9	31	1.7	-	136	Robb, 1989
25	Chrysanthemum	5	3	2-3	1-2	3-4	14-17	15	3	12	100	Arzone <i>et al.</i> , 1989
25	Chrysanthemum	2	2.1	4.4	1.7	2	12.2	30	3	25	30-40	Del Bene and Gargani, 1989
25	Pepper	3.2	2.44	4.9	1.8	4.1	16.4	332	2.5	28	33	Lacasa, 1990b
25	Bean	-	-	-	-	-	14.8	-	-	-	-	Brødsgaard, 1994b
25	Cucumber	-	-	-	-	-	14.7	-	-	-	-	Gaum <i>et al.</i> , 1994
25	Chrysanthemum	-	-	-	-	-	12.9	-	-	-	-	Robb and Parrella, 1991
25	Cucumber	-	-	-	-	-	12.4	-	-	-	-	Rijn <i>et al.</i> , 1995
26.7	Radish	4	2.3	3.8	1.1	2.7	13.9	40	-	-	-	Bryan and Smith, 1956
27	Cucumber	-	-	-	-	-	15.4	-	-	-	-	Soria and Mollema, 1995
27	Cucumber	-	-	-	-	-	13.9	-	-	-	-	Jarosik <i>et al.</i> , 1997
27	Pepper + pollen	-	-	-	-	-	10.5	-	-	-	-	Teulon, 1992
27.2	Chrysanthemum	3	(---4-2----)	0.9	2.3	10.2	34	1.7	-	-	229	Robb, 1989
30	Chrysanthemum	2.5	1.3	2.6	0.9	2	9.3	13	1.6	-	42	Robb, 1989
30	Bean	4.3	1.1	4.3	1.4	1.6	12.6	27.5	2.4	25	43.8	Lublinkhof and Foster, 1977
35	Chrysanthemum	2.4	1.4	3.3	1	1.9	10.7	9.5	1.4	-	5	Robb, 1989
35	Chrysanthemum	-	-	-	-	-	10.7	-	-	-	-	Robb and Parrella, 1991
36.7	Chrysanthemum	3	1	2	2	2	8	30	-	0	150	Robb and Parrella, 1987
18.5-36	Chrysanthemum	2.8	(---4-5----)	1.1	2.6	11.2	26.8	1.4	-	-	129	Robb, 1989

1.3.1.4 Infestation

F. occidentalis feeds on foliage and is anthophilous, even though it can also prey on *Tetranychus* spp. (Trichilo and Leigh, 1986; Pickett *et al.*, 1988). As Bailey (1938), Pickett *et al.* (1988) and Yudin *et al.* (1988) have observed, *F. occidentalis* prefers plants with flowers and in particular it prefers smaller and more intricate flowers (Bryan and Smith, 1956). In fact, when the photoperiod is unfavourable for the plant and prevents blooming, WFT populations diminish even to the point of not developing further (Arzone *et al.*, 1989). Most of the population colonizes the upper parts of the plant, where it settles until the crop is harvested (Lacasa, 1990b). Being an extremely polyphagous species, the insect feeds and reproduces on a wide range of wild plants, which are the vehicle through which crops are subsequently infested. In several crops, the edges of the cultivated fields are the first to be infested, while in orchards initial infestation of the flowers occurs from the weeds. Peak population is encountered in the hottest months of the year, while in temperate regions the insect tends to go into diapause during the winter months. Along the coastal regions of southern Spain, however, climatic conditions are such that *F. occidentalis* is to be found active even during winter months (Lacasa, 1990b). In Portugal, outbreaks of *F. occidentalis* were recorded in March-April and it increased during the summer (Mateus, 1993).

1.3.1.5 Host plants

Two hundred and forty four species of plants belonging to sixty two different families, and which include open-field ornamental, fruit, garden and agricultural crops, have been found to host *F. occidentalis* in the United States (Anonymous, 1989), a selection of which is listed in table 3.

Amongst non-European Mediterranean countries, data of crop infestation by *F. occidentalis* are available for Israel, where the insect has been reported on the following crops: *Rosa* L. spp. (rose), *Dianthus* L. spp. (carnation), *Gypsophila* L. spp., *Limonium* Miller spp., *Aster* L. spp., *Chrysanthemum* L. spp., *Ruscus* L. spp., *Solidaster* spp., *Impatiens* L. spp. (waxflower) (Gokkes, 1991).

In Europe, *F. occidentalis* has till now been found mostly on protected crops as indicated in table 4. During the last years, WFT occurred on an increasing number of plant species, including fruit trees, in different European countries (Nicolas and Bennis, 1993; Lacasa *et al.*, 1993; Torres Vila *et al.*, 1993; Leclant, 1994; Moleas *et al.*, 1996).

In Italy, *F. occidentalis* can also be found on weeds and indigenous wild plants, like *Anagallis arvensis* L., *Senecio vulgaris* L., *Papaver rhoes* L. (Del Bene & Gargani, 1989) and *Amaranthus*, *Chenopodium*, *Solanum nigrum* L., *Heliotropium europaeum* L. (Marullo, 1991). Recently I found *F. occidentalis* also on nectarine in northern Italy. In glasshouse areas in The Netherlands adults have been found during the summer period on garden plants like *Liathris* L. cultivars, *Aconitum napellus* L., *Aster novi-belgii* L.. Larvae were recorded from *Rosa* sp. (Mantel and Van de Vrie, 1988).

1.3.2 Other species

Morphological, biological and epidemiological characteristics of the main thrips species found in protected crops will be described, as these thrips species can occur concurrently with *F. occidentalis*, and can be controlled with the same natural enemies as used for *F. occidentalis*.

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Table 3: List of crops, ornamentals and fruit crops which are commonly infested by *F. occidentalis* in the United States.

Group	Host plant species	Reference
Crops	<i>Gossypium</i> L. spp., cotton	Hightower and Martin, 1956
	<i>Allium cepa</i> L., onion	Elmore, 1949
	<i>Carthamus tinctorius</i> L., safflower	Carlson, 1962; Anonymous, 1989
	<i>Fragaria vesca</i> L., strawberry	Allen and Gaede, 1963
	<i>Brassica oleracea</i> L., cabbage	Oatman and Platner, 1969
	<i>Lactuga sativa</i> L., lettuce	Yudin <i>et al.</i> , 1988
	<i>Capsicum annuum</i> L., pepper	
	<i>Lycopersicon esculentum</i> Miller, tomato	
	Cucurbitaceae	
	<i>Beta vulgaris</i> L., beet	
ornamentals	<i>Ducus carota</i> L., carrot	
	<i>Gladiolus</i> L. spp.	Weigel and Smith, 1933
	<i>Phurshia tridentata</i> , bitterbrush	Ferguson <i>et al.</i> , 1963
	<i>Leucaena glauca</i> Benth.	Yudin <i>et al.</i> , 1986
	<i>Rosa</i> L. spp., rose	
fruit trees	<i>Dianthus</i> L. spp., carnation	
	<i>Lathyrus odoratus</i> L., sweet-pea	Anonymous, 1989
	<i>Ficus carica</i> L., fig	Baker, 1939
	<i>Vitis</i> L. spp., grapevine	McNally <i>et al.</i> , 1985
	<i>Malus domestica</i> Borkh., apple	Venables, 1925
	<i>Prunus</i> L. spp., plum	
	<i>Armeniaca vulgaris</i> Lam., peach	
	<i>Prunus persica nucipersica</i> Scheid., nectarine	Anonymous, 1989

1.3.2.1 *Thrips tabaci* Lindeman (Terebrantia, Thripidae, Thripinae)

T. tabaci (onion thrips) is one of the species which features greatest intraspecific variability with regards to wing and body colour, ranging from light yellow to dark brown. The number of antennal segments is always equal to seven, of which the first is paler than the others. The main vein of the front wings features from 4 to 5 distal bristles, while no bristles are found on the abdominal sternites (Bournier, 1983). Insects born in winter are darker than their summer counterparts. Many biological studies have been conducted on this pest (Sakimura, 1932, 1937c; Harris *et al.*, 1936; Dimitrov, 1976b; Zawirska, 1976).

T. tabaci reproduction is by constant thelytokous parthenogenesis (Table 4). Males have never been found on protected crops in British and French populations (Morison, 1957; Bournier, 1983) and probably neither in the rest of Europe. Morison (1957) found some males in open fields in the UK, but not in greenhouses, and concludes that this thrips was incapable of bisexual reproduction in protected environments. Bournier (1983) has even gone so far as to hypothesize the existence of two strains, one of which is made up only of females and the

other of bisexual individuals with a sex ratio of 1:1. O'Neil (1960) suggests that parthenogenesis is the most common reproductive strategy employed by imported species as it is the easiest and most direct method of reproduction. A possible confirmation to O'Neil's hypothesis comes from the Near East, for example Iran, where this thrips is endemic and the sex ratio has been found to be 1:1 (Bournier, 1983), while in other parts of the world males are decidedly rare, for example in Hawaii, where 1 male has been found for every 1000 females (Sakimura, 1932), and in Sudan where out of 3000 females not one male was found (MacGill, 1927). According to O'Neil this species has originated in Central Asia, and, in fact, it was already known to be present in Egypt at the time of the Pharaohs (Chittenden, 1951). As with all thrips, the female lays eggs within plant tissues.

T. tabaci emerge from plant tissue through the tunnel drilled by the ovipositor. The first instars feature fewer antennal segments than the adults, while the integument, initially almost transparent, quickly develops pigmented spots depending on feeding patterns. Both first and second instars are extremely voracious. Pupal moulting normally takes place in the soil or humus around the hostplant within cells or on the plant itself. Duration of pre-imaginal stages is obviously a function of temperature (see Table 5).

The species features a number of ecotypes, each of which is polyphagous and can be hosted by a wide range of plants. In France, the insect has been found to reproduce parthenogenetically, and while it has never been found on tobacco, it has been reported on a variety of vegetable plants, mainly those belonging to the Liliaceae family, and in particular on onions, but also on cucumbers and roses. Zawirska (1976) has observed two strains to be present in Poland, one autochthonous, which reproduces parthenogenetically and which was not found on tobacco, and the other which was found to spread gradually across the territory beginning from the Ukrainian border. The latter ecotype reproduces bisexual and is capable of transmitting virus-induced diseases, such as Tomato Spotted Wilt (see paragraph 1.5 for further details).

T. tabaci is an extremely polyphagous species, it is known to infest about 300 plant species including, leek, tobacco, vegetables of the Liliaceae family, cabbage, pea, melon, lettuce, potato, tomato and carnation. It is particularly harmful to cotton crops, especially in the Balkans, Asia Minor and Egypt. It has been studied in many countries with special reference to factors affecting the growth of the insect, extent of damage and control methods (Bailey, 1938; Ghabn, 1938, 1950; Gawaad and Shazli, 1969, 1970, 1971; Gawaad and Soliman, 1972; Gawaad *et al.*, 1973; Grasselly *et al.*, 1990).

1.3.2.2 *Thrips palmi* Karny (Terebrantia, Thripidae, Thripinae)

T. palmi is similar to *T. flavus* Schrank (Palmer *et al.*, 1989), which is an economically unimportant and cosmopolitan flower thrips. The morphological differences between the two species are reported by Anonymous (1989a). *T. palmi* called 'palm thrips' or 'melon thrips', is about 1.3 mm long and has a pale yellow body with blackish setae (II urotergite with four lateral setae, VIII with complete comb in both sexes).

The life cycle of *T. palmi* is slightly different in respect to other thrips species, in fact the second instar larvae move into the ground where they develop and pupate. In Japan this species can overwinter on outdoor vegetation only in a limited area of the South (Anonymous, 1989a).

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Table 4: European countries and their crops most commonly infested by *F. occidentalis*.

Country	Ornamental	Vegetable	Fruit trees	Reference
The Netherlands	Saintpaulia, Chrysanthemum, Gerbera, Kalanchoe, Rademarchera			van de Vrie, 1987
Sweden	Poinsettia, Chrysanthemum, Cyclamen, Saintpaulia, Kalanchoe, Fuchsia, Gerbera, Impatiens			Nedstam, 1991
Finland	Saintpaulia, Rose	Cucumber and others (a)		Tiitanen and Markkula, 1989; Brax and Lindqvist, 1989; Kurppa, 1989
Hungary	Gerbera, Carnation	Cucumber, Tomato, Sweet Pepper		Jensen and Ceglarska-Hodi, 1991
Poland	Gerbera, Rose, Chrysanthemum, Carnation, Pot Plant Crops	Cucumber		Labanoswki, 1991; Piatkowski, 1991
Germany	Saintpaulia, Geranium, Rose (b)			Zur Strassen, 1986; Gundel, 1988
Denmark	Sintpaulia			Brødsgaard, 1989a; Pilgaard, 1990
Great Britain	Chrysanthemum			Buxton and Wardlow, 1991
France	Saintpaulia, Chrysanthemum (c) Cyclamen, Rose, Azalea, Gerbera, Begonia, Hibiscus, Geranium, Carnation, Lisianthus, Dahlia, Fuchsia, Impatiens, Zinnia, Orchid, Gloxinia	Egg-plant, Cucumber, Lettuce, Tomato, Melon, Bean, Strawberry, Vegetable narrow (c)	Nectarines	Bournier and Bournier, 1987; Fougeoux, 1988;
Belgium	Chrysanthemum (d)	Strawberry		Nicolas and Kouta, 1991
Spain		Pepper, Tomato, Egg-plant, Bean, Cucumber, Melon, Water-melon, Strawberry		Sterk, 1990; De Clercq, 1991
Portugal	Chrysanthemum, Rose, Carnation, Gerbera, Saintpaulia	Melon, Tomato, Bean, Strawberry	Apple, Plus-tree, Peach	Rodriquez and Belda Suarez, 1990
Italy	Saintpaulia, Geranium, Chrysanthemum, Cirsium, Sonchus, Gipsophila, Gladiolus, Azalea, Statice, Poinsettia, Gillyflower, Carnation, Rose, Cyclamen, Gerbera, Lisianthus (e) Gloxinia	Parley, Pumpkin, Pepper, Egg-plant, Cucumber, Bean, Green Bean, Vegetable narrow, Strawberry		Rampinini, 1987 and 1989; Arzone <i>et al.</i> , 1989; Del Bene and Gargani, 1989; Ciampolini <i>et al.</i> , 1990; Bellardi and Vicchi, 1990; Lisa <i>et al.</i> , 1990; De Sena and Asero, 1991; Ciampolini <i>et al.</i> , 1991
			Table grapes, Nectarine	Marullo, 1991; Tommasini and Burgio, in press

a) *F. occidentalis* has also been found in open-field crops during the summer months;
 b) WFT is currently one of the main nursery ornamental crop pests in Germany;
 c) Open-field crops infested by WFT besides Gladiolus, Pansy and *Reine-Marguerite*;
 d) WFT has been found on 20 different families of 50 species of nursery-grown vegetable and ornamental crops;
 e) Some ornamental plants are known to have been infested in open-field during the summer months.

Table 5: Examples of the mean egg production and approximate rate of oviposition of some thrips species (from Lewis, 1973) (B= normal bisexual, T= thelytokous).

Species	Type of Reproduction	Temp. (°C)	Total eggs	Rate (eggs/day)	References
<i>Heliothrips haemorrhoidalis</i>	T	15.5-20	25	0.6	Rivnay, 1935
<i>Heliothrips haemorrhoidalis</i>	T	25.5-28	47	1.4	Rivnay, 1935
<i>Taeniothrips dianthi</i>	B	223	55	3.0	Pelikan, 1951
<i>Thrips tabaci</i>	T	18	80	1.8	Sakimura, 1937

The insect was collected in 1921 from tobacco in Sumatra, Indonesia (Karny, 1925) and it was introduced in Japan in 1978 (Sakimura *et al.*, 1986). Many studies regarding integrated and biological control were carried out in this country (e.g. Kawai and Sakimura, 1990). *T. palmi* was found in Hawaii in 1982, in Puerto Rico in 1986 and in Florida in 1991 (Anonymous, 1991; Childers and Beshear, 1992). The life cycle of *T. palmi*, from egg to egg, lasts only 17.5 days at 25°C (Anonymous, 1989a). The crops attacked by *T. palmi* in these countries are mainly cucumber, watermelon, cantaloupe, Chinese spinach, lettuce, sweet pepper, eggplant, bean species, ornamental plants and citrus (Johnston, 1986; Childers and Beshear, 1992). Presently the melon thrips is a key pest of cucurbits and solanaceous plants in several temperate and tropical regions. It was accidentally introduced in Central Europe probably by imported ornamentals and potted plants (Schliephake, 1990) and was intercepted on cut flowers in Finland in 1989 and recently it was discovered in several nurseries on *Ficus benjamina* in The Netherlands after it had passed initial quarantine controls (Walker, 1994; Loomans, pers. comm.). Nowadays, *T. palmi* is considered as an EPPO and EU quarantine organism (van Lenteren and Loomans, 1998). Recently it was found also in Italy on some imported flowers (Marullo, 1997).

The damage caused by this thrips are those typical of the order. *T. palmi* is polyphagous and is a vector of TSWV on watermelon in Japan and is therefore an important quarantine pest. Integrated control is recommended in greenhouses in Japan since it was demonstrated that none of the repeatedly used insecticide applications caused a mortality higher than 80% (Anonymous, 1989a).

1.3.2.3 *Thrips fuscipennis* Haliday (Terebrantia, Thripidae, Thripinae)

T. fuscipennis can be easily confused with *T. tabaci*, from which it differs, however, in a number of morphological features including darker wings. Moreover, while the antennae are also divided into seven segments as in *T. tabaci*, the first is darker than the others. Around the

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edge of the pronotum, three small hairs can also be seen, while on the back edge of the eighth tergite the hair comb breaks off at the centre.

The insect reproduces by thelytokous parthenogenesis. The females overwinter on dry stems or in the bark, but never in the soil. In rose nurseries, they continue living on the foliage, feeding and moving without, however, laying eggs (Speyer, 1932, 1936). This tends to demonstrate that the insect goes into a winter diapause which lasts until the end of March. Egg-laying begins in early April, when the eggs are deposited in sprouts or in the bracts and sepals of buds. The number of generations which can develop during the reproductive period is unknown. Albeit polyphagous, this species is known to prefer roses, but carnations are also frequently infested. It has been found in all palearctic regions (Bournier, 1983).

1.3.2.4 *Thrips simplex* Morison and *Thrips meridionalis* Pr. (Terebrantia, Thripidae, Thripinae)

Both are similar in appearance. The adult of *T. meridionalis* is brown or black, only at the base of the fore wings the colour is paler. Antennae present 8 segments and the final two are smaller. Two hairs are in the posterior corner of the prothorax. On the eighth tergite a comb of hairs is present. *T. meridionalis* is commonly found in fruit orchards. Morphological differences between *T. simplex* and *T. meridionalis* include 5 to 6 distal hairs instead of 3, located on the main vein of the front wing as well as three antennal segments shorter by 20 to 21 mm and only a single row of accessory hairs on the seventh sternite instead of the two featured by *T. meridionalis* (Bournier, 1954).

T. simplex is amongst the species which reproduce by arrhenotokous parthenogenesis (Bournier, 1956a). Females can lay their eggs in any part of the plant, including the bulb, the leaves and the flowers. Discovered before 1930, and originating in Australia, it spread worldwide following the trade of gladiolus bulbs, which is the plant it most commonly infests and upon which it overwinters. It begins to reproduce at temperatures above 12°C (Bournier, 1983). During development, the insect does not appear to go into diapause and at 30°C the growth cycle is completed within 11 days (see Table 5). Pupation takes place either on the plant itself, into the soil or among bulb scales. This species is almost exclusively encountered on gladiolus, although it may occasionally be found also on carnation, iris, narcissus, freesia and tritoma.

1.3.2.5 *Taeniothrips dianthi* Priesner (=*Pesothrips dianthi* (Priesner))(Terebrantia, Thripidae, Thripinae)

T. dianthi is also similar in appearance to *T. meridionalis* from which it differs morphologically in the fact that it features a crown of thick and dark hairs around the tip of the third segment of the antennae. After winter, mated females emerge from the litter or from the soil around April and settle on carnation seedlings. Moving towards the heart of the seedling, they lay an average of three eggs per day (see Table 5). Development times at 23°C are shown in table 5. The second instars move down the plant and go deep down into the litter or the soil. During the reproductive period, three complete generations and a fourth partial one have been observed to develop in Central European countries (Pelikan, 1951). *T. dianthi* is related only with other species belonging to the *Dianthus* genus, which originate from south and south-eastern Europe. It is a particularly thermophilic species, and was introduced from the colder regions, such as the South-West of Poland, into the rest of Europe, where it found an ideal environment for its development, through the trade of carnation cuttings.

The species is practically monophagous and found only on carnations, where it causes considerable damage, morphologically altering the flowers and conferring on them a particular appearance called "bird's head" (Pelikan, 1951; Bournier, 1983).

1.3.2.6 *Heliothrips haemorrhoidalis* (Bouché) (Terebrantia, Thripidae, Panchaetothripinae)

Heliothrips haemorrhoidalis takes its name from the colour, featuring a black body (although the immature stages are paler), and a red abdomen tip. The surface of the body is covered throughout by a clearly distinguishable reticular pattern. The legs are glassy in appearance and the wings, when at rest, form a white contrast against the black body. Antennae are divided into eight segments, the first two being light brown, the other three yellow, the sixth brown in the distal portion and the last two pale and filiform. *H. haemorrhoidalis* reproduces itself by obligatory thelytokous parthenogenesis and males are extremely rare (Bournier, 1956a; Ananthakrishnan, 1993) (Table 5).

Some females deposit a drop of excrement on the egg, probably in order to seal the hole drilled by the ovipositor, while others lay their eggs deeper into the plant tissues, which then close themselves over the eggs. Larval instars of this species are known to secrete a rectal liquid which frightens away potential predators. This peculiar characteristic has probably been developed as larvae move very slowly especially when feeding.

Five to seven generations are found in Mid-Mediterranean countries between June and October, and up to 15 are known to develop in nursery environments as under these conditions the insect does not go into diapause. The adults overwinter on fallen dead leaves and bark.

This species is cosmopolitan and polyphagous and found in all countries with favourable climatic conditions as well as on a wide variety of plants, such as, *Viburnum* spp. L., *Photinia* spp., azalea, *Ficus* spp. L., *Dracaenae* spp. L., orchids, roses, *Croton* spp. L., avocado, citrus fruit, grapevine, tobacco, *Eucalyptus* spp. L'Hér., etc. In Mid-Mediterranean countries, it is most frequently found on *Viburnum tinus* L. High infestation may cause complete defoliation of the plant.

1.3.2.7 *Parthenothrips dracaenae* (Heeger) (Terebrantia, Thripidae, Panchaetothripinae)

Parthenothrips dracaenae is light brown in colour with a reticular pattern over the body similar to that of *H. haemorrhoidalis*. The legs feature dark femurs and pale tibias, while the wings are characterized by two black transversal spots which are clearly visible when the wings are folded, the antennae has 8 segments. The initial five segments being light brownish yellow, the sixth and seventh dark brown and the last filiform. *P. dracaenae* is the first species which has been observed to reproduce by parthenogenesis, a fact which accounts for its name. Populations encountered in glasshouses with temperatures ranging between 25 to 28°C are made up almost exclusively of females, while some males have been found in populations at lower temperatures, namely between 18 and 20°C (Lewis, 1973). An interaction, between photoperiod and feeding seems to induce deuterotokous parthenogenesis.

Immediately after moulting, second instar larvae are smaller than first instars but develop into adult size upon reaching maturity. This characteristic is similar to that of *F. occidentalis*. If temperature remains within 18 to 20°C, approximately one generation a month can develop. Females lay their eggs into leaves, and the larvae live gregarious (Bournier, 1983).

Although cosmopolitan, this species needs milder winters than *H. haemorrhoidalis* for survival. Not surprisingly, therefore, in Europe it is only found in greenhouse environments.

The polyphagous insect infests a number of plants, including *Dracaenae* spp. Vand., *Aralia* spp. L., *Begonia* spp. L., *Canna*, *Croton* spp. L., *Ficus* spp. L., *Kentia* spp. Moore et Mueller, *Pandanus* spp. Parkinson, *Phoenix* spp. L., etc.

1.3.2.8 *Haplothrips cottae* (Vuillet) and *Haplothrips tritici* (Kurdjumov) (Tubulifera, Phlaeothripidae, Phlaeothripinae)

These species belong to the sub-order Tubulifera and are similar in appearance. *H. tritici* is found particularly on Gramineae. The female of *H. tritici* is

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black and 1.5 mm long, the end of the front tibia and tarsus are pale. The antennae present 8 segments, but the end of the second, the third and the first part of the fourth segment are paler than the other. The wings are hyaline, without veins, fringed along the margin. The front wings have a double line of 5-8 hairs posteriorly. The tenth abdominal segment is shaped as a long tube. *H. cotti* differs from *H. tritici*, however, in that it has a longer head. Moreover, the tenth abdominal segment (or tube) is shorter and the insect does not exhibit the double fringe around the back portion of the front wings. This species can be found in a number of different forms, namely brachypterous at temperatures below 17°C, macropterous at 30°C and 87 to 100% relative humidity, and brachypterous at 30°C and 17% relative humidity, with the entirely brachypterous generation being found only in winter (Ghabn, 1932). The development times are showed in table 6.

Similarly to *T. dianthi*, this species only infests carnation and it is thermophilic. It has been found in Egypt, Spain and all other Mediterranean coastal regions.

1.3.2.9 *Liothrips vaneeckei* Pr. and *Liothrips oleae* Costa (Tubulifera, Phlaeothripidae, Phlaeothripinae)

Both are similar in appearance. The adult of *L. vaneeckei* is black and it differs from the latter, however, in the colour of its front tibiae which are completely yellow instead of black. Moreover, the middle and back tibiae are both yellow in their distal portions. The abdominal segment or tube is longer, *i.e.* 285 instead of 210 mm. The third antennal segment is shorter (84 mm) than that of *L. oleae* (105 mm). Wings are without veins, with a double line of 15-18 hairs. It reproduces by arrhenotokous parthenogenesis (Bournier, 1956b). In Europe, it is known to develop at least four generations a year (Hodson, 1935; Bailey, 1939; Titschack, 1960). It can be found world-wide, where it has spread following with the flower bulb trade. Bulb-induced contamination seems to take place via wind-borne intermediaries which have moved up from the soil onto the stems of the lilies (Titschack, 1960). First being limited to wild *Lilium martagon* L., *L. vaneeckei* has subsequently colonized lily crops. *L. oleae* infests olive trees.

1.4. Direct damage caused by Thysanoptera

1.4.1 Damage caused by Thysanoptera in general

All phytophagous Thysanoptera cause direct damage to plants due to the mechanical action of the mouthparts during feeding and in Terebrantia as a result of oviposition as well. In more detail feeding and egg-laying behaviour entail:

- perforation of plant tissues as a consequence of the introduction of mouth stylets;
- injection of saliva into plant tissues and consequent cell lysis;
- sucking up of cellular contents;
- ovipositor penetration and egg-laying into plant tissues.

Each puncture into the plant tissues causes the destruction of on average 1 epidermal cell and between 1-2 underlying parenchymal cells. Moreover, cells are often injected with a phytotoxic substance which can determine specific tissue reactions as observed by Kloft and Ehrhardt (1959) using radioactive isotopes. These attacks bring about cell dehydration and discoloration, resulting in superficial necrosis.

Amongst the various thrips species described above, some species are monophagous, like *T. dianthi* which only infests carnation, and *T. simplex* which is only found on gladiolus.

Typically polyphagous species, on the other hand, include *T. tabaci* and *F. occidentalis* (Bournier, 1983; Grasselly *et al.*, 1990).

Another peculiar characteristic of thrips is that, while some species can be extremely harmful to a certain crop in a certain region, they are completely harmless in other regions. An example is *T. tabaci* that is widespread in all temperate and sub-tropical regions of the northern hemisphere. While attacking several varieties of tobacco in Turkey and Greece, it does not seem to infest tobacco crops in France (Bournier, 1983).

The type of damage which thrips can cause to crops depends on a number of factors including:

- the organ of the plant infested;
- the growth stage of the plant;
- the degree of toxicity of the saliva of the species considered in relation to host-plant characteristics.

1.4.1.1 Damage caused to fully developed leaves, or leaves with a thick cuticle

The surface of the leaf exhibits emptied and discoloured cells, initially taking on a mother-of-pearl appearance and subsequently turning brown. In the case of a massive infestation, the leaves wither and fall. It sometimes appears to be similar to that caused by mites but, in addition to larval exuviae, the presence of brownish transparent faecal drops is a clear indication of thrips infestation. This type of damage to leaves is often encountered in protected crops (Moulton, 1928), caused especially by the action of *H. haemorrhoidalis* and *P. dracaenae*, which are known to infest in particular ornamental crops such as *Ficus* spp., *Philodendron* spp., *Croton* spp., *Dracaenae* spp., *Phlox* spp., etc.

1.4.1.2 Damage to developing leaves

This damage is more frequently encountered than the previous one. The reaction of the leaves to the toxic saliva of the thrips normally differs according to plant species, and often also to plant variety. If the saliva does not penetrate below the surface layer, then the leaf continues to grow, exhibiting only necrotic spots in the immediate vicinity of the puncture. On the other hand, if the saliva penetrates further, both sides of the leaf limb are deformed. In fact, as the leaf grows it takes on the form of a half-open umbrella. *T. tabaci*, can destroy all the epidermal cells of an onion, thus causing the leaf to completely wither (Ghabn, 1948). In other cases, the leaf can continue to develop, taking on an undulated form resulting from the impossibility of growing normally along the damaged parts. *T. tabaci* on leek always causes silvery, mottling or blotching on the affected surfaces of leaves, through feeding punctures, sometimes in longitudinal stripes along the growing leaf. The major part of damage of *T. tabaci* is caused during warm summers (Theunissen and Legutowska, 1991). On cabbage, the visible injury, caused by *T. tabaci*, consists of papillary callus proliferation on the lower and upper surfaces of the leaves, and reducing the quality of the crop (Giessmann, 1988). Another example of this kind of damage is found on carnation plants infested by *T. dianthi* (Bournier, 1983).

Table 6: Duration (in days) of stages of the life-cycle of some thrips species at different temperatures (°C) (modified after Lewis, 1973).

Species	Tempe- rature	Eggs	1st instar	2nd instar	Prepupa	Pupal stage	Youth stages total no.	Pre- oviposition	Imago	Source
At constant temperatures										
<i>Taeniothrips dianthi</i>	23	7.0	5.5	8.0	1.0	5.0	26.5	-	-	Pelikan, 1951
<i>Thrips simplex</i>	15	12.8	(--- 18.6 ---)		(--- 11.7 ---)		23.4	-	-	Herr, 1934
<i>Thrips simplex</i>	30	2.9	(--- 3.9 ---)		(--- 3.5 ---)		10.3	-	-	Herr, 1934
<i>Thrips tabaci</i>	17.5	15.1	(----- 15.3 -----)				30.4	5.7	-	Edelson and Magaro, 1988
<i>Thrips tabaci</i>	20	8.4	(----- 11.9 -----)				20.4	3.2	-	Edelson and Magaro, 1988
<i>Thrips tabaci</i>	25	6.0	(----- 7.3 -----)				13.3	1.1	-	Edelson and Magaro, 1988
<i>Thrips tabaci</i>	25	6.0	(--- 6.1 ---)	1.2	2.8		16.1	-	-	Harris <i>et al.</i> , 1936
<i>Thrips tabaci</i>	27.5	4.3	(----- 6.8 -----)				11.1	1.0	-	Edelson and Magaro, 1988
<i>Thrips tabaci</i>	30	4.0	(--- 4.2 ---)	1.0	2.0		11.2	-	19.9	Harris <i>et al.</i> , 1936
<i>Haplothrips cottlei</i>	30		(----- 23 -----)				23.0	-	13.0	Bournier, 1983
<i>Haplothrips cottlei</i>	23		(----- 43 -----)				43.0	-	-	Bournier, 1983
<i>Haplothrips cottlei</i>	18		(----- 67 -----)				67.0	-	-	Bournier, 1983
At fluctuating-temperature (mean)										
<i>Thrips tabaci</i>	30.8	4.8	(--- 5.9 ---)	1.4	2.4		13.9	-	20.2	Lall and Singh, 1968
<i>Thrips tabaci</i>	26.7	4.6	(----- 8.6 -----)				14.4	1.0	-	Edelson and Magaro, 1988

1.4.1.3 Damage to stems and to terminal buds

Damage to the stem, caused by punctures at its vegetative apex, only occurs when this part of the plant is still young and tissues are, therefore, soft. Suberisation of the tissue is similar to that caused to the leaves. In France, attacks of this kind have been reported on grapevines beginning after mid-August (Bournier, 1957). Given their size, thrips are capable of penetrating into the heart of buds. In this case, their punctures may destroy small leaves and meristems. *T. tabaci*, is known to attack and damage cotton crops when these are still at the cotyledon stage of development (Bournier, 1983).

1.4.1.4 Damage to flowers

Damage to flowers may include damage to petals, stamens, pistils and peduncles.

Petals: Thrips may attack a wide variety of flower species. When infested, petals exhibit white spots which subsequently turn brown, after which the petals become deformed. Not infrequently, the insects penetrate into the flower buds before blooming, completely destroying them. A typical example of this kind of damage is found in carnations, where infestation causes deformation of the bud into the shape of a "bird's head" (Pelikan, 1951; Bournier, 1983).

Stamens: A single puncture in the stem may cause total destruction of the stamen. Moreover, as anthers are a source of food for various species of thrips, another dehiscence may ensue, as is the case, for example, with *F. occidentalis* infested plants.

Pistils: *Kakothrips robustus* (Uzel) is known to also puncture the pistil and the ovary, thus causing destruction of certain parts of the young fruit which, upon subsequent development, appears deformed with only a few seeds (Bühl, 1936).

Peduncles: Damage to the peduncles of flowers is less frequently caused by the thrips species considered in this paper, this type of damage is mainly induced by tree-infesting thrips.

1.4.1.5 Damage to fruit

Damage to fruit may include that to the fruit proper as well as to the pericarp.

Developing fruit: Developing fruit is most frequently damaged as at this stage the fruit still features a very soft epidermis. Epidermal suberisation ensues which, in turn, causes deformation of developing fruit. This kind of damage is usually encountered in peaches, which are thus made unmarketable, as well as in grapes, plums and cherries (Bournier, 1983).

Pericarp: Damage of this kind is known to cause a change in colour of the wheat pericarp. Even if controversial, it has also been reported in mushroom following on punctures by *H. tritici*.

1.4.1.6 Damage to bulbs and rhizomes

A bulb can be described as a bud consisting of fleshy leafy scales or layers, while a rhizome is a scaly underground stem. It is these scales which are subject to thrips attack. In lilies, for example, *L. vaneeckeai* punctures the superficial scales, thus permitting micro-organisms in the soil to penetrate into the bulb, infesting it and causing its decay (Schopp, 1936; Titschak, 1960). Wounds inflicted by *T. simplex* to gladiolus cause, instead, dehydration and subsequent darkening (Bournier, 1954).

1.4.1.7 Intoxication and growth of galls

When punctures are inflicted on young stems and especially at the growth apex, saliva induced intoxication may result. In addition to leaf deformation caused by *T. dianthi*, Bournier (1983) also observed a considerable shortening of internodes and most of deformed whorls of

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the plant. In most cases, the effects of intoxication diminish or disappear with subsequent plant growth. Saliva toxicity can induce abnormal cell multiplication in the plant, in particular in the parenchymal tissues. Vessel bundles are destroyed due to circulating cell proliferation and the collenchyma and sclerenchyma develop irregularly throughout the plant. The leaf mesophyll hardens due to tannin and anthocyanin build-up. The leaves may still fold in on themselves, thus forming mantle or overcoat galls, as has been observed in *Ficus microcarpa* Vahl growing in the Mediterranean basin, punctured by *Gynaikothrips ficorum* Marchal (Bournier, 1983).

1.4.2 Damage caused by *F. occidentalis*

1.4.2.1 General damage symptoms

Damage to crops caused by *F. occidentalis*, as with that caused by other thrips, features different characteristics according to extent and period of attack, as well as to plant parts involved. Generally, the major symptoms of *F. occidentalis* infestation include a discolouration of the upper leaf surface where attack occurs. The pattern of damage is more coarse than damage by *T. tabaci*. Silvering, deformity, growth malfunction and brown-coloured bumps may also be present on the foliage of ornamental plants. Halo spotting is another symptom of thrips damage consisting of small dark scars surrounded by whitish tissue. On some host plants (sweet pepper), oviposition causes a reaction of the surrounding plant tissue. Thrips' feeding causes discolouration and scarring of open blooms and petals. It also results in deformation of buds if the feeding occurs before they start opening. Kloft and Ehrhardt (1959) have shown that the action of the saliva injected into plant cells is the real cause of damages for its toxic effects on plant tissues. This was demonstrated by the use of radioactive tracers (P32), which show how saliva spreads abundantly through the cell walls, thus invading and destroying the entire region around the puncture. The cytoplasm of the dead cells dehydrates and the cells lose their pigmentation, turning to a mother of pearl whitish colour before becoming brown. The damage caused by WFT, as with other thrips, already described is often hard to distinguish from spider mite damage, but a good indication of thrips attack is the appearance of liquid faecal deposits which cause dark-green speckling, while spider mites produce black granules. Female WFT can lay their eggs in petal tissue which causes a "pimpling" effect in flower such as orchids (Anonymous, 1989b).

1.4.2.2 Damage symptoms on specific host plants

Chrysanthemum- *Chrysanthemum* flowers attacked by *F. occidentalis* exhibit, for example, distorted petals, discolouration, and extensive streaking, especially on dark flowers. Unlike *Saintpaulia* and *Gloxinia* spp. flowers, which wither as a consequence of pollen dispersion, attacks to *Chrysanthemum* pollen granules do not seem to affect the flower. Two types of alterations have been observed in the foliage depending on the age of affected tissues. As regards buds, for example, attacks by *F. occidentalis* cause irregular growth of small leaves as well as distortion and failure to open of the parenchymal foliage. Attacks to open leaves, on the other hand, only cause necrotic scars and silvering, as is also the case on rose and gerbera sepals (Fougeroux, 1988; Ciampolini *et al.*, 1990).

Geranium - Damage caused by *F. occidentalis* to geranium (Rampinini, 1989) can already be detected on the young leaves, which grow deformed, curling upwards and exhibit whitish and suberose bumps on the upper leaf surface which are even more marked on the lower leaf surface, on the peduncles, petioles and stems. Flowers can abort and, if they bloom, display deformed petals with long or marginal discolouration. These symptoms tend to worsen at

higher temperatures such as those found in glasshouses. Humidity is also an important factor in aggravating these symptoms, which do not diminish, however, even when the plant is transferred outside. *F. occidentalis* causes typical corky spots on the lower surface of the leaves, and lateral necrotic spots were also found (Gundel, 1988).

Grapevine - In 1990, *F. occidentalis* was reported to infest this crop in southern Italy (Ciampolini *et al.*, 1991; Laccone, 1992), causing in particular considerable damage to table grapes. The extent of the damage from one region to another varies according to a number of ecological factors such as climate, humidity, type of soil and the presence of grass covers which are the source of inoculation of the infesting organism. The pest attacks almost exclusively the grape bunch at the growth stage between flower bud separation and post-setting, and in particular during full blossom. This causes peduncle and grape withering as well as a slight deformation of the rachis. The most serious damage, however, is caused to the grape by wounds due to oviposition. This leads to tissue necrosis which, as the grape grows, becomes more and more marked until a dark spot appears as a consequence of suberization of the epicarp and of the underlying layers. The thrips can lay more than one egg in each single grape, so that the damage can be even more extensive. Apart from damage to the grape, other parts of the plant do not show significant damage.

Strawberry - Infestation of this crop mainly affects the flowers, while damage to the leaves is negligible. Damage to flowers is typically caused by punctures due to feeding. Initial symptoms are rusty spots at the base of the flowers above the sepals, which can also be observed in the unripe fruit. The fruits damaged are typically deformed or they become 'bronze' coloured in the calyx area. The major damage, however, is represented by the flowers showing necrosis and withering (Ribes, 1990).

Rodriguez and Belda Suarez (1989), who examined the damage caused by thrips to a number of vegetable crops in Spain, describe the symptoms as follows:

Bean - The population is mainly localized on the lower leaves of the plant where punctures of both adults and the larvae can be seen. Albeit only occasionally, damage to fruit can be considerable, appearing as a markedly white halo around the punctures. The population on the flowers consists mainly of adult, but this does not seem to adversely affect the fruit-bearing capacity of the plant or to cause pod deformation.

Egg-plant - Thrips infestation peaks when the plant is in full bloom. Other parts of the plant are less sensible to infestation, a fact accounted for by the presence of tomentous layers with which the plant is endowed, especially on the leaves. The damage on the leaves is given by silvery spots close to the veins, which become necrotic. This damage is particularly evident in the upper foliage, where the adults are localized. The larvae are uniformly distributed throughout the plant. Upon blossoming, adults attack the flower and especially the ovary. Whitish punctures can be seen at the tip of the fruit. The peduncle may exhibit damage from feeding punctures, with spots becoming necrotic and then rusty.

Cucumber - Thrips populations increase progressively as the plant grows, being localized on the leaves and fruits but above all on the flowers, where adults are found, particularly on the petals. The typical symptoms of damage caused by feeding punctures are observed on the leaves, the spots becoming larger and larger and forming extensive necrosis, thus hampering the regular physiological processes of the plant. The flower and the fruit are known to host all thrips species. However, no apparent relationship seems to exist between the damage caused by thrips and the eventual bending observed on the fruit. The fruit's marketability decreases as a result of the necrotic spots located around the peduncle or in areas directly in contact with the leaves.

Melon - Thrips are found mainly on the leaves. In the extensive areas in which this crop is grown during the summer months, the instar population is greater than the adult one. Damage

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caused by feeding punctures increases as the leaf surface area grows larger, eventually causing the leaf to wither. The older leaves are infested first, after which infestation spreads to the rest of the plant, which becomes damaged in all its parts to the point of damaging the whole crop. The fruit is the least susceptible to thrips attack and its marketability is not affected.

Pepper - Infestation is initially restricted to the leaves. As the plant grows, the adults progressively move towards the younger parts of the plant, finally settling on the blooming flowers. Silvering and subsequent necrosis are the most evident damage displayed by the leaves, of which the older are the most affected. Punctures only occasionally occur on the fruit; these are localized at the point of intersection between the calyx and the fruit itself, where the larvae shelter. Feeding punctures initially cause silvering, followed by necrosis and rusty spotting especially in the peduncle and are much more marked on red than on green fruits. This damage is extremely serious as it decreases the fruit's market value, especially in cases where feeding is extensive.

Tomato - Most of the population is found on the lower leaves of the plant, with larvae settling in particular under folded leaf edges. Damage to leaves caused by feeding punctures is characterized by silvery spots which subsequently become necrotic. In case of massive attacks, withering may result. When punctured, both green and ripe fruits display a whitish halo around the punctures. In addition to feeding punctures, fruits also display punctures caused by oviposition.

Zucchini - The greatest damage is caused to leaves in the early stages of plant growth. The thrips subsequently move into the flower in order to feed on the pollen, and it is at this stage that infestation reaches its peak. The typical spots due to thrips feeding appear on the leaves, localized around the limb and petiole. Damage to the fruit is negligible except for a few silvery spots on the peduncle.

Watermelon - Thrips distribution is more or less uniform over the leaves. The typical spots caused by feeding punctures can easily be detected on the leaves but are less evident on the fruit and almost invisible on the ripe fruit.

1.5. Indirect thrips-induced damage caused by Thysanoptera

1.5.1 Viruses

Thysanoptera feed by first injecting saliva into plant cells and then sucking the contents of the destroyed cells resulting from the action of the lysins. With such a way of feeding, the insects can acquire and consequently transmit viruses. Many authors have therefore assumed that thrips are carriers of plant virus-induced diseases. For example, Bondar (1924) studied the mosaic disease of the manihot, Kreutzberg (1940, 1955) the rosette disease of the pistachio, and Messieha (1969) the ring spot of tobacco. Heinze (1959) has made a list of 19 species of thrips considered to be common carriers of plant infesting viruses. It should be noted, however, that in most cases virus transmission is not as evident as may be thought. It seems that Tobacco Streak Virus (TSV) can be transmitted by *F. occidentalis* and *T. tabaci* (Kaiser *et al.*, 1982). The authors report that additional studies will be needed to determine whether *F. occidentalis* or *T. tabaci* is the primary vector of TSV and to clarify other aspects of the virus-vector relationship.

A clearly established case of transmission of virus-induced disease with thrips as carriers concerns the disease caused by the tomato spotted wilt virus (TSWV) (Pittman, 1927; Samuel *et al.*, 1930; Bonnemaison, 1939; Sakimura, 1962; Reddy and Wightman, 1988; Marchoux *et al.*, 1991; Ananthakrishnan, 1993; Peters *et al.*, 1996). In this case, the carriers were found to

include: *T. tabaci*, *Frankliniella schultzei* (Trybom), *F. occidentalis*, *Frankliniella fusca* (Hinds). Marchoux *et al.* (1993) found an increase in the range of thrips hosts, even if *F. occidentalis* remains the most important. Using ELISA testing it has been established that over 50% of adult *F. occidentalis* are infected by TSWV (Marchoux, 1990). Studies about virus transmission by WFT are in progress. Wijkamp *et al.* (1993) have recently shown that less than one-day-old first instar of *F. occidentalis* can acquire the virus and that 80% of larvae could transmit the virus before pupation. This particular viral disease was first observed in Australia in 1915, spreading afterwards to America and Asia (De Sena and Asero, 1991). Smith observed TSWV in the United Kingdom in 1932. Diffusion of this virus in several regions of North America was reported, for example, by Paliwal (1974, 1976), Allen and Broadbent (1986), Broadbent *et al.*, (1987) and Miller (1989).

One of the main channels of transmission of TSWV is via thrips. In India, TSWV has been found to be transmitted by two other species of thrips, namely *Scirtothrips dorsalis* Hood and *Thrips palmi* Karny (Amin *et al.*, 1981; Marchoux, 1990). TSWV can affect a wide variety of plants: 299 species of 48 botanic different families (Edwardson and Christie, 1986; Berling *et al.*, 1990) and in particular vegetable, flower and ornamental crops (Allen *et al.*, 1990). After reaching Europe, the virus went through a period of relative dormancy, but in recent years a number of European countries, including The Netherlands (Van der Hoeven, 1988; Verhoeven and Roenhorst, 1992), France (Gébré-Sélassié *et al.*, 1989; Berling *et al.*, 1992; Marchoux *et al.*, 1993), Italy (Bellardi and Bertaccini, 1989; Lisa *et al.*, 1990; Vicchi and Fini, 1992; Vovlas *et al.*, 1993; Vicchi and Talamè, 1994; Tomassoli and Barbra, 1994; Carbone *et al.*, 1995; Vicchi *et al.*, 2001), Spain (Peña, 1990), Portugal (Mateus, 1993), Great Britain (Fletcher, 1990), Hungary (Jenser *et al.*, 1996) as well as Greece and Crete (Tsakiridis and Gooding, 1972; Poditakis, 1991 pers. comm.; Poditakis *et al.*, 1993; Chatzivassiliou *et al.*, 1996; 2000), have been particularly hard-hit by this disease (De Sena and Asero, 1991), a fact probably resulting from the diffusion of *F. occidentalis*. Allen and Matteoni (1991) suggest the use of Petunia as an indicator plant to monitor TSWV carried by thrips in greenhouses. The damage by TSWV to susceptible plants is more significant than the feeding activity of WFT, as was demonstrated by Broadbent *et al.* (1990). It is often difficult to make a correct diagnosis of the infection by TSWV only by observing the plants. The necrosis and the concentric chlorotic rings, like on Gloxinia and Begonia (hosts of the virus), are easily confused with symptoms due to fungal infections (for example *Phytophthora parasitica* Dast. on Gloxinia) and bacterial infections (for example *Xanthomonas campestris* (Pammel) Dowson on Begonia). Besides, on Saintpaulia and Gloxinia the concentric chlorotic rings used for diagnosis, can be seen only sometimes because they are related to a special strain of TSWV, and depends the environmental condition at that moment of the infection (Vicchi *et al.*, 1992). Symptoms of this virus vary widely among plant hosts. Daughtrey *et al.* (1997) provided a table comparing symptom of TSWV and INSV, of which is discussed later, for several crops.

Not all forms of *T. tabaci* are capable of transmitting the virus (Zawirska, 1976). In France, for example, TSWV is not found at all in the southern regions where research conducted on indigenous strains of *T. tabaci* has shown that these are incapable of transmitting the virus (Nkouka, 1977). TSWV is transmitted in a persistent way (Sakimura, 1962b) even though it is more correct to say that viral transmission patterns are typically circulatory. Larvae puncture the virus-infected plant, thus absorbing viruses which go into the haemocoelic cavity through the digestive tube and finally into the salivary glands, from which they are then reinjected into healthy plants. Lent *et al.* (1993) demonstrated that salivary glads are the major site of TSWV replication. Fifteen minutes are necessary for the larvae to acquire the virus. The time necessary for the virus to reach the salivary glands usually coincides with the time taken for

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the insect to develop into an adult, at which stage the virus has become highly virulent. The maximum period of transmission of the virus is 3-4 weeks after acquisition (Bellardi and Vicchi, 1990). The period between acquisition and transmission, *i.e.* in which the thrips is not infectious, ranges from 4 to 18 days for *T. tabaci* and 4 to 12 days for *F. fusca* (Sakimura, 1963). In cases where development of first instar larvae into second instar larvae is slowed down by temperature factors, the second instar larvae are already themselves infesting agents (Bournier, 1983). If the infection by the insect has not occurred at the larval stage, adults do not contract the virus. Both females and males are capable of picking up the virus (Sakimura, 1962a), but according to van de Wetering *et al.* (1996) males transmit TSWV more efficiently than females. It takes the larvae 5 to 15 minutes to get inoculated with the virus but once infested the insect can remain virulent throughout its life-span without however transmitting the viral cells to its offspring (Ie, 1970; De Sena and Asero, 1991).

T. tabaci is also a carrier of "Pineapple Yellow Spot". The larva is the stage during which the virus is picked up. Then 10 days of incubation are required for transmission in respect to 5 days circa for TSWV. The transmission of TSWV is easier than Pineapple Yellow Spot (Bailey, 1935).

Wijkamp and Peters (1993) demonstrated the capability of *F. occidentalis* to be a vector of another important tospovirus, the Impatiens necrotic spot virus (INSV). It was discovered that INSV is just a new serotype of TSWV, formalized as INSV (van Driesche *et al.*, 1998). This virus shows a closer association with ornamentals compared to TSWV (Daughtrey *et al.*, 1997).

1.5.2 Bacteria

It can be safely assumed that thrips are vectors of a large number of bacteria. The bacteria can probably penetrate into the plant through the punctures made by thrips. Bacterial infection due to thrips has definitely been reported for non-European countries. As far as Europe is concerned, at least three cases of plant infection have been reported as possibly due to thrips-borne bacteria. These include infections induced by *Erwinia amylovora* (Burr.) which causes pear bacterial fire (Bournier, 1983), two bacteria which predispose plants to attack by *Fusarium moniliforme* Sheld. *fici* and which seem to be borne by *T. tabaci*, reported in Provence (Caldis, 1927) as well as a bacterium affecting bean crops and carried by *Hercinothrips femoralis* Reuter (Buchanan, 1932).

1.5.3 Fungi

Thrips have often been reported to be fungal-vectors. Spores can easily be trapped in the bristles of several thrips species and consequently deposited on healthy plants. Bournier (1983) cites a number of examples including Yarwood (1943) who observed a number of thrips- associated mildews such as: *Uncinula necator* (Schw.) Burr. in grapevine, *Sphaerotheca pannosa* (Wall.) Lév. in roses, *Sphaerotheca humuli* (De Candolle) Burr. in strawberries, *Erysiphe cichoracearum* D.C. in melon, etc. Ghabn (1932) found that carnations were inoculated by a *Haplothrips cottei* borne *Alternaria* Nees. Ondrej (1973) made the same observation with regards *Botrytis fabae* Sard. Many other such reports have come in from the United States, and it can be safely assumed that the list is far from being complete.

1.6. Sampling of thrips

Many of the records and biological data provided in this chapter have been obtained with various sampling methods. The most important methods are summarized below. Sampling techniques which are mainly useful for collectors are reported by Lewis (1973) and Loomans (2000). In applied entomology sampling is directed towards survey and monitoring of harmful insects. Lewis (1973) reports also sampling and extraction methods that give qualitative and quantitative estimates of the size and distribution of thrips populations. For detection of thrips different methods can be employed. One of the easiest techniques to collect thrips is by shaking the flower above a sheet of paper or by extracting them from leaf-litter and soil. Lacasa (1990b) and Mateus (1993) suggest several kinds of sampling and collecting techniques. They distinguish direct and indirect methods:

1. Direct methods, by collecting the plant and subsequently counting the number of individuals, which allows the determination of the exact distribution of the various types of thrips on the plant.
2. Indirect methods, using special traps which exploit the insect's behaviour and reactions to specific colour stimuli, or with other traps such as transparent sheets.

A wide number of studies using chromotropic traps have yielded contrasting results. Lewis (1973) is of the opinion that, as *F. occidentalis* belongs to the Thripidae family, it is attracted to white. This assumption is supported by Yudin *et al.* (1986 and 1987) and Moffit (1964), who showed that for adults of *F. occidentalis*, the colour white is a much stronger attractant than yellow. Other authors, however, such as Fougeroux (1988), Del Bene and Gargani (1989), Robb and Parrella (1989) and Torres del Castillo *et al.* (1989), are of the opinion that yellow is the most attractive colour to this insect, whereas Brødsgaard (1989b) and Mateus (1993), found special shades of blue to be most effective. Brødsgaard (1989b), observed that in a mixed culture of white, rose pink, dark blue and light blue, *S. ionantha* and *F. occidentalis* always preferred the light blue flowers. Vernon and Gillespie (1990b) studied the response of WFT to sticky traps coloured with different reflective intensity, and WFT seemed similarly attracted by the same reflective intensity. WFT appears to be attracted strongest by a blue colour with a reflection between 430 and 490 nm (Mateus, 1993). This fact can be explained considering the polyphagy of *F. occidentalis*: adults are expected to be attracted by the colours of a wide range of flowers. Vernon and Gillespie (1990a), also tested the difference between fluorescent and non-fluorescent coloured sticky traps, but found no significant differences in attractiveness between the two kinds of traps.

Presently, blue sticky traps are sold to growers, because it is the most effective technique for detecting *F. occidentalis* in protected crops. Blue sticky traps are good tools for detecting initial attacks and for monitoring population fluctuations of WFT (Brødsgaard, 1993a; 1993b). In several crops, yellow sticky traps are also employed for catching WFT as they also capture other pests such as *Liriomyza* spp., *Trialeurodes vaporariorum* (Westw.) and *Bemisia tabaci* (Genn.).

Other indirect trapping methods involve semiochemicals. It is known that many insects species are attracted by the odour of plants on which they feed and oviposit. Several synomones such as floral scents are important sources of information mainly for pollinators and some of these allelochemicals have been studied also for thrips. Kirk (1985) reports about components which attract several species of thrips. The potential use of synthetic odours to collect thrips in greenhouses, either for monitoring or for control purposes, is reviewed by Teulon and Ramakers (1990). Studies on the influence of scent on flying thrips have been carried out for the chemical components benzaldehyde, anisaldehyde, salicaldehyde or cinnamaldehyde, and for other not clearly defined chemicals. *T. tabaci* and some species of

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the genus *Frankliniella* were attracted and collected in traps in great numbers when anisaldehyde was added to the trap compared to unbaited traps. Brødsgaard (1990) demonstrated that for *F. occidentalis*, anisaldehyde increases the number of thrips caught on scented window traps compared to unscented window traps. A similar result was obtained by Cameron *et al.* (1993), Teulon *et al.* (1993) and Roditakis *et al.* (1996). A model to estimate thrips infestation on sweet pepper has been studied and is described in chapter 5.

1.7. Thrips control

1.7.1. Chemical control

In many crops, chemical control is the most important way of controlling thrips pest outbreaks. Due to their hidden lifestyle (eggs in plant tissue, pupae in soil or like larval stages hidden in buds or between leaf- and flower structures), their short life-cycle and zero-tolerance for some export products, chemical treatments have to be repeated often. They not only upset regular IPM programs for greenhouse crop, they also result in a quick development of insecticide resistance.

The resistance of *F. occidentalis* to an array of chemical products is illustrated by many authors (Race, 1961; Shorey and Hall, 1962 and 1963; Carlson, 1964; Morishita *et al.*, 1969; Beryabin *et al.*, 1979; Anonymous, 1981; Dintenfass *et al.*, 1987; Bohmer and Eilenbach, 1987; Robb *et al.*, 1988; Freuler and Benz, 1988; Devesa and Dow Elaco Hib., 1990; Grasselly *et al.*, 1991; Brødsgaard, 1991a; Nasruddin and Smitley, 1991; Georghiou and Lagunes-Tejeda, 1991; Immaraju *et al.*, 1992; Bohmer *et al.*, 1992; Pasini *et al.*, 1993; Robb *et al.*, 1993; Brødsgaard, 1994; Robb *et al.*, 1995; Zhao *et al.*, 1995). Several studies in the laboratory and in the field were undertaken by different authors on the toxicity of insecticides on *F. occidentalis* (Table 7).

The major part of the pesticides included in table 7 are of limited value for their use on crops in several European countries. Some of them are not registered at all, some are registered in some countries and not in others. The major part of the insecticides cited in table 7, as well as many other more recently tested, are not selective for the natural enemies which are commonly used in integrated pest management (IPM) on vegetable and ornamental plants (Ramakers, 1990; van de Veire *et al.*, 2002).

In conclusion, it seems that chemical control cannot resolve the problem of WFT for the European greenhouses industry. The level of control achieved with insecticides is not sufficient to provide an adequate reduction in thrips numbers or TSWV disease (Yudin *et al.*, 1991; van Driesche *et al.*, 1998). Therefore, alternatives to insecticidal control of thrips are needed. Potential alternatives that could be integrated with chemical control include cultural control, host-plant resistance and biological control. Developing monitoring systems, establishing treatment threshold levels and application of biological control measures will lead to a decrease in the number of sprays.

1.7.2. Cultural control

Mechanical barriers (e.g., meshes, netting, plastic sheets) provide a type of cultural control which has been used to restrict insect vectors from landing on their hosts (Broadbent, 1969; Cohen and Marco, 1973, 1979; Harpaz, 1982). Yudin *et al.* (1991) studied the effect induced by aluminium polyvinyl netting (1.5 m high from the soil) on the reduction of WFT numbers

in a field of lettuce crop. They obtained 10% decrease in thrips numbers when these mechanical barriers were used. In a study carried out by Berlinger *et al.* (1993), commercial woven screens in aluminium colour were used to avoid the entrance of *F. occidentalis* into greenhouses. It reduced the penetration of thrips to 20-40% of the number found in the control. These results seem to be due more to the repulsive effect of the aluminium colour than to the mesh size used.

Also the use of sticky traps as a mass trapping tool was proposed by some authors (Murai, 1988; Brødsgaard, 1993a). The largest effect of mass trapping can be obtained by suspending the traps near ground level, because at this height not only large numbers of thrips can be caught, but thrips can be caught before they have the opportunity to reproduce in the crop (Brødsgaard, 1993a). However, use of vast amounts of sticky traps is probably not compatible with the normal cultural activities in many vegetable and ornamental plants. Using a proper screen and/or sticky traps, can obviously contribute as a monitoring device and sometimes to reduce population of WFT. Complementary control measures which are more efficient, like biocontrol, are, however, needed (Berlinger *et al.*, 1993; Brødsgaard, 1993a).

The use of trap plants like gloxinia and impatiens for WFT control was studied by Hoyle and Saynor (1993), but without great effectiveness.

Table 7. Insecticides tested against WFT, in laboratory or greenhouse experiments (test period 1985 - 1995).

INSECTICIDE	CLASS	CONTROL	REFERENCES
Endosulfan	Chlorinated hydrocarbon	+-	1, 5, 7, 12, 16
Chlorpyriphos-methyl	Organophosphate	+-	1, 4, 7, 10, 12, 13, 15
Dichlorvos	Organophosphate	* +-	4, 5, 6, 7, 8, 18
Etrimphos	Organophosphate	++	3
Malathion	Organophosphate	+-	8, 12
Methamidophos	Organophosphate	++	1, 2, 4, 5, 7, 14, 16
Monocrotophos	Organophosphate	+-	1, 13
Omethoate	Organophosphate	+-	2, 7, 14
Formetanate	Carbamate	* ++	4, 7, 9, 10, 14
Furathiocarb	Carbamate	++	3
Methiocarb	Carbamate	* ++	4, 10, 11, 12, 13, 14, 17
Methomyl	Carbamate	* +-	1, 5, 7, 19
Deltamethrina	Pyretroid	--	2, 8
λ -cyhalothrin	Pyretroid	+-	5, 10, 14
Abamectine	Macrocyclic lactone	--	5, 13, 14, 15

++ excellent control; +- good control; - marginal control; * phytotoxic

Legenda: 1 -Hamrick, 1987; 2 -Bohmer and Eilenbach, 1987; 3 -Freuler and Benz, 1988; 4 -Paitier, 1990; 5 -Bournier, 1990; 6 -Ramakers, 1990; 7 -(Heungens *et al.*, 1989; Heungens and Butaye, 1990); 8 -Ribes and Silla, 1990; 9 -Jover *et al.*, 1990; 10 -Ferrer *et al.*, 1990; 11 -Puiggròs *et al.*, 1990; 12 -Devesa and Dow Elaco Hib., 1990; 13 -Gokkes, 1991; 14 -Grasselly *et al.*, 1991; 15 -Nasruddin and Smitsley, 1991; 16 -Bohmer *et al.*, 1992; 17 -Pasini *et al.*, 1993; 18 -Staay and Uffelen, 1988; 19 -Heungens, 1994.

Note: Abamectine showed a good control of young instars (Bohmer *et al.*, 1992; Pasini *et al.*, 1993), but a first documented case of resistance to this chemical was reported by Immaraju *et al.*(1992)

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1.7.3. Host-plant resistance

There is little knowledgeable about resistance of plant species or cultivars to thrips. Some studies were carried out for vegetable crops (Fery and Schalk, 1991; Mollema, 1992; Robb, 1992), but no good results were obtained. Research on chrysanthemum was undertaken by Broadbent *et al.* (1990), who recorded that yellow-flowers were preferred by WFT over white-flowers. But Dijken *et al.* (1993) found that flower colour was not important to attract thrips. A chrysanthemum cultivar resistant to the direct damage caused by thrips was found by Jager and Butôt (1993). However, it is not easy to come up with a host-plant resistance solution, because finding a resistant species or cultivar is not the same as finding a plant which is relatively unattractive to thrips. Furthermore, WFT is also a vector of viruses and this problem makes it more difficult in establishing effective host-plant resistance.

1.7.4. Biological control

The implementation of biological control in greenhouses has been influenced by a number of factors. When biological control of one pest is initiated, the use of pesticides against other pests has to be avoided. To allow the natural enemies to survive, alternative control methods have to be used against other pests and diseases. For example, in The Netherlands chemical control of WFT and leafminers interrupted the biological control of whitefly (van Lenteren *et al.*, 1979; Ravensberg *et al.*, 1983). On the other hand, pesticide resistance to the most common insecticides showed in pests like WFT, gave a big impulse to develop IPM (Robb, 1989; Paitier, 1990; Ramakers, 1990; Bournier, 1990; Brodsgaard, 1991b). Presently, the use of IPM programmes is also stimulated by many governments in order to reduce the use of chemicals and to lower residues on products (Ramakers, 1989). Finally, the application of bumble bees for pollination in sweet pepper, eggplant and tomato crops limits the use of many pesticides (Ramakers, 1989).

Generally, natural enemies include pathogenic microbes, parasitic insects, predaceous arthropods and in some cases, competitors (Ehler, 1990). Many natural enemies of thrips pests are known. Generally they are polyphagous species. The most important groups of natural enemies which are more or less specific for *F. occidentalis* and *T. tabaci*, will briefly described here. One of the main problems to develop biological control is that only for a few natural enemies data about the effectivity of reducing WFT populations are available.

1.7.4.1. Pathogens

The following pathogens of *F. occidentalis* and *T. tabaci* are known: the fungi *Zoophthora radicans* (Brefeld) Batko.; *Neozygites parvispora* (Macleod et Carl) (Keller and West, 1983); *Entomophthora thripidum* Samson, Ramakers and Oswald (Samson *et al.*, 1979; Ananthakrishnan, 1993); *Beauveria bassiana* Bals. (Dyadechko, 1964; Lipa, 1985; Ananthakrishnan, 1993); *Verticillium lecanii* (Zimm.) (Nedstam, 1991); *Metharizium anisopliae* (Metsch.); *Paecilomyces fumosoroseus* (Wize) Brown and Smith, and the nematods *Howardula aptini* (Sharga) (Wilson and Cooley, 1972); *Thripinema nicklewoodii* Siddiqi (Greene and Parrella, 1993) and *Steinernema feltiae* (Filipjew) (Tomalak, 1991).

Gillespie (1984, 1986) investigated the use of *V. lecanii*, *B. bassiana*, *M. anisopliae* and *P. fumosoroseus* for controlling *T. tabaci*; *M. anisopliae* and *B. bassiana* proved to be very pathogenic under ideal laboratory conditions. In the former USSR, *B. bassiana* reduced the thrips population by 83% after only two applications (Lipa, 1985). Against *F. occidentalis* a high mortality was induced by *V. lecanii* in the laboratory (Gillespie, 1989a) and in

greenhouses on chrysanthemum, where humidity was raised, 95% mortality was observed (Helyer, 1993). *V. lecanii* was, however, not effective for *F. occidentalis* in pot plant and cucumber crops, because of a low humidity (Nedstam, 1989; Helyer, 1993).

The nematode *S. feltiae* was studied with variable success to control *F. occidentalis* from several authors (Tomalak, 1991; Helyer *et al.*, 1995; Chyzik *et al.*, 1996).

Pathogens do not seem to provide good solutions for the control of WFT, mainly because they need a high relative humidity to develop and this is often a serious problem for the crops, because the plants become susceptible to several diseases under such conditions. Moreover, problems exist in the mass-production of these entomopathogens (Wilding and Latteur, 1987; Bartlett and Jaronski, 1988)

1.7.4.2. Parasitoids

Thrips parasitoids all belong to the superfamily Chalcidoidea. Most of them are solitary endoparasitoids of larvae (Eulophidae) or eggs (Mymaridae, Trichogrammatidae) of thrips. Except for some odd species in the genus *Thripastichus* (Euliphidae: Terastichinae) and *Podiobius* (Euliphidae: Enterodontinae), all larval parasitoids can be found in four closely related genera: *Ceranisus*, *Goetheana*, *Thripobius* and *Entedonastichus* (Euliphidae: Entodontinae). They all are solitary, internal parasitoids of the larval stages, although sometimes the prepupae and/or pupae may be attacked. Parasitoids belonging to the genus *Megaphragma* (Hymenoptera: Trichogrammatidae) and *Podibius indicus* (Hymenoptera: Mymaridae) are known to parasitize thrips eggs. Relatively little is known about most parasitoids attacking thrips, and *F. occidentalis* in particular (Loomans, 1991). Only *Ceranisus menes* (Walker) and *Ceranisus americensis* (Girault) are known to attack and develop on *F. occidentalis* and *T. tabaci*, and most attention was paid to a common wide-spread species *C. menes* (Murai, 1990; Galazzi *et al.*, 1991-92; Loomans *et al.*, 1992; Loomans *et al.*, 1993; Loomans and van Lenteren, 1995; Fourez, 1995; Loomans, 2003) and *C. americensis* (Girault) (Loomans and van Lenteren, 1996; Loomans, 2003).

The distribution of *C. menes* can be considered as cosmopolitan (Loomans *et al.*, 1992). It can parasitize larvae of many thrips species, including important pest species, but the actual host preferences were not established (Sakimura, 1937b; Viggiani, 1977; Murai, 1990; Loomans and van Lenteren, 1995).

Murai (1990) showed that *C. menes* can be reared on thrips of the genus *Frankliniella*, and other authors (Loomans, 1991; Galazzi *et al.*, 1991-92) showed can it can develop also on *F. occidentalis*.

Development time for *C. menes*, as well almost all thrips parasitoid species, is relatively long and its longevity rather short compared to that of *F. occidentalis* and *T. tabaci*. For example, the development time for *F. occidentalis* and *T. tabaci* varies from 14-21 days between 20-25°C, and *C. menes* takes at least two weeks more to complete its life-cycle (Loomans, 1991; Galazzi *et al.*, 1991-92; Greene and Parrella, 1993; Loomans and van Lenteren, 1995; Fourez, 1995). Temperature strongly mediates development time and in particular pupal development. At 20°C or lower, the life-cycle is very long (Loomans and van Lenteren, 1995). At low temperature, pupae probably are not in diapause, but in a quiescent state, because pupae started hatching relatively fast when transferred to higher temperature (Murai, 1988).

C. menes has been found on a wide range of host plants in different biotopes, also in Europe (Loomans, 1991; Galazzi *et al.*, 1991-92; Gabarra, 1992; Mateus, 1993): it seems that no specific biotope is preferred. It has been collected mostly from flowering plants, representing more than 20 different families. Plant structure can influence host-searching

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efficiency and overall parasitization success to a large extent (Loomans and van Lenteren, 1995).

High levels of parasitization have been reported from Asia (Sakimura, 1937b), but in Europe they were recorded only occasionally and in particular on *T. tabaci*. *C. menes* seems not to contribute significantly to thrips control in greenhouses (Loomans and van Lenteren, 1995). Classical biological control of thrips pests by releasing parasitoids in an inoculative way was tried against *T. tabaci* in Hawaii, but without success (Sakimura, 1937a). *C. menes*, as well *C. americensis*, showed a very limited searching efficiency and obtained low parasitization levels when it was released against *F. occidentalis* in an experimental greenhouses with roses in The Netherlands (Loomans *et al.*, 1995).

In conclusion, *C. menes* cannot be considered as a suitable candidate for seasonal inoculative biological control of *F. occidentalis*, but might be useful in inundative release programmes (Loomans and van Lenteren, 1995). For more details on thrips parasitoids, I refer to review by Loomans and van Lenteren (1995) and Loomans (2003).

1.7.4.3. Predators

The literature on natural enemies provides much information on predators of Thysanoptera (e.g. Thompson and Simmonds, 1965; Herting and Simmonds, 1971; Lewis, 1973; Ananthakrishnan, 1973, 1979, 1984; Ananthakrishnan and Sureshkumar, 1985; Fry, 1987; Riudavets, 1995; van Driesche *et al.*, 1998). Many arthropods are known to be predators of thrips and a large part is cited as predators of *F. occidentalis* and *T. tabaci*. They belong to several families of Heteroptera like Anthocoridae, Miridae, Nabidae and Lygaeidae, as well some species of the Thysanoptera order, and species of the orders Diptera, Neuroptera (Chrysopidae), Coleoptera and Araneida (Acari) (Lewis, 1973; Ananthakrishnan, 1979). But often biological control data and information about their biology when exposed to these pest species is lacking. The most studied families of thrips predators are Phytoseiidae and Anthocoridae.

1.7.4.3.1. Thysanoptera. Few species of Thysanoptera are thrips predators, and they belong mainly to the genera *Aeolothrips* Haliday (Lewis, 1973; Lacasa, 1988b), *Haplothrips* Amyot and Serville, *Scolothrips* Hinds and *Franklinothrips* Back. Few of them are described as predators of *F. occidentalis* and *T. tabaci*: e.g. *Aeolothrips fasciatus* L (Baker, 1988; Ferrari 1980; El Serwi *et al.*, 1985) and *Aeolothrips intermedius* Bagnall (Lacasa, 1980).

A. intermedius was studied as predator of *T. tabaci*, on which it can complete its development (Bournier *et al.*, 1978, 1979; Lacasa, 1980; Lacasa *et al.*, 1982). This species can be considered cosmopolitan and it is common in many biocoenoses of cultivated and wild plants such as strawberries (Ribes, 1990) and onions (Lacasa *et al.*, 1989). The first instar of *A. intermedius* is already feeding on prey, and it consumes on average 25 *T. tabaci* larvae in order to complete its preimaginal development. In Southeast Spain, predation by *A. intermedius* is fairly limited and not quantitatively important (Lacasa *et al.*, 1989). *A. fasciatus* appeared insufficient to control outbreaks of *T. tabaci* (Ferrari, 1980). *A. intermedius* is omnivorous, as most thrips predators and can complete their development by feeding only on pollen (Bournier *et al.*, 1979; Lacasa, 1980). These predators do, however, not seem useful for biocontrol of thrips mainly because they frequently cause damage to the plants, they are difficult to rear and are not compatible with other natural enemies. Several natural enemies attack *A. intermedius* including other species of the genus *Aeolothrips* (Lacasa, 1980). Recently some studies were carried out on *F. vespiformis* (Crawford) as predator of thrips. This thrips showed to be able to locate and feed on eggs of *T. palmi* and *Echinothrips americanus* Morgan (Loomans and Vierbergen, 1999; Loomans and Heijboer, 1999). *E.*

americanus is a nearctic pest species introduced in North Europe in 1993. Nowadays it is causing strong outbreaks mostly on sweet pepper crops (Vierbergen, 1998). Only adults of *F. vespiformis* showed to be able to prey on thrips eggs and only when eggs are laid on plant with soft leaves, for example *Ficus* (Loomans and Heijboer, 1999). Nevertheless the importance of *F. vespiformis* and other thrips predators to control thrips pests, their use appear still very hard and limiting because of their polyphagous habits (van Lenteren and Loomans, 1998). Furthermore, laboratory rearing of thrips predators is difficult due to the high percentage of cannibalism (Bournier *et al.*, 1978; Bournier *et al.*, 1979; Lacasa, 1980; Lacasa *et al.*, 1982).

1.7.4.3.2. Phytoseiidae. Several genera preying on thrips are included in Phytoseiidae, among which are *Amblyseius* (Berlese), *Neoseiulus* (Hughes), *Euseius* (Wainstein), *Typhlodromus* (Scheuten) and *Phytoseiulus* (Evans). They are mainly polyphagous and feed on small arthropods. The most important species of this family for biological control of thrips belong the genus *Amblyseius*. The species of Phytoseiidae which have been described as predators of *F. occidentalis* or *T. tabaci* are: *A. addoensis* van der Merwe and Ryke, *A. barkeri* (Hughes) (=*A. mckenziei*) (Schuster and Pritchard), *A. potentillae* (Garman), *A. sessor* Delon, *A. urescens* A. and H., *A. degenerans* Berlese and *N. cucumeris* (Oudemans).

Most attention for control of *F. occidentalis* was paid to the following three species: *A. barkeri*, *N. cucumeris* and *A. degenerans*.

N. cucumeris and *A. barkeri* are cosmopolitan species and prey on *F. occidentalis* and *T. tabaci* (MacGill, 1939; Rodriguez-Reina *et al.*, 1992), as well as on other thrips and mites (Riudavets, 1995).

N. cucumeris and *A. barkeri* have been studied on many crops and in laboratory experiments. Some biological parameters are shown in table 8 (for more details see Riudavets, 1995).

Both *N. cucumeris* and *A. barkeri* can eat large amounts of prey (Gillespie, 1989b; Kajita, 1986; Bakker and Sabelis, 1987; Hansen and Geyti, 1987; Guyot, 1988; Bakker and Sabelis, 1989), but they prey only on first instars of thrips (Gillespie and Ramey, 1988; Gilkeson, 1990; Claudio, 1991). Due to its attack of first instar thrips only, it takes a long time before *N. cucumeris* can reduce *T. tabaci* populations (Gilkeson, 1990). Females and males of *A. barkeri* consume an average of 89 and 82 larvae of first instar larvae of *T. tabaci* (Bonde, 1989), or 48 and 20 first instar thrips larvae of *F. occidentalis* (Sengonga and Bendiek, 1988) respectively during their lifespan. *A. barkeri* cannot develop completely feeding on *F. occidentalis* (Sengonga and Bendiek, 1988).

The introductions of these two predators for thrips control in greenhouses in several countries show contradictory control results. For *N. cucumeris* the success rate has been lower on cucumbers and eggplant than on sweet peppers, and success was less for the control of *F. occidentalis* than for *T. tabaci* (Ramakers, 1978; de Klerk and Ramakers, 1986; Ravensberg and Altena, 1987; Ramakers, 1990; Jacobson, 1995; Dissevelt *et al.*, 1995; Riudavets, 1995). The effectiveness of *N. cucumeris* depends on its speed of reproduction, which, on its turn, is dependent upon availability of pollen (Altena and Ravensberg, 1990; Ramakers, 1990; van Rijn and Sabelis, 1993). *N. cucumeris* is able to establish itself on the crop even before the pest appears when pollen are available (Ramakers, 1983; Ramakers, 1990), but it fails to control *F. occidentalis*, because of its low predation capacity (Gerin and Hance, 1993). The females enter reproductive diapause during winter, and the egg hatching success drops at low humidity conditions (Gilkeson *et al.*, 1990; van Houten, 1991; Morewood and Gilkeson, 1991; Sunderland *et al.*, 1992; van Rijn *et al.*, 1993; van Houten *et al.*, 1993; van Houten and van Lier, 1995). *A. barkeri* seems less sensitive than *N. cucumeris* to diapause induction (Claudio, 1991). Good thrips control was obtained with *A. degenerans* on sweet pepper (van

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Houten and van Stratum, 1993). This species showed to be less sensitive to low humidity condition than *N. cucumeris* (van Houten, 1993; van Rijn *et al.*, 1993; van Houten *et al.*, 1995). Recently a new strain of *A. degenerans* was found, which does not go into diapause (van Houten and van Stratum, 1993; van Houten, 1993; van Houten *et al.*, 1995), but more information still needs to be obtained on the thrips control effectiveness of this strain.

A recent study on the introduction of *A. degenerans* in sweet pepper greenhouses using 'banker plants' (*Ricinus communis* L.) was carried out by Ramakers and Voet (1995). The pollen of the banker plants allow the development of a predatory mite population when sweet pepper plants are young and have a low prey density. The first results were promising and *A. degenerans* established on the crop before thrips outbreaks.

In conclusion, predatory mites are able to control thrips infestations on sweet pepper, while contradictory results were obtained for cucumber (Lindhagen and Nedstam, 1988). They do not seem to obtain good control of WFT on other crops like ornamentals (Glockemann, 1991; Buxton and Wardlow, 1991; Nedstam, 1989; Wardlow, 1989; Bertaux, 1989; Del Bene *et al.*, 1993; Buxton and Finlay, 1993).

Natural enemies producers in Europe now rear *N. cucumeris* and *A. degenerans*. Mass-production using thrips as prey is uneconomic. Predatory mites can be easily reared with *A. farris* that feed on wheat bran (Ramakers and Lieburg, 1982; Ravensberg and Altena, 1987; Gillespie and Ramey, 1988; Hessein and Parrella, 1990).

Table 8 - Development, reproduction and predation capacity of the predatory mites *N. cucumeris*, *A. barkeri* and *A. degenerans* (Fo = *F. occidentalis*, Tt = *T. tabaci*) (after Riudavets, 1995, revised)

Predator	Prey	Preimaginal development time			No. of eggs/fem./day	Consumption of thrips larvae/day	References
		20°C	25°C	30°C			
<i>N. cucumeris</i>	Fo	11.1	8.7	6.3	1.5		Gillespie and Ramey, 1988
	Fo				1.8	6.6	Castagnoli <i>et al.</i> , 1990
	Fo				2.2	6.0	van Houten <i>et al.</i> , 1993
	Tt		8.2		2.0	3.6	Castagnoli <i>et al.</i> , 1990
	Tt		6.2		2.3	3.0	Bonde, 1989
<i>A. barkeri</i>	Tt		6.0		2.0		Beglyarov and Suchalkin, 1983
	Fo				1.4	4.4	van Houten <i>et al.</i> , 1993; 1995
<i>A. degenerans</i>							

1.7.4.3.3. *Heteroptera*. Many families of Heteroptera are known as predators. Only some species of the Anthocoridae, Lygaeidae, Nabidae and Miridae have been mentioned as predators of *F. occidentalis* and *T. tabaci*. The family Anthocoridae contains quite a number of thrips predators.

The major part of the species which belong to the genus *Geocoris* (Fallen) (Lygaeidae) are phytophagous (Carayon, 1961) and only two species, *Geocoris pallens* (Stal), and *Geocoris atricolor* Montandon (both nearctic) have been described as predators of *F. occidentalis* (Benedict and Cothran, 1980; Riudavets, 1995). *Geocoris* spp. are not effective against *F. occidentalis*. They are in fact omnivorous and frequently consume plant juices (Yokoyama, 1978; Benedict and Cothran, 1980; González and Wilson, 1982). Details on the development time of *G. pallens* were studied by Butler (1966). A laboratory rearing of *G. pallens* is described by Yokoyama (1980).

Among *Nabis* (Latreille) (Nabidae), which are mainly predatory species, four species have been described as predators of Thysanoptera. *Nabis alternatus* (Parshley) and *Nabis americoferus* (Carayon) have a nearctic distribution (Canada, USA and Mexico). *Nabis ferus* (L.) (Euro-Siberia, rare in the Mediterranean region) and *Nabis pseudoferus* Remane (throughout all Central and southern Europe and in southern England and southern Scandinavia) (Riudavets, 1995) have a palaearctic distribution. Only the first two species prey on *F. occidentalis* and they are found mainly on alfalfa and bean (Benedict and Cothran, 1980; Stoltz and McNeal, 1982), while the other two species are found on *T. tabaci* (Dimitrov, 1975a). Both adults and nymphs are predatory (Benedict and Cothran, 1980). No studies of their biology when feeding on Thysanoptera have been made. To obtain water, they use plant saps which may cause plant damage (Ridgway and Jones, 1968). They are difficult to rear mainly because of cannibalism between nymphs (Perkins and Watson, 1972).

In the Miridae family, the palaearctic species *Deraecoris pallens* Reuter, *Dicyphus eckerleini* Wagner, *Dicyphus tamaninii* Wagner, *Macrolophus rubi* Woodroffe (= *M. costalis* Fieber), and *Macrolophus caliginosus* Wagner, are polyphagous and they have been described as preying upon *T. tabaci* and *F. occidentalis* (Riudavets, 1995).

M. rubi and *D. eckerleini*, which feed on *T. tabaci*, showed to be the most numerous beneficial insects of the predator complex on Bulgarian tobacco and they keep *T. tabaci* at low population densities (Dimitrov, 1975a, 1975b, 1976a, 1977; Dirimarov and Dimitrov, 1975).

D. tamaninii and *M. caliginosus* are able to complete preimaginal development and to lay eggs when feeding on *F. occidentalis* (Riudavets, 1993; Riudavets *et al.*, 1993a; b). On cucumber, releases of *D. tamanini* controlled *F. occidentalis* populations in cage trials (Gabarra *et al.*, 1995), but in the field it mainly is present on tomato (Riudavets *et al.*, 1993) on which WFT is not so important as a pest. *D. tamaninii* showed to be effective to control an experimental infestation of WFT on cucumber crop (Riudavets, pers.comm.). This species can, however, be phytophagous in absence of prey. In laboratory trials, *M. caliginosus* consumed a lower amount of WFT larvae (3,1 per day) compared to other predatory bugs like *Orius majusculus* (Reuter) (4,9 per day), *Orius laevigatus* (Fieber) (4,2 per day) and *D. tamaninii* (4,2 per day) (Riudavets *et al.*, 1993a). In the same experiment, the two mirid bugs showed a longer development time and a lower fecundity when feeding on WFT than the two *Orius* species with which they were compared.

In the family Anthocoridae, the genera *Orius* Wolff, *Anthocoris* Fallen, *Montandoniola* Poppius, *Xylocoris* Dufour and *Scoloposcelis* Fieber, are known as predators of several pest species (Carayon, 1961; Sohm, 1981; Schmitt and Goyer, 1983; Ananthakrishnan and Sureshkumar, 1985). The most important species known to prey on *F. occidentalis* and *T. tabaci* are found in the genera *Orius* (Ravensberg, 1991) and *Anthocoris* (L.) (Buxton and

Wardlow, 1991). Knowledge about these polyphagous predators (*Orius* spp.) was limited at the start of this study (1991-92) and was mainly limited to nearctic species *Orius tristis* White (Butler, 1966; González and Wilson, 1982; Salas-Aguilar and Ehler, 1977; Stoltz and Stern, 1978; Shields and Watson, 1980; Gonzales *et al.*, 1982; Stoltz and McNeal, 1982; Hollingsworth and Bishop, 1982; Letourneau and Altieri, 1983; Letourneau, 1990; Tellier and Steiner, 1990; Gilkeson, 1990; Gilkeson *et al.*, 1990), and *O. insidiosus* (Say) (Barber, 1936; Isenhour and Yeargan, 1981; Isenhour and Marston, 1981; Kingsley and Harrington, 1982; Isenhour and Yeargan, 1982; Ananthakrishnan and Sureshkumar, 1985; Kiman and Yeargan, 1985; McCaffrey and Horsburgh, 1986; Ruberson *et al.*, 1991; Brødsgaard, 1991b). Ryerson and Stone (1979) reviewed the biology of these two species. Before 1991-92 only a few studies were carried out on the palearctic species *O. majusculus* (Reuter) (Péricart, 1972; Alauzet *et al.*, 1990; Ramakers, 1990; Trottin-Caudal *et al.*, 1991), *O. laevigatus* (Fieber) (Péricart, 1972; Tawfik and Ata, 1973a; 1973b; Afifi *et al.*, 1976; Ramakers, 1978; Villevieille and Millot, 1991; Tavella *et al.*, 1991) and *O. albipennis* (Reuter) (Puchkov, 1961; Saxena, 1977; Ananthakrishnan and Sureshkumar, 1985; Peña, 1987). In Europe *O. albipennis* is found rarely in southern Spain only, while it is common on the Canarian Islands and in North Africa (Péricart, 1972), where it has its origin. Two other palearctic species preying on thrips are *O. niger* Wolff (Péricart, 1972; Akramovskaya, 1978) and *O. minutus* (L.). *O. minutus* is rare in Middle and South Europe, while it is common in eastern Europe and above all in Asia (Péricart, 1972). No studies were carried out for these two species as predators of WFT. Furthermore, Fulmek (1930) states that *O. minutus* can feed on plant juices and in fact can complete its development when fed only with plant material.

1.7.4.3.5. *Orius* spp. as thrips predator. A short summary of the knowledge of *Orius* species up to 1991 is given below and in table 9. During recent years, the interest of several researchers on thrips biological control has turned to different species of the genus *Orius*. Studies published after 1991 will be discussed in other chapters of this thesis.

Orius spp. can prey on all the different stages of thrips, and they can be found on several plant species, cultivated or not (Péricart, 1972; Tawfik and Ata, 1973; Ramakers, 1990; Trottin-Caudal *et al.*, 1991; Villevieille and Millot, 1991). The development time and the fecundity of these predators are strongly influenced by a wide range of factors, like prey and environmental conditions and in particular temperature (see Tab. 9) (for more details of each species, see Riudavets, 1995).

Adults and nymphs are frequently found in flowers. These observations suggest that their presence on floral structures corresponds to their feeding on thrips or pollen, or both, (Salas-Aguilar and Ehler, 1977). The preference for thrips as prey was demonstrated by Hollingsworth and Bishop (1982) for *O. tristis*.

The oviposition behaviour of *O. insidiosus* as well as the other *Orius* species can cause some damage to a pepper crop. Females lay eggs in or adjacent to the growing tips. Very few eggs are laid in flowers and fruits (van den Meiracker and Ramakers, 1991). Péricart (1972) observed that *O. majusculus* was occasionally phytophagous on chrysanthemums in Holland. Occasionally *O. tristis* was observed to probe plant tissue, perhaps to take in moisture.

However, *O. tristis* is not able to live only on plant tissue (Askari and Stern, 1972; Salas-Aguilar and Ehler, 1977). The literature provides no information on which kind of damage *Orius* may induce on different plants.

O. albipennis was suggested to be a promising general biocontrol agent due to its wide distribution, its continuous presence in cotton agroecosystems in fairly high abundance, its wide range of prey, its high predation capacity and its ability to survive even in the absence of prey (Salim *et al.*, 1987). In Italy *O. laevigatus* adapts very well to a protected environment,

ad it can survive even without thrips prey (Tavella *et al.*, 1991). Good control of WFT was obtained on cucumber in France using *O. majusculus* (Trottin-Caudal *et al.*, 1991). *O. insidiosus* was one of the main species studied to control WFT. On soybeans in the U.S.A. it represented 55% of the total predator population (Barry, 1973). In conjunction with *Aeolothrips fasciatus* (L.) (Robinson *et al.*, 1972) or *Nabis* spp. (Bechinski and Pedigo, 1981) it is one of the most abundant predatory insects present on many plant species. On sweet pepper plants, the persistence of low predator populations at very low prey densities can be explained by the provision of alternative food sources such as pollen (van den Meiracker and Ramakers, 1991). Also *O. tristiscolor* showed good control of WFT on cucumber (Gilkesson *et al.*, 1990). *O. niger* is important in the biological control of *A. gossypii* and *T. tabaci* on eggplants and on several Cucurbitaceae (Akramovskaya, 1978). Greathead (1976) states that this species may be interesting for controlling thrips in greenhouses.

Studies on the interactions of *O. insidiosus*, *O. laevigatus* and *O. tristiscolor* with others predators indicate that they are fully compatible (Parrella *et al.*, 1980; McCaffrey and Horsburgh, 1982; Afifi *et al.*, 1976; Tellier and Steiner, 1990).

Not much was known on the induction of diapause in *Orius* spp. when this research project started. *O. albidipennis* appears to have no diapause (Péricart, 1972; Salim *et al.*, 1987). *O. laevigatus* hibernates as adult in European climates (Péricart, 1972). In Armenia the adults of *O. niger* were found in hibernation during all Winter (Akramovskaya, 1978). For *O. minutus* hibernation occurs in the adult stage (Fulmek, 1930; Puchkov, 1961; Ramakers, 1978). In Canada, *O. tristiscolor* does show diapause, which seems to be induced in the adult female stage, early in Autumn (Tellier and Steiner, 1990).

In conclusion, Anthocoridae seem to be promising candidates for the control of thrips pests and they are currently receiving much attention. *O. tristiscolor* has been successfully tested on greenhouse cucumbers in Canada and *O. insidiosus* has been introduced for thrips control into Europe. Less attention was paid to other *Orius* species such as the palearctic species before my studies started.

1.8. Main conclusions concerning thrips pests and their control

Based on the information provided in this chapter we can conclude that direct damage due to thrips attack is usually less important than its indirect damage caused as virus vector. *F. occidentalis* (Western Flower Thrips) is able to acquire viruses, the most important being Tomato Spotted Wilt Virus, and to transmit it in a persistent way. Also other thrips species are able to transmit viruses. Nowadays problems induced by viruses in several protected crops are very severe, forcing growers to control thrips when they occur at very low densities.

Knowledge of bionomics, life-cycles and biological traits is essential for effective control of thrips. In Europe, the most common pest species of many crops is *F. occidentalis*. The pest status of *F. occidentalis* is still increasing. It occupies new habitats and substitutes other thrips pest species.

Table 9. Development time, fecundity and presence of diapause in several *Orius* spp. fed with different prey.

Prey	Development time in days (T°C) nymph	Development time in days (T°C) egg + nymph	Fecundity No. of eggs/female (T°C)	Diapause	References
<i>O. albidipennis</i>	22.9 (20°C) 20.7 (23°C) 11.1 (24-28°C)		143.4 (24-28°C)	Yes ?	Zaki, 1989
<i>O. insidiosus</i>		34.0 (17°C) 33.6 (20°C) 13.9 (23°C)		yes	Isenhour & Yeargan, 1985 Kiman & Yeargan, 1985 McCaffrey & Hoursburgh, 1986a-b
		20.0 (24°C) 12.6 (28°C) 9.5 (29°C) 12.1 (32°C) 8.3 (35°C)	106.4 (24°C)		
<i>O. laevigatus</i>	13.2 (24-28°C) 13.9 (26°C)		160.6 (24-28°C) 112.4 (25°C)	yes ?	Tawfik & Ata, 1973 Zaki, 1989
<i>O. majusculus</i>	45.2 (12°C) 10.4 (30°C)	44.0 (15°C) 25.7 (20°C) 16.6 (25°C)	195.3 (15°C) 158.2 (20°C) 236.9 (25°C)	yes	Alauzet <i>et al.</i> , 1990
<i>O. tristicolor</i>	26.4 (21°C) 13.9 (24°C)			yes	Askari & Stern, 1972 Salas-Aguilar & Ehler, 1977
	14.4 (25°C)		129.0 (25°C)		Hollingsworth & Bishop, 1982
thrips	9.3 (26°C) 8.4 (33°C)		59.6 (26°C)		

WFT has spread throughout Europe because of the market distribution of plants or plant parts. Spread was also enhanced by development of resistance to most pesticides. Further, Europe may be invaded by new thrips species like *Thrips palmi* Karny which is already resistant to many pesticides. It is spreading around the Pacific Basin of the USA (Mau *et al.*, 1989) and was recently introduced in continental USA (Anonymous, 1991, Childers and Beshear, 1992). Such potential invasions once more stress the need to obtain in depth knowledge of thrips natural enemies. Biological control, in combination with host plant resistance breeding and agroecology, can offer important tools in the development of suitable control strategies.

1.9. Aim and scope of the research described in this thesis

The overall aim of this research project is to develop biological control of *F. occidentalis* through the selection of an efficient beneficial arthropod. The large number of natural enemies of thrips makes it impossible to evaluate all of them on their usefulness for biological control of *F. occidentalis* in a single project. On the basis of available literature data which are summarized in table 10, it was concluded that predators have the best prospect for use in thrips biological control programmes. Research was directed towards on the Anthocorid predators of the genus *Orius* (Rhyncota: Heteroptera), which seems to be the most promising category of predators of *F. occidentalis*. Of the *Orius* genus, the most common species of the Mediterranean regions of Europe were chosen as candidates for biological control of the exotic *F. occidentalis*. It is quite common to find naturally occurring native natural enemies which exploit an exotic pest species (Ehler, 1990; Luck *et al.*, 1988). Furthermore, the use of native natural enemies may avoid negative effects of importation of exotic natural enemies on the native environment (Howarth, 1991; van Lenteren *et al.*, 2003). I followed the general sequence for development of biological control as described by van Lenteren (1989):

- collection of literature data for natural enemy and pest;
- making an inventory of natural enemies and first selection of potential candidate agents;
- detailed study of candidates, selection of best candidate(s);
- mass production and release;
- evaluation of control capacity in release area.

The most difficult part of this sequence is the selection of potentially good candidate species. The criteria for evaluation and selection of biocontrol agents have been studied and described by several authors (Huffaker and Messenger, 1976; van Lenteren, 1986; Hokkanen, 1989; Bigler, 1989; Mackauer *et al.*, 1990). The criteria to be used depend on the type of biological control programme to be developed: classical biological control programmes for exotic or indigenous pests (Hokkanen and Pimentel, 1984; Waage, 1990; Ehler, 1990; Waage and Mills, 1992; Pimentel, 1963; Carl, 1982) or conservation and augmentation of indigenous or exotic natural enemies (Luck, 1992; Luck *et al.*, 1988). Most of these criteria have been developed for parasitoids, but several of them can be used for evaluation of predators as well.

Based in the criteria available for parasitoids, I propose that a good predator for control of thrips species in the Mediterranean area (Table 10):

- 1) is able to search effectively for thrips on different plant parts and on several economically important plant species;
- 2) can develop without entering diapause;
- 3) does not damage the plant;
- 4) has a preference for the pest;

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- 5) is able to survive at low prey density;
- 6) is compatible with the use of other natural enemies;
- 7) can be mass produced economically.

Most of these criteria have not been studied yet for the predators discussed earlier in this chapter.

The research described in this thesis was divided into the following steps:

- First, the distribution of *Orius* species present in Italy was studied (**Chapter 2**). Also, occurrence of *F. occidentalis* together or in absence of *Orius* spp. predators was checked on vegetable and ornamental crops, in order to detect if there might be crops which are unsuitable for the predators.
- Next, the main biological parameters of several *Orius* species (*O. majusculus*, *O. laevigatus*, *O. niger* and *O. insidiosus*) were studied, like development time, fecundity, longevity and predation activity on WFT and on a factitious prey, both during younger and adult stages. Also, a mass rearing system for *Orius* was developed and evaluated. (**Chapter 3**).
- This was then followed by a study on the occurrence of diapause in *O. laevigatus*, by evaluation of the influence of photoperiod and temperature on the reproductive activity of this species (**Chapter 4**).
- Following, the capacity of *O. laevigatus* to control thrips pests (*F. occidentalis* and *T. tabaci*) was studied by releases of this predator on vegetable crops in commercial greenhouses (**Chapter 5 and 6**).
- Finally, the findings are summarized and discussed in **Chapter 7**.

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42 Table 10. Potential quality of different natural enemies for thrips (*F. occidentalis*) control in Europe.

Natural enemies	Climatic adaptation	Predation upon most stages of target pest	Search capability on different plants	Survival at low prey density	No diapause	No negative effects on plant	Preference for target pest	Compatible with other nat. enemies	Economic to rear
PATHOGENS									
Fungi	--	++	--	/	/	++	+-	++	++
Nematoda	--	++	--	/	/	++	+-	++	+-
PARASITOIDS									
Eulophidae	++	--	+-	--	--	++	++	++	--
PREDATORS									
Thysanoptera	++	--	++	++	+-	--	+-	--	--
Phytoseidae	+-	--	+-	++	+-	+-	+-	--	++
Lygaeidae	+-	+-	+-	++	--	--	--	--	+-
Nabidae	+-	++	--	++	+-	--	--	+	--
Miridae	++	++	++	++	/	--	--	+-	+-
Anthocoridae	++	++	++	++	+-	+-	+-	++	+-

(++ good; +- reasonable; -- bad; / unknown)

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Chapter 2. COLLECTION OF *ORIUS spp.* IN ITALY

Abstract

Predators belonging to the genus *Orius* were collected in several areas in Italy on 18 species of vegetable crops, 10 species of ornamental crops, on tobacco and prickly pear, and on 6 species of wild plants. Five *Orius* species which prey on small arthropods (thrips included) and one species, *O. pallidicornis* (Reuter), which feeds on pollen of the wild plant *Ecballium elaterium* Rich. were found. The most common species were *O. niger* Wolff, *O. laevigatus* (Fieber) and *O. majusculus* (Reuter). No clear host-plant preferences of these thrips species were recorded. The species showed different geographic distributions. *O. niger* was found to be widely common in all the Italian regions. *O. laevigatus* was frequently found, was the most abundant species in central and southern regions, but was rare in the northern regions. *O. majusculus* decreased in abundance from northern to central Italy, and was absent below 38° N latitude. *O. horvathi* (Reuter) and *O. vicinus* (Ribaut) were recorded only once on raspberry (in northern Italy) and on sweet pepper (on Sicily), respectively. The phytophagous species *O. pallidicornis* was found only on Sicily. The distribution map of the predators indicates that *O. laevigatus* is the predominant species in the warmest areas, *O. majusculus* in the coldest areas, while *O. niger* occurs all over Italy in similar amount. The survey indicates that *O. niger* and *O. laevigatus* are well adapted to the Mediterranean area which may make them good candidates for biological control of thrips.

2.1. Introduction

The host-plant range of the thrips pest *F. occidentalis* in Europe is very large and includes both cultivated and non-cultivated plants. Vegetable as well as ornamental crops are damaged by thrips directly and indirectly (like the transmission of viruses) (see chapter 1). The list of host plants also includes table grapes, where severe outbreaks have been recorded in Southern Italy (Laccone, 1992), and some fruit trees like nectarine in both South (Marullo, 1991) and North Italy (Tommasini and Ceredi, 2001; Tommasini and Burgio, in press).

The first step in the evaluation of natural enemies for biological control, is to search in the area of origin to determine if an efficient predator, parasitoid or pathogen is present (van Lenteren, 1989; Luck *et al.*, 1988). A collection of one group of thrips natural enemies, heteropteran *Orius* spp., was carried out in many Italian regions, including greenhouse crops and open field crops infested by *F. occidentalis*. An initial identification of the prey-predator association, the predator location within the habitat, and direct observations of predation activity on the target pest is helpful to discover new natural enemies (Luck *et al.*, 1988). The *Orius* species studied here are indigenous predators in Europe, while *F. occidentalis* is a pest imported from North America. Therefore, the approach followed here is not a search of natural enemies in the area of origin of *F. occidentalis*, but a study of potential endemic natural enemies of an introduced exotic pest. Such new combination can give very good biological control results (see *e.g.* van Lenteren, 1997).

Similar collection studies were carried out along the North-Eastern coast of Spain by Goula *et al.*, (1993), Riudavets and Castañé (1994) and Lacasa *et al.* (1996). A general survey on distribution of *Orius* spp. in Europe was first produced by Péricart (1972). Many authors provided information on *Orius* distribution in specific areas in Europe (González Zamora *et*

al., 1992; Gargani, 1993; Vacante and Tropea Garzia, 1993; Vacante, 1993; Chambers *et al.*, 1993; Frescata and Mexia, 1993; Lykouressis, 1993; Tavella *et al.*, 1994; Ivancich Gambaro, 1995; Lykouressis and Perdikis, 1997; Barbetaki *et al.*, 1999).

In this paper, the results of an intensive predator collection project in Italy are reported and the data are compared with other data on distribution of *Orius* species.

2.2. Materials and methods

A list of plants infested by thrips pests and particularly by *F. occidentalis*, was compiled by checking the literature and taking into account the observations of several crop protection specialists working in various Italian regions. The list included 18 vegetable crops (sweet pepper, eggplant, cucumber, melon, watermelon, zucchini, bean, French bean, pepper, basil, pumpkin, tomato, lettuce, onion, leek, strawberry, raspberry, black currant), 9 ornamental crops (gerbera, chrysanthemum, oleander, rose, dahlia, gladiolus, geranium, impatiens and hibiscus), tobacco, prickly pear and 6 wild plants (*E. elaterium* Rich., *Cirsium* spp., *Sinapsis alba* (L.), *Crepis* spp., *Inula viscosa* (L.) and a few species of crucifers). Collection of predators belonging to the genus *Orius* was carried out in 30 Italian Provinces from North to South in both protected and open field crops. The collection was undertaken during the summer periods from June to September during four years (1991-1994). In order to follow a standard methodology for each crop, mainly the flowers were monitored and *Orius* adults were collected with a 'mouth aspirator'. Sampling continued for at least 20 minutes per plant, even when no *Orius* were found.

Specimens were preserved in 75% alcohol. Adult males were dissected in the laboratory for identification by comparing the parameres of their sexual organs using a stereomicroscope. The keys of Péricart (1972) were mostly used for taxonomic identification. A morphological key for identification of live female adults belonging to the three *Orius* species predominant in Italy was designed in order to simplify identification in the future (Table 2).

2.3. Results and Discussion

During the survey of four years, 518 samples were taken resulting in the collection of 4,931 individuals, which comprised 6 *Orius* species. In the Mediterranean basin plastic tunnels are generally used for growing protected crops, and they usually remain open for a large part of the crop cycle. The result is a continuous exchange of pests and natural enemies between outdoors and indoors. Therefore, samples collected in the open field and in the greenhouse were considered together. The sampling data are reported in tables 1a and 1b and figure 1, and show that *O. laevigatus* (Fieber) (subgenus *Orius* s. str.), *O. niger* Wolff (subgenus *Orius*) and *O. majusculus* (Reuter) (subgenus *HeterOrius* Wagner) were the species most frequently found. They formed 57.58%, 37.51% and 4.05% respectively of the total number of specimens checked. The other three species, *O. horvathi* (Reuter) (subgenus *HeterOrius*), *O. vicinus* (Ribaut) (subgenus *HeterOrius*) and *O. pallidicornis* (Reuter) (subgenus *Orius*), were collected in very low numbers (0.82%, 0.02% and 0.02% respectively of the total).

Péricart (1972) described *O. pallidicornis* as species feeding on pollen, clearly associated with its host plant *E. elaterium*. Goula *et al.* (1993) found this species also on *Amaranthus blitoides* (L.) in Spain. *O. pallidicornis* was found only in some areas on Sicily (37-38° N latitude) on *E. elaterium*.

Chapter 2

When *O. pallidicornis* is excluded from the analysis, no strict link appears to exist between *Orius* species and plants or a groups of plants (Tables 1a and 1b), so it can be concluded that no strong host-plant preferences exist in these *Orius* species.

In general, *O. laevigatus* was the most abundant species in Italy, particularly on vegetable crops. This confirms the findings of Tavella *et al.* (1994) who sampled *Orius* spp. on sweet pepper at the North-western Italian coast, and Vacante and Tropea Garzia (1993a) who collected *Orius* species on sweet pepper on Sicily (southern Italy). Similar data were recorded in Spain (Gonzàles Zamora *et al.*, 1992; Goula *et al.*, 1993; Riudavets and Castañé, 1994), Portugal (Frescata and Mexia, 1993) and Greece (Lykouressis and Perdikis, 1997; Barbetaki *et al.*, 1999), indicating a probable dominance of *O. laevigatus* in the Mediterranean basin. In Italy *O. laevigatus* numbers were highest on basil, sweet pepper, eggplant, melon and french bean. In Spain, *O. laevigatus* was the most abundant species on strawberry, sweet pepper, cucumber and rose (Goula *et al.*, 1993; Riudavets and Castañé, 1994). In England, it was frequently found on local patches of nettles (Chambers *et al.*, 1993).

O. niger was frequently found on strawberry in the North-eastern Italian regions (Ivancich Gambaro, 1995). I found that this species was the most abundant also on wild plants where *O. laevigatus* and *O. majusculus* were rarely found. Wild plants outside the crop may positively influence occurrence of natural enemies on the crop as wild plants provide alternative food as well as shelter for overwintering (van Emden, 1990). The rare presence of *O. laevigatus* and *O. majusculus* on wild plants might be explained by the higher attraction of the nearby crops infested with thrips, compared to the non-cultivated plants with few thrips. This preference for cultivated plants is a positive parameter for natural enemies. *O. majusculus* was rarely found on ornamental crops. The crops showing the highest attraction for the three most common *Orius* species were sweet pepper, followed by eggplant, strawberry and French bean (Table 1a and 1b). *Orius* predators were rarely found on tomato which confirms the results of Riudavets *et al.* (1993a, b).

O. horvathi and *O. vicinus* were recorded only once on raspberry in northern Italy, and on sweet pepper on Sicily, respectively. *O. horvathi* was also rarely found in Spain (Riudavets and Castañé, 1994).

The various species showed differences also in their geographic distribution (Fig. 1 and Table 2). *O. niger* was widely spread over all the Italian regions. *O. laevigatus* was frequently found in central and southern regions. It was the most abundant species in Ligury, Tuscany, Umbria, Abruzzo, Calabria and Sicily. It was rarely found in the northern regions. *O. majusculus* decreased in its relative abundance from northern to central Italy, and was absent below 38° N latitude. The distribution map of the predators indicates that *O. laevigatus* is predominant in the warmest areas and near the coasts, *O. majusculus* in the coldest areas such as the Po valley, while *O. niger* appears occurs all over Italy. The present data confirm the studies of Alauzet *et al.* (1992; 1994) showing that *O. laevigatus* is more adapted to high temperatures than *O. majusculus*. These data also suggest that *O. laevigatus* and *O. niger* may be good candidates for control of *F. occidentalis* in the warmest areas of the Mediterranean basin. *O. majusculus* might be a good candidate for more northern areas.

No specimens of the exotic *O. insidiosus* (Say) were found, not even in the greenhouses where this nearctic species was released for biological control of thrips together with *O. albidiipennis*. *O. insidiosus* is apparently unable to establish itself on sweet peppers in greenhouses or on wild plants in the field. This finding is in agreement with Tavella *et al.* (1994). Recently, I again checked samples collected on Sicily in 2000 on vegetable crops and a high number (>300 individuals) of *O. albidiipennis*, native of the Canary Islands, was recorded, but no *O. insidiosus* were found (Tommasini, 2002, unpublished data).

Figure 1. Distribution of *Orius* species collected in Italy (518 samples, 4931 individuals).

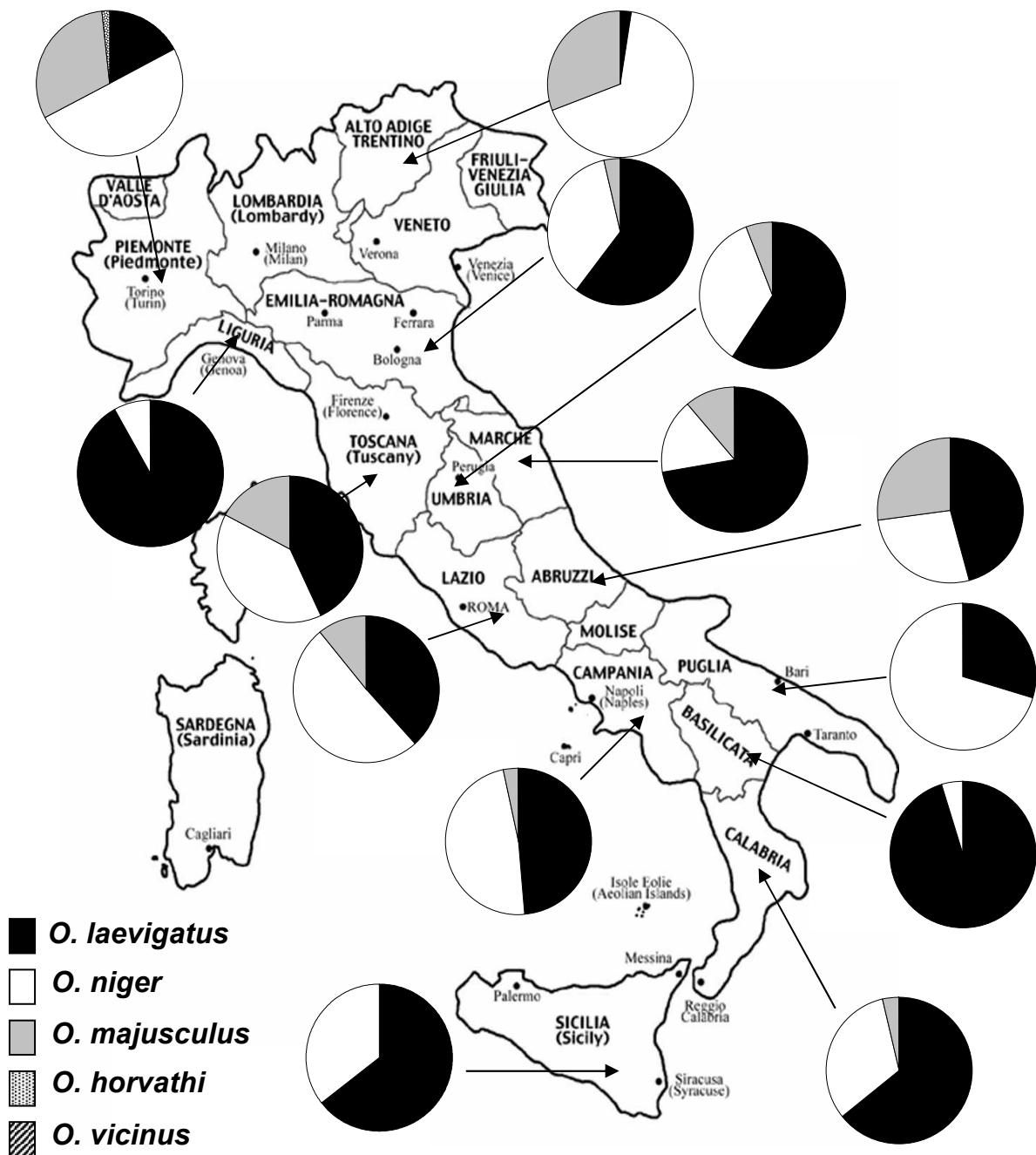


Table 1a. Relative abundance of *Orius* species collected in Italy on several plants.

Plants	<i>O. laevigatus</i>	<i>O. majusculus</i>	<i>O. niger</i>	<i>O. pallidicornis</i>	<i>O. horvathi</i>	<i>O. vicinus</i>
Sweet pepper	+++	+++	+++	-	-	+
Eggplant	+++	++	+++	-	-	-
Melon	+++	++	++	-	-	-
French bean	+++	++	+++	-	-	-
Zucchini	++	++	++	-	-	-
V Pepper	+	++	++	-	-	-
E Pumpkin	+	+	+	-	-	-
G Basil	+++	+	++	-	-	-
E Strawberry	+++	++	+++	-	-	-
T Cucumber	++	+++	++	-	-	-
A Tomato	-	+	-	-	-	-
B Lettuce	-	+	+	-	-	-
L Water melon	++	+	++	-	-	-
E Bean	+	+	+	-	-	-
Raspberry	+	+	++	-	+	-
Black currant	-	+	-	-	-	-
Onion	-	+	-	-	-	-
Leek	+	+	+	-	-	-
Tobacco	+	+	++	-	-	-
O Oleander	++	++	++	-	-	-
R Rosa	++	+	+	-	-	-
N Gerbera	+	+++	+++	-	-	-
A Impatiens	-	+	+	-	-	-
M Dalia	-	+	+	-	-	-
E Gladiolus	-	+	+	-	-	-
N Hibiscus	+	++	++	-	-	-
T Geranium	+	+	+	-	-	-
A Chrysanthemum	+	++	++	-	-	-
L Prickly pear	+	-	-	-	-	-
O <i>Ecballium elaterium</i>	-	+	+	+++	-	-
H <i>Cirsium</i>	+	+	+	-	-	-
E <i>Sinapis alba</i>	+	+	+	-	-	-
R <i>Crepis</i>	-	-	-	-	-	-
<i>Inula viscosa</i>	+	++	++	-	-	-

Legend: - never found, + rare (1-3 samples occurrence), ++ common (4-10 samples occurrence), +++ abundant (> 10 samples occurrence).

Table 1b. Number specimens of *Orius* species collected in Italy on several plants.

Plants	<i>O. laevigatus</i>	<i>O. majusculus</i>	<i>O. niger</i>	<i>O. pallidicornis</i>	<i>O. horvathi</i>	<i>O. vicinus</i>
Sweet pepper	1360	54	572			1
Eggplant	91	18	68			
Melon	116	7	41			
French bean	1040	17	570			
Zucchini	32	9	28			
V Pepper	7	4	11			
E Pumpkin	3	1	6			
G Basil	101	2	54			
E Strawberry	43	5	199			
T Cucumber	22	32	16			
A Tomato		1				
B Lettuce		4	4			
L Water melon	16	3	65			
E Bean	46	6	9			
Raspberry	1	5	6		1	
Black currant		9				
Onion		1				
Leek	5	2	4			
Tabacco	6	6	14			
O Oleander	31	2	34			
R Rosa	10		6			
N Gerbera	12	1	41			
A Impatiens			1			
M Dalia			2			
E Gladiolus			2			
N Hibiscus	6	6	12			
T Geranium	1	2	3			
A Chrysanthemum	1	1	11			
L Prickly pear	1					
O <i>Ecballium elaterium</i>			1	40		
H <i>Cirsium</i>	1		5			
E <i>Sinapsis alba</i>	1		1			
R <i>Crepis</i>			1			
<i>Inula viscosa</i>	4		37			
Total	2857	198	1834	40	1	1
%	57.9	4.0	37.2	0.8	0.02	0.02
Total				4931		

Table 2. Number of specimens of *Orius* species collected in Italy (1991-1995 survey).

Region	Latitude	<i>O. laevigatus</i>		<i>O. niger</i>		<i>O. majusculus</i>		<i>O. pallidicornis</i>	<i>O. horvathi</i>	<i>O. vicinus</i>
		Male	Female	Male	Female	Male	Female	Male	Male	Male
N	Trentino	46.1	0	1	24	4	4	9	0	0
O	Piemonte	44.9-44.4	1	9	17	12	14	4	0	1
R	Emilia-	44.8-44.1	58	785	263	254	36	14	0	0
T	Romagna									
H	Ligury	44.3-43.9	29	17	3	1	0	0	0	0
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C	Toscany	43.8-42.8	25	42	16	46	6	21	0	0
E	Umbria	43.5	63	248	38	144	2	29	0	0
N	Marche	43.6	13	0	3	0	2	0	0	0
T	Abruzzo	43.7-42.2	10	0	6	0	6	0	0	0
R	Lazio	42.4-41.5	47	128	79	152	6	43	0	0
E										
<hr/>										
S	Campania	40.7	6	8	8	6	1	0	0	0
O	Basilicata	40.6	6	14	1	0	0	0	0	0
U	Puglia	41.5-40.4	11	0	26	0	0	0	0	0
T	Calabria	38.9-38.1	16	2	4	5	1	0	0	0
H	Sicily	37.5-37.0	420	898	96	626	0	0	40	1
<hr/>										
Total		705	2152	584	1250	78	120	40	1	1
Sex Ratio (within species)		24.7 %	75.3 %	31.8 %	68.2 %	39.4 %	60.6 %	100 %	100%	100 %
<hr/>										
4931										

Table 3. Morphological key to distinguish live females of *O. laevigatus*, *O. niger* and *O. majusculus*.

Characteristics	Subgenus <i>Heterorius</i> (<i>O. majusculus</i>)	Subgenus <i>Orius</i> (<i>O. laevigatus</i>)	Subgenus <i>Orius</i> (<i>O. niger</i>)
<i>Macrochetae</i>	Absence	Presence	Presence
Colour of legs			
1 st pair	Totally yellowish	Totally yellowish or Femur brown in the proximal part, the other part yellowish or Femur black and knee and tibia yellowish or Femur and tibia black with light-brown knee	Totally black or Femur and tibia black with light-brown knee or Femur black and knee and tibia yellowish
2 nd pair	Totally yellowish	Totally yellowish or Femur brown in the proximal part, the other part yellowish or Femur black and knee and tibia yellowish or Femur and tibia black with light-brown knee	Totally black
3 rd pair	Totally yellowish or Femur brown in the proximal part, the other part yellowish	Totally yellowish or Femur brown in the proximal part, the other part yellowish or Femur black and knee and tibia yellowish or Femur and tibia black with light-brown knee	Totally black

The adults of the species belonging to the family Anthocoridae are so variable in size and colour of body and wings (Péricart, 1972) that the determination of species based only on phenotypic parameters is unreliable. To facilitate the determination of the three most common *Orius* species collected in Italy (*O. majusculus*, *O. laevigatus* and *O. niger*), more than 1,000 predators were carefully studied, observing morphological features of the specimens without killing them. Morphological characteristics can be used to distinguish between *O. majusculus* (subgenus *HeterOrius*) on the one hand and *O. niger* and *O. laevigatus* (subgenus *Orius*) on the other hand. The subgenus *Orius* presents four macrochetae in the angular margins of the pronotum, which are absent in subgenus *Heterorius* (Péricart, 1972). The distinction between *O. niger* and *O. laevigatus* was more problematic. The colour of the legs was the unique morphological characteristic discriminating between the two species.

Generally, in *O. laevigatus* the legs were completely yellowish or light yellow-brown, as reported also by Tavella *et al.* (1991). In some specimens the yellowish colour was observed at least at the prothoracic legs or at the tibia of both the prothoracic and mesothoracic legs. In *O. niger* the legs were generally entirely black, even if some specimens showed the tibia or the knee and the distal part of the prothoracic femur to be lightly yellow-brown (Table 3). This simple morphological key for separation of the species has been verified by the observation of the male genital parameres in more than 1,000 specimens of the three species, confirming the correspondence of the identification in circa 95% of the adults examined.

2.4. Conclusions

This survey indicates that at least three Italian species of the genus *Orius* have become natural enemies of the imported thrips pest *F. occidentalis*. So a new associations between an imported pest and a group of native predators has developed. According to Hokkanen and Pimentel (1984; 1989), new predator-prey association show generally a higher rate of success in biological control when compared to old association, because specific natural enemy defence mechanisms of the pest against its natural enemy have not yet evolved. In southern Europe, a similar example of an effective new association was recently recorded after the introduction from north America of the leafminer *Liriomyza trifolii* (Burgess) (Diptera Agromyzidae) which is naturally controlled by the native parasitoid *Diglyphus isaea* (Walker) (Hymenoptera Eulophidae) (Vacante, 1993). During the past 25 years, many more new associations have shown to result in good biological control (van Lenteren, 1997).

O. laevigatus was found to be the most common *Orius* species in Italy and it was often found on all vegetable crops on which *F. occidentalis* is an important pest, and it showed a wide natural distribution in the warmest Italian regions. *O. niger* showed a wide distribution all over Italy and occurred on a large range of host plants. *O. majusculus* was confined to the northern regions and generally occurred at low densities. The survey indicates that *O. laevigatus* and *O. niger* are well adapted to both climate and the main vegetable and ornamental crops grown in the Mediterranean area. Therefore, these two species seem good candidates for biological control of thrips pests.

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Chapter 3. BIOLOGICAL CHARACTERISTICS AND PREDATION CAPACITY OF FOUR *ORIUS* SPECIES ON TWO PREYS SPECIES

2

Abstract

Biological characteristics and predation activity of four *Orius* species (the paleartic *O. majusculus*, *O. laevigatus* and *O. niger* and the neartic *O. insidiosus*) were determined in the laboratory at $26 \pm 1^\circ\text{C}$; RH= $80 \pm 5\%$; photoperiod = 16L:8D). The *Orius* species were fed *ad libitum* with two preys: frozen *Ephestia kuehniella* (Zell.) eggs and live *Frankliniella occidentalis* (Perg.) adults. Newly-hatched *Orius* nymphs were isolated in plexiglass cylinders and mortality, development time and predation were checked. Newly-emerged *Orius* adults were isolated in pairs in cylinders and longevity, oviposition and predation were recorded. The intrinsic rates of natural increase (r_m) were calculated for the four *Orius* species on the two preys and the r_m was 0.094 (on *F. occidentalis*) and 0.068 (on *E. kuehniella*) for *O. laevigatus*, 0.097 (on *F. occidentalis*) and 0.080 (on *E. kuehniella*) for *O. majusculus*, 0.116 (on *F. occidentalis*) and 0.101 (on *E. kuehniella*) for *O. insidiosus*, 0.035 (on *F. occidentalis*) and -0.003 (on *E. kuehniella*) for *O. niger*, respectively. The killing rates (k_m) for all four *Orius* species was determined using the formula $k_m = \ln k_0/t_k$. The k_m was 0.23 for *O. laevigatus*, 0.21 for *O. majusculus*, 0.25 for *O. insidiosus*, 0.19 for *O. niger*, respectively. In all species, the females that fed on *E. kuehniella* showed greater longevity and higher reproduction than those fed on *F. occidentalis*. *O. niger* was the most difficult species to rear, both during immature stages and as adults. *O. niger* showed a high preimaginal mortality, high consumption of *E. kuehniella* eggs, low predation of *F. occidentalis* adults, long development time, low fecundity and low r_m on both preys. The development time of *O. majusculus* and *O. laevigatus* was similar when feeding on *F. occidentalis*. The total consumption of *E. kuehniella* eggs was significantly higher for *O. laevigatus*. *O. majusculus* showed a higher fecundity compared to *O. laevigatus* when fed *E. kuehniella* eggs, but no differences were recorded when both species were fed *F. occidentalis* adults. Most data for the neartic *O. insidiosus* were similar to those of *O. laevigatus* and *O. majusculus*. Mass rearings of *O. insidiosus*, *O. laevigatus* and *O. majusculus* were successfully developed, while mass rearing of *O. niger* was difficult due to its low reproduction rate. In addition to the experiments at 26°C , the rate of development as well as the fecundity and longevity of *O. laevigatus* were studied also at 14, 22 and 30°C . From these experiments we can conclude that performance of *O. laevigatus* was best at 26°C . A mass-rearing method for *O. laevigatus* was developed and the main quality control parameters for this species were defined.

According to the biological characteristics of the four *Orius* species, the endemic species with the highest k_m and good culturing possibilities, *O. laevigatus*, was chosen for further evaluation as predator of the thrips pest *F. occidentalis*.

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3.1. Introduction

Since the accidental introduction from USA, western flower thrips, (*Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae)) has disrupted Integrated Pest Management systems developed and applied successfully for several vegetable and ornamental crops in Europe (Tommasini and Maini, 1995). Among the natural enemies of this pest, several species belonging to the genus *Orius* (Heteroptera: Anthocoridae) appeared to be promising candidates for biological control (Riudavets, 1995). In Italy, wild populations of indigenous *Orius* species (*O. majusculus* (Reuter), *O. laevigatus* (Fieber) and *O. niger* Wolff) limit *F. occidentalis* outbreaks, especially during summer. The Nearctic species *O. insidiosus* has been released in Europe by several natural enemy producers for control of *F. occidentalis*.

Several studies have been conducted to obtain knowledge about *Orius* species. In table 1 the main biological characteristics found in the literature are summarized for the *Orius* species subject of the present study. Similar biological characteristics for other Palearctic and Nearctic *Orius* species are available in the literature, but are not summarized here: *O. tristis* (White) (Salas-Aguilar and Ehler, 1977; Stoltz and Stern, 1978), *O. albidipennis* (Reuter) (Tawfik and Ata, 1973a; Zaki, 1989; Carnero *et al.*, 1993), *O. limbatus* Wagner (Carnero *et al.*, 1993) and *O. minutus* L. (Lichtenauer and Sell, 1993). Studies for these species concentrated on development time and/or fecundity at different temperature regimes and when offered different types of prey. *O. tristis* and *O. minutus* were studied as predators of *F. occidentalis*, while the other species were fed with *E. kuehniella*.

Until 1992, research was carried out mainly for the Nearctic species *O. insidiosus* and *O. tristis* as predators of *F. occidentalis*. Later several studies included Palearctic species as *O. majusculus* and *O. laevigatus*. No specific studies on the biology of *O. niger* were done before this project research started. Generally, the effect of temperature on development time, fecundity and longevity were studied. Most authors agree that temperature and food play an important part in the development time and adult activity of *Orius* spp.. Isenhour and Yeargan (1981a), Kingsley and Harrington (1982), McCaffrey and Horsburgh, (1986a, b) and Bush *et al.* (1993) studied bionomics of *O. insidiosus*. Alauzet *et al.* (1990; 1992), Fischer *et al.* (1992) Rudolf *et al.* (1993), Alvarado *et al.* (1997) and Riudavets and Castañé (1998) worked on *O. majusculus* and only recently aspects of the biology of *O. laevigatus* were studied (Rudolf *et al.*, 1993; Tavella *et al.*, 1994; Alauzet *et al.*, 1994; Tommasini and Benuzzi, 1996; Cocuzza *et al.*, 1997a, 1997b; Alvarado *et al.*, 1997; Riudavets and Castañé, 1998). Studies on the last three *Orius* species as predators of *F. occidentalis* are limited (Husseini *et al.*, 1993; Riudavets *et al.*, 1993a, b; Riudavets, 1995; Vacante and Tropea Garzia, 1993a, b; Cocuzza *et al.*, 1997a). No comparisons were made of the development of several *Orius* species on different prey species.

Very few data are available about the life histories of *Orius* spp. Van den Meiracker (1994b), studied the life history of *O. insidiosus*, Riudavets (1995) calculated the intrinsic rate of natural increase for *O. laevigatus* and *O. majusculus* when feeding on *F. occidentalis* nymphs at 25°C and Alauzet *et al.* (1994) studied bionomics of *O. laevigatus*.

The best available single description of the population growth potential of a species under given conditions is still the intrinsic rate of natural increase (r_m) (Southwood, 1966). It might also be a useful parameter to compare the capacity of parasitism of various parasitoids in inoculative releases, because in parasitoids each egg laid means that a host is killed (van Lenteren, 1986b). A parameter to compare predators might be the kill rate (k_m), where the predation capability with *ad libitum* prey is considered instead of the fecundity of predators, as fecundity in predators is not directly related to prey killing as in parasitoids (van Lenteren, pers. com.). The kill rate is a parameter with which the capability of a predatory species, in

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Table 1. Data from the literature on biological characteristics of *Orius* spp. (+ ample data, +/- only few data, - no data).

<i>Orius</i> Species	prey species	Immature development	Immature mortality	Fecundity	Longevity	Predation capacity	r_m	Source
<i>O. insidiosus</i>	c, d, f	+	+	-	-	-	-	1, 2, 3, 4
	f	-	-	+	-	+	-	17
	d, e	-	-	+	+	-	-	3, 4, 18
	a	+	-	+	-	-	-	9
	b	+	+/-	+	+/-	-	+	20
	b, g, n	+	-	+	+	+	-	22
	g	+	-	-	-	+	-	21
<i>O. majusculus</i>	a	+	-	-	-	-	-	9
	a	+	+	+	+	+	+	10
	a, m	+	-	-	-	+	-	8
	b	+	-	+	-	-	-	5, 7
	b	+	-	+	+	-	-	6
	l	+	-	-	-	-	-	5
	g	+	-	-	-	+	-	21
<i>O. laevigatus</i>	a	+	-	-	-	-	-	9
	a	+	+	+	+	+	+	10, 23, 25
	a*	-	-	-	-	+	-	16
	b	+	-	+	+	-	-	11, 12, 15,
	b	-	-	+	+	-	-	16
	i, j	+	-	+	+	-	-	24
	g, h, k	+	-	+	+	+/-	-	15
	g, h, k	+	-	-	-	-	-	13
	g	+	-	-	-	+	-	14
<i>O. niger</i>	?	-	-	-	+/-	-	-	19

Prey species: a = *F. occidentalis* (nymphs), a* = *F. occidentalis* (adult), b = *E. kuehniella* (eggs), c = *Panonichus ulmi* (Kock), d = *Heliothis virescens* (Fabr.), e = *H. obsoleta* (Fabr.) (eggs), f = *Sericothrips variabilis* (Beach) (larvae, adult), g = *Aphis gossypii* Glov., h = *Spodoptera littoralis* Boisd. (eggs), i = *Tribolium confusum* Duv. (paralyzed larvae), j = *Phthorimaea operculella* (Zell.) (larvae), k = *Tetranychus telarius* L., l = *Rhopalosiphum padi* (L.), m = *Tyrophagus putriscentiae* Schr., n = *Caliothrips phaseoli* (Hood).

Sources: 1 = McCaffrey and Horsburg, 1986a, 2 = Isenhour and Yeargan, 1981a, 3 = Bush *et al.*, 1993, 4 = Kiman and Yeargan, 1985, 5 = Alauzet *et al.*, 1990, 6 = Fischer *et al.*, 1992, 7 = Alauzet *et al.*, 1992, 8 = Husseini *et al.*, 1993, 9 = Castaño and Zalom, 1994, 10 = Riudavets, 1995, 11 = Alauzet *et al.*, 1994, 12 = Tavella *et al.*, 1994, 13 = Tawfik and Ata, 1973a, 14 = Tawfik and Ata, 1973b, 15 = Zaki, 1989, 16 = Vacante and Tropea Garzia, 1993b, 17 = Isenhour and Yeargan, 1981c, 18 = Barber, 1936, 19 = Akramovskaya, 1978, 20 = van den Meiracker, 1994b, 21 = Alvarado *et al.*, 1997, 22 = Mendes *et al.*, 2002, 23 = Cocuzza *et al.*, 1997a, 24 = Cocuzza *et al.*, 1997b, 25 = Sanchez and Lacasa, 2002.

this case of *Orius* species, to reduce a pest species can be estimated during one generation of the predator.

Information about biological characteristics, including the prey kill rate, is needed also for development of mass rearing methods. Methodologies for culturing Anthocoridae, including some *Orius* species, were reported by Samsøe-Petersen *et al.* (1989), Takara and Nishida (1981), Isenhour and Yeargan (1981a), Kiman and Yeargan (1985), Alauzet *et al.* (1990), van den Meiracker and Ramakers (1991), Husseini *et al.* (1993), Frescata *et al.* (1994), Castañé and Zalom (1994), van den Meiracker (1994b), Blümel (1996) and Yano (1996). With new knowledge to be obtained from this study, it is expected that the mass rearing of *Orius* species can be improved.

In this chapter, biological characteristics of four *Orius* species (*O. majusculus*, *O. laevigatus*, *O. niger* and *O. insidiosus*) and their predation capacity of two prey species (*F. occidentalis* and *Ephestia kuehniella* eggs), are presented. The biological parameters studied (development time, mortality, sex ratio, female lifespan, fecundity and predation of *F. occidentalis* by each *Orius* species) were used to determine the intrinsic rate of natural increase (r_m) and the kill rate (k_m) of each *Orius* species. For r_m I used Southwood's (1966) formula: $r_m = \ln R_0/T$, where R_0 is the net reproductive rate and T is the generation time. For the kill rate (k_m) I developed the formula $k_m = \ln K_0/T_k$, where K_0 is the number of prey killed during both the nymphal and adult stages and T_k is the generation time. This information is, among others, very useful to compare the prey reduction capacity and needed also to develop a mass rearing.

3.2. Material and Methods

3.2.1. Rearing of predators

Separate rearings of *Orius* species were set up in a climate room at $26 \pm 1^\circ\text{C}$, RH $75 \pm 10\%$ and 16L:8D, using the three species most frequently found in Italy on plants infested by thrips (see chapter 2), and the Nearctic species *O. insidiosus*. *O. majusculus* was collected in northern Italy (Emilia-Romagna region), *O. laevigatus* and *O. niger* were collected in southern Italy (Sicily), while *O. insidiosus* was supplied by a natural enemy producer.

Identification of the field-collected predators was carried out in the laboratory. Egg-laying females (> 200) were isolated in a plexiglass cylinder (4 cm high, 4 cm diameter), with a fine gauze lid on the top. The offspring of each female was checked in order to find at least one male, which was then identified after dissection with keys of Péricart (1972) and Herring (1966). Then, ca. 50 newly emerged adults of the same species were put together in larger plexiglass cylinders (9 cm high, 9 cm diameter) covered with fine cotton gauze to start pilot rearings (the so-named adult unit). To prevent cannibalism, some strips of paper were added to each cylinder, and water was supplied by adding moist cotton. Frozen eggs of the flour moth *Ephestia kuehniella* (Zell.), glued on paper with Arabic gum, were used to feed both nymphs and adults. This prey was successfully used for other Anthocoridae also by Samsøe-Petersen *et al.* (1989), Alauzet *et al.* (1990; 1992), Frescata *et al.* (1994) and van den Meiracker (1994b). Bean pods were used as oviposition substrates like reported by Isenhour and Yeargan (1981a), van den Meiracker and Ramakers (1991), Riudavets *et al.* (1993a), Tavella *et al.* (1994) and van den Meiracker (1994b). Bean pods with *Orius* eggs were removed from the adult units three times per week and were placed in a new cylinder (the so-

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named nymphs unit) to start the pre-imaginal rearing. Food and water were supplied up to adult emergence.

3.2.2. Pre-imaginal characteristics

The experiments were carried out in a climatic cell at $26\pm1^{\circ}\text{C}$, $75\pm10\%$ RH and $16\text{L:}8\text{D}$ photoperiod. Three palearctic species, *O. majusculus*, *O. laevigatus* and *O. niger*, and the Nearctic species *O. insidiosus* were tested. All populations were reared in the laboratory for seven to ten generations before the start of the experiments.

More than 600 eggs per *Orius* species laid into bean pods during an interval of 6 hours were isolated in petri dishes. After hatching, which was checked every 3-4 hours, several first-instar nymphs were isolated in plexiglass cylinders (4 cm high, 4 cm diameter) covered by a plastic cap with small-mesh steel wire netting (200 mesh). Nymphs were fed *ad libitum* on either of two different species of preys, *i.e.* on *E. kuehniella* frozen eggs (>500 eggs per *Orius* nymph) glued onto pieces of cardboard with Arabic gum, or on *F. occidentalis* adults (>40 adults per *Orius* nymph) feeding on a piece of a bean pod. Mortality from egg hatch to adult emergence, development time and predation for each instar, and sex ratio of emerged adults were recorded for both species of prey. Nymphal development was checked every 3-4 hours until the adult stage. When exuviae were found, the number of *E. kuehniella* eggs or *F. occidentalis* adults consumed were counted for 35 predators of each *Orius* species and for both prey species. The natural mortality of *E. kuehniella* eggs and *F. occidentalis* adults was estimated by keeping an equal amount of prey at the same rearing conditions without predators (20 replications per prey).

3.2.3. Adult characteristics

Newly-emerged pairs of *Orius* species (*O. majusculus*, *O. laevigatus*, *O. niger* or *O. insidiosus*) were isolated in transparent plexiglass cylinders (9 cm high, 9 cm diameter), capped with a wad of fine cotton. Every two days, adults were fed *ad libitum* on frozen *E. kuehniella* eggs (>500 per *Orius* pair) glued onto pieces of cardboard with Arabic gum, or on *F. occidentalis* adults (>80 adults per *Orius* pair). At the same time, a bean pod was placed in each cylinder, to provide a substrate for oviposition of the predators and as food for *F. occidentalis*. Survival of *Orius* females, and the number of eggs laid were checked. Dead males were replaced with fresh ones. Starting from the day of emergence, the predation of the *Orius* pairs was calculated once a week by counting the number of prey consumed during 24 hours. The natural mortality of *E. kuehniella* eggs and of *F. occidentalis* adult was estimated by keeping an equal amount of prey at the same conditions without predators (12 replications per prey type).

Life table parameters were studied following the methodology explained by Southwood (1966). Age in day (including immature stages) (x), age-specific survival (including immature mortality) (l_x), age-specific fertility (m_x), estimated as the expected number of female eggs produced per females alive at age x, were determined in order to calculate the net reproductive rate ($R_0 = \sum_x l_x m_x$) and the intrinsic rate of natural increase r_m ($r_m = \ln R_0/T$), where T is the generation time ($T = \sum_x l_x m_x x / R_0$) and x the age expressed in units of time (a class unit is composed from an interval of 4 days). The kill rate (k_m) of the four *Orius* species when fed with *F. occidentalis* *ad libitum*, was calculated using the same formula of r_m , but substituting the age-specific fertility (m_x), with the age-specific predation

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both during the nymphal and the adult stages. Thus $k_m = \ln K_0/T_k$, where T_k (generation time) is the period during a generation where the predator may prey ($T_k = \sum_x l_x K_x x / K_0$) and K_0 is the net consumption rate ($K_0 = \sum_x l_x K_x$), *i.e.* the number of preys killed (K_x) during a generation of the predator, corrected by natural mortality.

3.2.4. Effect of temperature on the development and fecundity of *O. laevigatus*

The main biological parameters of *O. laevigatus* were studied at several constant temperatures. The experiment was carried out by using predators reared in the laboratory for ca. 18 generations as described in section 3.2.1. Experimental rearings of *O. laevigatus* were set up at different constant temperatures (14, 22 and 30°C), RH 75±10% and 16L÷8D (at 14°C the photoperiod was set at 12L÷12D). The egg development time, the total immature development time, the fecundity and female longevity were recorded. More than 500 eggs of *O. laevigatus* were isolated in petri dishes for each temperature regime. Eggs were laid on bean pods during a 24-hours interval. Egg-hatching and adult emergence were checked twice a day. Groups of 20 newly-hatched nymphs were isolated in transparent plexiglass cylinders (9 cm high, 9 cm diameter) capped with a wad of fine cotton. Twice a week, predators were fed with frozen *E. kuehniella* eggs glued onto pieces of cardboard with Arabic gum. After emergence *Orius* pairs were isolated (>30 pairs per temperature regime) in smaller plexiglass cylinders (4 cm high, 4 cm diameter). Survival and oviposition of females were checked three times per week, and dead males were replaced with fresh ones. Total development time against temperature were calculated, considering also the data recorded during the previous experiment at 26°C with the same species (section 2.2.1). Furthermore, our data were combined with those of Alauzet *et al.* (1994) who studied *O. laevigatus* at a different constant temperature when fed with *E. kuehniella* eggs, to define the threshold temperature of development for each instar as well as for the total development time and pre-oviposition period.

Statistical analysis

Each predator, or pair of predators of the four *Orius* species feeding on one of the two prey species, was considered as an experimental unit. The pre-imaginal mortality (expressed as % of adult emerged), the sex ratio (% of females) as well as the total development time of females and males at the different temperatures, were analysed by the chi-square test ($p < 0.05$). The embryonic and post-embryonic development time for each prey species as well as at each temperature, the predation capacity on *E. kuehniella*, the pre-oviposition time and total fecundity, were compared with the Kruskal-Wallis test followed by the distribution free multiple comparison test (Dunn's procedure valid for unequal sample size). The predation capacity on *F. occidentalis* for young *Orius* instars and the adult pairs of *Orius* were compared by ANOVA and the Tukey test. The performance of the same species when fed on different prey was compared by using the Mann-Whitney U test.

3.3. Results

3.3.1. Pre-imaginal characteristics

Development and immature mortality. All four species completed the development on both prey species, *E. kuehniella* eggs and *F. occidentalis* adults (Table 2 and 3). Diet affected the development time of all four *Orius* species: *F. occidentalis* adults as prey induced a faster

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development of all *Orius* species compared to *E. kuehniella* eggs as prey. *O. niger* had the longest egg development period. The other three species had similar development times. During immature development (Table 2), *E. kuehniella* eggs induced a significantly higher mortality than *F. occidentalis* adults in all species, except for *O. insidiosus* where mortality with the two prey species was similar. No significant differences were found in the sex ratio for all the *Orius* species on both prey species (Table 2). The development times recorded for all the pre-imaginal instars of the four *Orius* species are given in table 3. Differences among species were recorded in the total post-embryonic development time when *E. kuehniella* was used as prey: it increased from *O. insidiosus* (10.9 days) to *O. niger* (13.0 days). The same differences were recorded when the predators were fed with *F. occidentalis* adults.

Predation. Because natural mortality of the prey was very low, the number of spontaneously collapsed *E. kuehniella* eggs (1.6 ± 0.11 in 24 hours; means \pm SE), or the natural mortality of *F. occidentalis* adults (1.7 ± 0.35 in 24 hours; means \pm SE) were not subtracted from the daily predation data. The amount of prey consumed by each instar during the pre-imaginal development is reported in table 4. It shows an increase in predation rates from the first (9.6 prey eaten) to the fifth instar (34.4 preys eaten) for all species on the two prey species. Differences among the four species were found in the total predation of *E. kuehniella* egg. *O. niger* and *O. laevigatus* consumed significantly more eggs than *O. majusculus* and *O. insidiosus*. Slight differences were found in the predation capacity on *F. occidentalis* adults. On average *O. majusculus* ate the highest number and significantly more thrips than *O. insidiosus* and *O. niger*.

Table 2. Pre-imaginal mortality and sex ratio at emergence of four *Orius* species on two different prey species.

Species	No. nymphs	Mortality (%)	No. Females emerged	No. Males emerged	Sex ratio (% females)
<i>Prey: Ephestia kuehniella eggs</i>					
<i>O. majusculus</i>	77	59.7	12	19	38.7 a
<i>O. laevigatus</i>	183	78.1	23	17	57.5 a
<i>O. niger</i>	189	93.7	5	7	41.7 a
<i>O. insidiosus</i>	83	37.3	25	27	48.1 a
<i>Prey: Frankliniella occidentalis adults</i>					
<i>O. majusculus</i>	84	41.7	17	32	34.7 a
<i>O. laevigatus</i>	84	46.4	25	20	55.6 a
<i>O. niger</i>	103	42.7	25	34	42.4 a
<i>O. insidiosus</i>	84	46.4	23	22	51.1 a

3.3.2. Adult characteristics

Fecundity and longevity. Individual females of the four species mate several times during their reproductive life. The average longevity, pre-ovipositional period and the total oviposition per female of the four *Orius* species fed on *E. kuehniella* eggs or on *F. occidentalis* adults is presented in tables 5 and 6. In all four *Orius* species, the

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Table 3. Development time (days) of four *Orius* species on two different prey species (means \pm SE).

Species	Eggs	1 st instar	2 nd instar	3 rd instar	4 th instar	5 th instar	Total development
<i>Prey: Ephestia kuehniella</i> eggs							
<i>O. majusculus</i>	4.2 \pm 0.02 a	2.1 \pm 0.03 b	1.8 \pm 0.04 a	1.6 \pm 0.05 a	1.9 \pm 0.05 ab	3.6 \pm 0.05 ab	15.4 \pm 0.11 ab
<i>O. laevigatus</i>	4.2 \pm 0.02 a	2.4 \pm 0.04 c	1.7 \pm 0.04 ab	1.8 \pm 0.03 a	2.1 \pm 0.03 b	3.8 \pm 0.04 b	16.0 \pm 0.14 bc
<i>O. niger</i>	4.8 \pm 0.12 b	2.8 \pm 0.13 c	2.0 \pm 0.10 b	2.0 \pm 0.06 b	2.2 \pm 0.11 b	3.9 \pm 0.12 b	17.8 \pm 0.22 c
<i>O. insidiosus</i>	4.2 \pm 0.02 a	2.0 \pm 0.03 a	1.6 \pm 0.05 a	1.6 \pm 0.03 a	2.0 \pm 0.03 a	3.6 \pm 0.04 a	15.0 \pm 0.10 a
<i>Prey: Frankliniella occidentalis</i> adults							
<i>O. majusculus</i>	4.0 \pm 0.01 a	2.1 \pm 0.03 a	1.6 \pm 0.03 a	1.6 \pm 0.06 b	2.1 \pm 0.05 c	3.7 \pm 0.07 b	15.1 \pm 0.11 b
<i>O. laevigatus</i>	4.1 \pm 0.02 b	2.3 \pm 0.04 b	1.7 \pm 0.02 b	1.6 \pm 0.05 b	1.9 \pm 0.03 b	3.6 \pm 0.07 ab	15.1 \pm 0.11 b
<i>O. niger</i>	4.6 \pm 0.03 c	2.6 \pm 0.05 c	1.8 \pm 0.04 b	1.7 \pm 0.04 c	2.0 \pm 0.04 b	3.8 \pm 0.07 c	16.5 \pm 0.12 c
<i>O. insidiosus</i>	4.1 \pm 0.02 b	2.1 \pm 0.05 a	1.5 \pm 0.06 a	1.5 \pm 0.04 a	1.5 \pm 0.05 a	3.4 \pm 0.04 a	14.1 \pm 0.07 a

Table 4. Pre-imaginal predation capacity expressed as number of prey eaten during the instars of four *Orius* species on two different prey species (means \pm SE).

Species	1 st instar	2 nd instar	3 rd instar	4 th instar	5 th instar	Total immature predation
<i>Prey: Ephestia kuehniella</i> eggs						
<i>O. majusculus</i>	7.7 \pm 0.3 a	13.4 \pm 0.8 a	13.5 \pm 0.7 a	23.4 \pm 0.9 a	40.7 \pm 1.6 a	99.4 \pm 2.7 a
<i>O. laevigatus</i>	19.4 \pm 1.0 b	23.9 \pm 1.3 b	30.6 \pm 1.8 b	35.2 \pm 1.8 b	65.3 \pm 4.1 b	174.6 \pm 8.6 b
<i>O. niger</i>	21.2 \pm 1.5 b	30.9 \pm 3.7 b	38.1 \pm 2.4 b	27.9 \pm 2.9 a	66.9 \pm 3.9 b	183.5 \pm 8.0 b
<i>O. insidiosus</i>	9.1 \pm 0.3 a	12.7 \pm 0.6 a	14.3 \pm 0.7 a	22.6 \pm 1.0 a	37.0 \pm 2.3 a	94.3 \pm 3.5 a
<i>Prey: Frankliniella occidentalis</i> adults						
<i>O. majusculus</i>	5.2 \pm 0.3 bc	5.7 \pm 0.2 ab	8.4 \pm 0.3 b	8.8 \pm 0.3 b	17.5 \pm 1.1 a	45.7 \pm 1.1 b
<i>O. laevigatus</i>	5.4 \pm 0.2 c	7.7 \pm 0.3 c	7.6 \pm 0.4 ab	6.3 \pm 0.4 a	15.6 \pm 0.7 a	42.6 \pm 0.9 ab
<i>O. niger</i>	4.3 \pm 0.4 ab	6.0 \pm 0.3 b	8.6 \pm 0.2 b	6.8 \pm 0.5 a	15.4 \pm 0.8 a	41.1 \pm 1.5 a
<i>O. insidiosus</i>	4.1 \pm 0.2 a	4.9 \pm 0.3 a	7.0 \pm 0.4 a	6.7 \pm 0.4 a	16.4 \pm 0.04 a	39.2 \pm 1.0 a

females fed on *E. kuehniella* lived significantly longer and showed higher rates of total oviposition than *Orius* females fed on *F. occidentalis*.

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When predators were reared on *E. kuehniella* eggs, the pre-oviposition period was longer than when reared on *F. occidentalis*. The difference was largest for *O. majusculus*, which showed a delay of about 2 days (Tables 5 and 6). *O. niger* showed the longest pre-oviposition period (6.7 days) on both prey species. No differences in pre-oviposition period were found among the other three species.

O. majusculus laid the highest number of eggs when fed with *E. kuehniella* eggs, but it was not significantly different from *O. insidiosus*. *O. insidiosus* did not show difference in oviposition activity compared to *O. laevigatus* on both prey species. *O. niger* laid the lowest number of eggs, both with *E. kuehniella* and *F. occidentalis* as prey. Among the three species *O. majusculus*, *O. laevigatus* and *O. insidiosus*, total fecundity was similar when thrips were used as prey (Table 6).

The age-specific survival for each species is shown in figure 1. Sixty percent of the females survived till the 28th day after emergence. Maximum survival was 60 days for *O. majusculus* on *E. kuehniella* eggs. Among the species fed on the same prey, significant differences in longevity were found among the species with *E. kuehniella* as prey, but not with *F. occidentalis* as prey (Tables 5 and 6). Different life spans were recorded for each species when fed with different prey. The highest longevity was recorded for both *O. majusculus* and *O. niger* when fed with *E. kuehniella* eggs. With *F. occidentalis* as prey no differences in longevity were found. The longevity of males was recorded for the four *Orius* species with *F. occidentalis* as prey, and no differences were found among the species (Kruskal Wallis, $P>0,05$). Only the females of *O. majusculus* lived longer than males. No difference was recorded in male and female longevity of *O. laevigatus* and *O. niger*. The males of *O. insidiosus* lived longer than the females.

Oviposition patterns of *Orius* females are presented in figure 2. Females usually began oviposition between 2-5 days after emergence, although sporadic cases of earlier oviposition were found. *O. majusculus*, *O. laevigatus* and *O. insidiosus* showed a high oviposition rate with both prey species. Oviposition rates in females fed on *F. occidentalis* started to decline ca.10 days earlier than females fed on *E. kuehniella* (day 16 and day 26 respectively). Differences were less marked in *O. niger*, because of its overall lower oviposition.

Predation. The predation per *Orius* pair during 24 hours, which was checked at 8 day intervals, is shown in table 7. Significant differences in predation among the four species were registered only at the beginning and the end of life of the predators when fed on *E. kuehniella*. No differences in predation were found with *F. occidentalis* as prey. All the predators ate a larger number of *E. kuehniella* eggs than *F. occidentalis* adults. It should be realised, however, that *E. kuehniella* eggs are smaller than *F. occidentalis* adults, so one *F. occidentalis* adult provides more food than one *E. kuehniella* egg. On average, the daily predation of the *Orius* species was 25 eggs of *E. kuehniella* and 22 adults of *F. occidentalis*.

Life tables. The life tables of the four *Orius* species are shown in table 8 and 9. The intrinsic rate of natural increase (r_m) of all the predators was higher when they were fed *F. occidentalis* adults than *E. kuehniella* eggs (Table 8). The type of prey has a strong influence on r_m , which was expected as these differences were also observed for development time, fecundity and longevity of the four *Orius* species. *O. niger* showed the lowest rate of natural increase (r_m), as well the net reproductive rate (R_0) of the *Orius* species for both types of prey. The highest r_m was found for *O. insidiosus*. *O. insidiosus* showed an R_0 value three times higher than *O. laevigatus* and almost double of that of *O. majusculus* when the predators were fed with *E. kuehniella*. *O. majusculus* and *O. laevigatus* fed with *F. occidentalis* showed a similar r_m and R_0 . Excluding *O. niger*, the other three *Orius*

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Table 5. Pre-oviposition period, total fecundity and longevity (Means \pm SD) of four *Orius* species reared at 26°C when fed with *E. kuehniella* eggs.

Species	No.	Pre-oviposition period (days)	Total fecundity (eggs/female)	Longevity of females (days)
<i>O. majusculus</i>	63	4.6 \pm 3.9 ab	174.0 \pm 106.0 c	47.0 \pm 21.8 b
<i>O. laevigatus</i>	64	3.2 \pm 1.8 a	118.6 \pm 75.1 b	38.6 \pm 18.5 a
<i>O. niger</i>	29	6.7 \pm 4.4 b	54.1 \pm 59.8 a	50.0 \pm 18.2 b
<i>O. insidiosus</i>	65	3.7 \pm 6.2 a	144.3 \pm 76.8 bc	42.3 \pm 14.0 ab

Table 6. Pre-oviposition period, total fecundity and longevity (Means \pm SD) of four *Orius* species reared at 26°C when fed with *F. occidentalis* adults.

Species	No.	Pre-oviposition period (days)	Total fecundity (eggs/female)	Longevity of females (days)	Longevity of males (days)
<i>O. majusculus</i>	36	2.8 \pm 2.7 a	87.1 \pm 50.6 b	19.7 \pm 7.7 a	16.6 \pm 6.9 a
<i>O. laevigatus</i>	42	2.7 \pm 1.1 a	55.6 \pm 50.4 b	18.0 \pm 9.7 a	18.9 \pm 12.1 a
<i>O. niger</i>	36	6.8 \pm 5.2 b	16.2 \pm 26.1 a	18.5 \pm 11.3 a	18.6 \pm 11.0 a
<i>O. insidiosus</i>	46	2.5 \pm 1.3 a	65.7 \pm 56.8 b	17.1 \pm 8.5 a	20.1 \pm 12.8 a

species showed a lower difference in the R_0 when they were fed with *F. occidentalis* compared to *E. kuehniella*.

The kill rates (k_m) of the four *Orius* species fed with *F. occidentalis* were from highest to lowest: 0.25 for *O. insidiosus*, 0.23 for *O. laevigatus*, 0.21 for *O. majusculus* and 0.19 for *O. niger*. The values of k_m are generally proportional to the net predation rates (k_0) and inverse to the generation time (T_k).

3.3.3. Effect of the temperature on the development and fecundity of *O. laevigatus*.

There were two reasons to carry out this experiment only with *O. laevigatus*. First, the *Orius* species most frequently found in the Mediterranean area were *O. laevigatus* and *O. niger* (see chapter 2), but *O. niger* showed a very low intrinsic rate of increase. Second, *O.*

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laevigatus does not appear to go into diapause (see Chapter 4) and it is, therefore, a better candidate for control of *F. occidentalis* in winter than the other *Orius* species.

Development time. The equations of the rate of development against temperature were calculated with the data of Alauzet *et al.* (1994). It was assumed that the mean developmental rates, *i.e.* the reciprocal of development times, were linearly related to the temperature between 15 and 30°C (Table 11 and Figure 3).

The threshold value for overall development was 11.3°C, which is higher than that of *F. occidentalis* (9.4°C - Gaum *et al.*, 1994). The slope of the regression of *O. laevigatus* and for *F. occidentalis* appear quite similar. The instars L1, L2, L3 and L4 seem more sensitive to temperature than the egg stage and L5. Their rates of development accelerated faster with the increase of the temperature than the egg stage and L5. The egg stage was least sensitive, showing the lowest threshold temperature (9.2°C). The highest threshold temperature was found during the pre-ovipositional period (14.2°C).

The egg development periods and the total development times of *O. laevigatus* are given in table 12. Differences in both egg and total development time were found at the three temperatures, with an inverse relation between development time and temperature. No differences were found in the development times of males and females at the same temperature. Sex ratios were the same at different temperatures. Immature mortality was influenced by temperature, mortality was lowest at 22°C (Table 12). Table 13 provides the rate of development of *O. laevigatus* at 5 temperatures. Here, the threshold temperature (9.8°C) was lower than the threshold temperature calculated from the data of Alauzet *et al.* (1994) (11.3°C).

Adult activity. The shortest pre-oviposition period was recorded at 30°C and the longest one at 14°C (Table 14). At 14°C only 30% of the females laid eggs, and only 1 egg per female was laid. The highest fecundity (172.8 eggs/female) and percentage of egg-laying females (94.6%) was recorded at 22°C. The percentage of egg-laying females at 30°C was lower, but not significant, than that at 22°C. Table 14 also provides the female's longevity at the three temperatures. The highest longevity was observed at 14°C, where few females lived more than 100 days and one female even lived 214 days.

In figure 4, the fecundity of *O. laevigatus* reared at three different constant temperatures is shown. At 30°C 80% of females laid eggs after 4 days from emergence. At 22°C 80% of females laid eggs after 16 days from emergence, while at 14°C oviposition remained low as well as the percentage of egg-laying females. At 14°C the photoperiod was 12L:12D and this photoperiod may have strongly reduced the fecundity (see chapter 4).

In figure 5 the survival of females at different temperatures is shown.

3.4. Discussion

3.4.1. Pre-imaginal characteristics

This study showed that the type of prey can strongly influence the rate of development and mortality of *Orius* species. *F. occidentalis* adults as food source resulted in a lower pre-imaginal mortality than *E. kuehniella* eggs for the European *Orius* species. Kiman and Yeargan (1985) found differences in the mortality during development time of *O. insidiosus* with different prey, and, contrary to our results, thrips was the poorest food among the types of prey tested. The present data on the development time of *O. insidiosus* are similar to those

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recorded by Kiman and Yeargan (1985) (15.8 days), who reared this species at 24°C on *Sericothrips variabilis* (Beach). They are also similar to data of McCaffrey and Horsburgh (1986a) who reared *O. insidiosus* on *Panonychus ulmi* (Koch) at 23 and 29°C (18.8 and 9.5

Fig. 1: Longevity of four *Orius* species fed on adults of *Frankliniella occidentalis* or *Ephestia kuehniella* eggs.

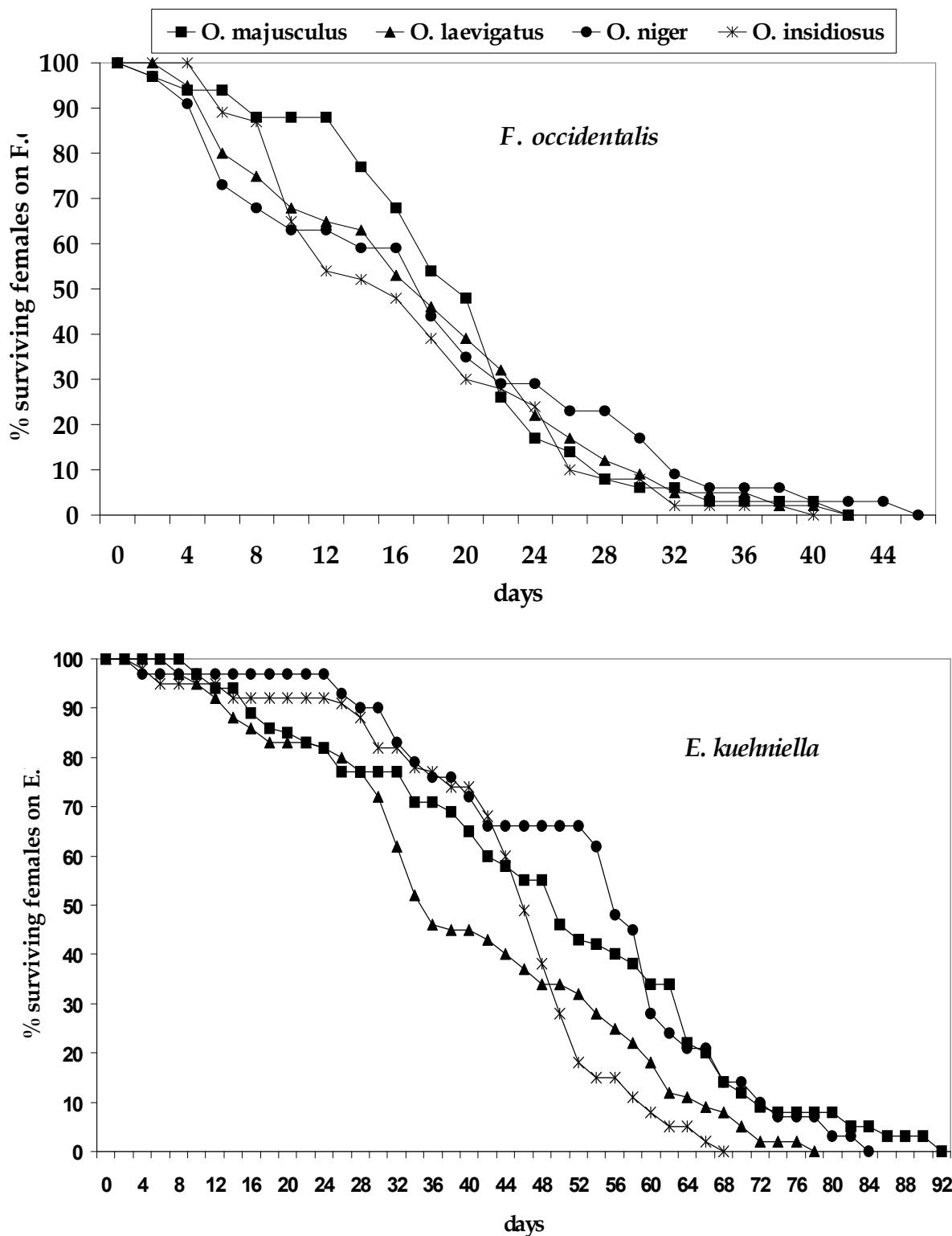
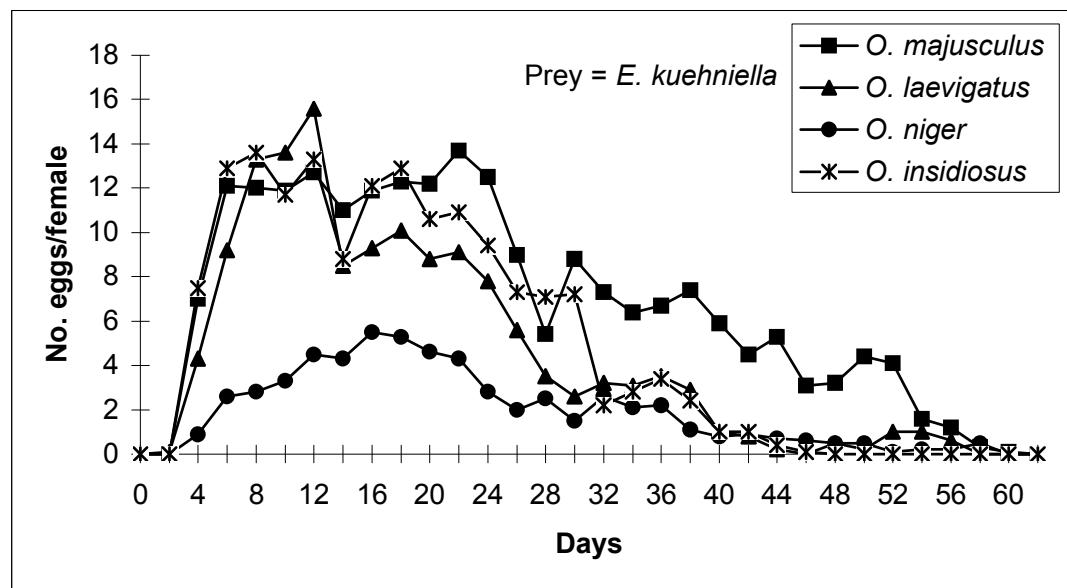
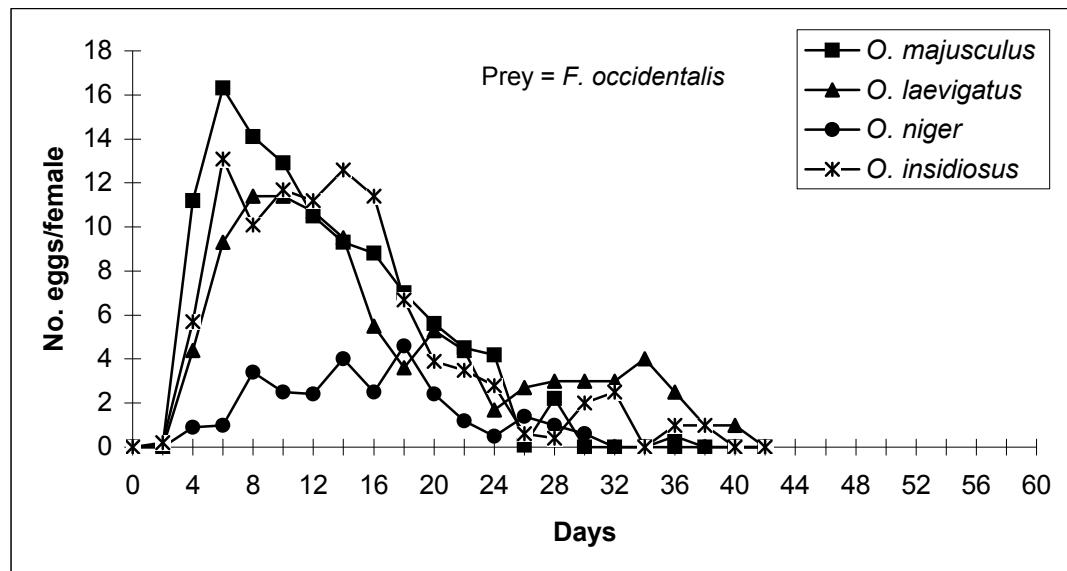


Figure 2. Oviposition of four *Orius* species fed on adults of *Frankliniella occidentalis* or *Ephestia kuehniella* eggs.



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Table 7. Predation by pairs of four *Orius* species fed on two different prey species. Different letters show significant differences between the data of the same day ($P < 0.05$); Kruskal-Wallis test, followed by distribution-free multiple comparison; Dunn's procedure valid for unequal sample size (Mean \pm SE).

Species	prey: <i>F. occidentalis</i>			
	1 st day	8 th day	16 th day	24 th day
<i>O. majusculus</i>	21.6 \pm 2.3 a	20.3 \pm 1.8 a	23.3 \pm 2.6 a	26.4 \pm 5.6 a
<i>O. laevigatus</i>	27.6 \pm 3.0 a	22.7 \pm 2.4 a	27.8 \pm 2.3 a	20.9 \pm 3.0 a
<i>O. niger</i>	24.5 \pm 2.5 a	25.0 \pm 1.7 a	21.2 \pm 0.9 a	17.0 \pm 2.3 a
<i>O. insidiosus</i>	21.7 \pm 2.4 a	29.8 \pm 3.1 a	25.3 \pm 1.9 a	20.0 \pm 1.9 a

Species	prey: <i>E. kuehniella</i>							
	1 st day	8 th day	16 th day	24 th day	32 nd day	40 th day	48 th day	56 th day
<i>O. majusculus</i>	21.9 \pm 0.9 a	81.4 \pm 3.7 a	57.4 \pm 4.7 a	49.9 \pm 3.7 a	57.6 \pm 4.2 a	47.8 \pm 1.9 ab	58.8 \pm 2.2 a	55.8 \pm 2.4 b
<i>O. laevigatus</i>	33.3 \pm 1.4 b	75.3 \pm 7.0 a	59.8 \pm 5.0 a	41.2 \pm 3.6 a	54.8 \pm 2.5 a	44.6 \pm 1.3 ab	55.2 \pm 2.0 a	57.6 \pm 2.9 b
<i>O. niger</i>	22.3 \pm 1.1 a	76.6 \pm 9.3 a	56.8 \pm 6.2 a	52.2 \pm 2.8 a	48.4 \pm 2.7 a	55.9 \pm 3.3 b	53.9 \pm 2.3 a	45.1 \pm 1.9 a
<i>O. insidiosus</i>	24.2 \pm 1.3 a	88.6 \pm 7.6 a	61.7 \pm 5.2 a	49.6 \pm 2.0 a	54.1 \pm 4.5 a	40.6 \pm 1.9 a	51.8 \pm 3.5 a	52.4 \pm 1.5 ab

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Table 8. Generation time (T), net reproductive rate (R_0) and intrinsic rate of natural increase (r_m) of four *Orius* species reared at 26°C on two preys (Ek = *E. kuehniella* eggs; Fo = *F. occidentalis* adults).

Species	Prey	R_0	T	$r_m = \ln R_0/T$
<i>O. majusculus</i>	Fo	12.5	26.0	0.097
<i>O. majusculus</i>	Ek	18.4	36.4	0.080
<i>O. laevigatus</i>	Fo	12.7	26.9	0.094
<i>O. laevigatus</i>	Ek	10.1	34.0	0.068
<i>O. niger</i>	Fo	3.0	30.8	0.035
<i>O. niger</i>	Ek	0.9	38.7	-0.003
<i>O. insidiosus</i>	Fo	17.9	24.9	0.116
<i>O. insidiosus</i>	Ek	30.1	33.6	0.101

Table 9. Predation period (T_k), net predation rate (K_0) and killing rate (k_m) of four *Orius* species reared at 26°C on *F. occidentalis* adults (see section 3.2.3).

Species	K_0	T_k	$k_m = \ln K_0/T_k$
<i>O. laevigatus</i>	68.8	18.3	0.23
<i>O. majusculus</i>	62.9	19.9	0.21
<i>O. niger</i>	59.4	21.0	0.19
<i>O. insidiosus</i>	76.5	17.2	0.25

Biological characteristics and predation capacity of four *Orius* species on two prey species

Table 10. Generation time, R_0 and r_m of *F. occidentalis* reared at 25°C on different crops.

Crop	R_0	T	$r_m = \frac{\ln R_0}{T}$	References
Chrysanthemum	99.5	26.9	0.171	Robb, 1989
Bean leaves	12.2	17.9	0.139	Brødsgaard, 1991a, 1994
Bean leaves	34.7	25.3	0.140	Gerin et al., 1994
Cucumber	6.0	4.6	0.300	Gaum et al., 1994
Cucumber	22.1	20.1	0.166	van Rijn et al., 1995
Chrysanthemum (flower)	91.3	32.0	0.141	Katayama, 1997

Table 11. Parameter values for rate of development ($y = a + bx$, and $y = 1/day$) of *O. laevigatus* reared on *E. kuehniella* (based on data of Alauzet et al., 1994).

Stage	A	b	R^2	T_0 (°C)
Egg	-0.1306	0.0142	0.99	9.2
L1	-0.2737	0.0255	0.99	10.7
L2	-0.5081	0.0425	0.93	12.0
L3	-0.5277	0.0444	0.98	12.0
L4	-0.2842	0.0288	0.97	9.9
L5	-0.2152	0.0184	0.97	11.7
Total development	-0.0619	0.0055	0.99	11.3
Pre-oviposition time	-0.3744	0.0264	0.93	14.2

Table 12. Development time, sex ratio and percentage of emergence of *O. laevigatus* at different temperatures (Means \pm SE) when reared on *E. kuehniella* eggs.

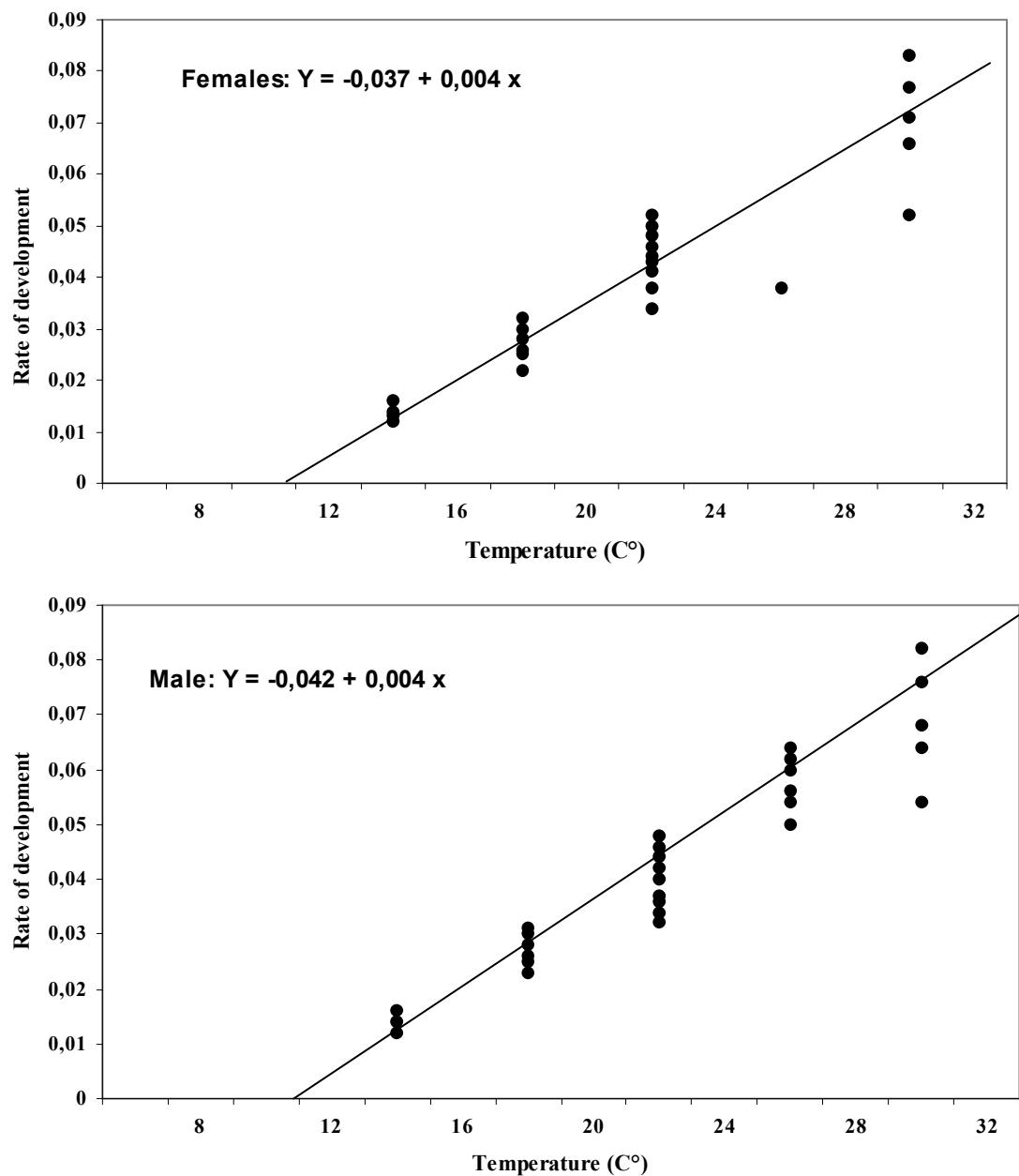
Temp. (°C)	No. eggs	Egg developmen t time (days)	Nymphal development time (days)	Total development time females (days)	Total development time males (days)	Immature mortality (%)	Sex ratio (% females)
14	1101	15.8 \pm 0.2 c	59.4 \pm 5.0 c	75.2 \pm 5.1 c	76.7 \pm 5.0 c	93.8	56.6
22	1248	5.3 \pm 0.5 b	15.4 \pm 2.3 b	20.7 \pm 2.2 b	20.7 \pm 2.2 b	52.2	51.1
30	1328	2.9 \pm 1.0 a	10.4 \pm 1.5 a	13.3 \pm 1.5 a	12.8 \pm 1.3 a	85.6	58.6

Table 13. Rate of development of males and females (Means \pm SD) of *O. laevigatus* reared at different temperatures on *E. kuehniella* eggs (data at 18°C determined in other experiment, see chapter 4).

Temperature (°C)	No. of eggs	Egg stage	Nymphal stage	Total rate of development
14	66	0,063 \pm 0,004	0,017 \pm 0,001	0,013 \pm 0,001
18	60	-	-	0,026 \pm 0,002
22	588	0,190 \pm 0,015	0,066 \pm 0,010	0,049 \pm 0,005
26	40	0,239 \pm 0,008	0,085 \pm 0,006	0,063 \pm 0,003
30	111	0,344 \pm 0,041	0,100 \pm 0,013	0,076 \pm 0,007

T_0 (°C)	11,1	8,8	9,8
R^2	0,90	0,77	0,88
$y = a + bx$	$y = -0,20 + 0,02x$	$y = -0,04 + 0,01x$	$y = -0,04 + 0,01x$
P	<0.001	<0.001	<0.001

Fig. 3. Rate of total development time of females and males of *O. laevigatus* respectively (by Alauzet *et al.*, 1994)



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Table 14. Pre-oviposition period, fecundity, longevity and percentage of egg-laying females of *O. laevigatus* at different temperatures (Means \pm SD) reared on *E. kuehniella* frozen eggs.

Temperature (°C)	No.	Pre-oviposition period (days)	Total fecundity (eggs/female)	Egg-laying females (%)	Female longevity (days)
14	26	53.3 \pm 39.7 c	1.0 \pm 2.2 a	30.0	75.6 \pm 53.4 b
22	33	8.9 \pm 8.3 b	172.8 \pm 107.5 c	94.6	62.2 \pm 29.2 b
30	41	2.9 \pm 6.0 a	77.0 \pm 66.9 b	80.4	18.0 \pm 10.1 a

days, with an interpolated average of 14.2 days at a temperature of 26°C). *O. insidiosus* showed a longer development time when fed with eggs of *Heliothis virescens* (Fabr.) at 24 and 28°C, with 20.0 and 12.7 days, respectively (Isenhour and Yeargan, 1981a). Bush *et al.* (1993) and Kiman and Yeargan (1985) recorded a shorter development time of *O. insidiosus* when fed on *H. virescens* eggs (11.1 days at 25°C and 13.4 days at 24°C respectively). Only van den Meiracker (1994b) studied *O. insidiosus* fed with *E. kuehniella* eggs at 25°C and he found a decrease in the nymphal development time of 3.6 and 4.9 days in females and males respectively, when he reared this species for 3 years in the laboratory. However, the data of van den Meiracker (1994b) show a longer nymphal development time (17.2 days) than that found in the present study where we fed *O. insidiosus* with the same prey. When *F. occidentalis* nymphs were provided as prey *O. insidiosus* showed a faster development time (9.8 days at 25°C) (Castañe and Zalom, 1994) than in our experiment.

The development time of *O. laevigatus* on *E. kuehniella* eggs was studied at a variable temperature between 24 and 28°C by Zaki (1989), at 25°C by Alauzet *et al.* (1994) and at 4 fluctuating thermoperiods by Tommasini and Benuzzi (1996). The nymphal development time was 14.8 Zaki (1989) and 13.1 days Alauzet *et al.* (1994) respectively at 24-28°C and 25°C, slightly longer than our result at 26°C. Similar development time data were recorded by Tavella *et al.* (1994) (10.6 days) at 25°C. On other prey, *O. laevigatus* showed a longer nymphal period of 13 and 16 days compared with *E. kuehniella* eggs as food (Tawfik and Ata, 1973a, b; Zaki, 1989). Riudavets (1995) studied the development time of *O. laevigatus* and *O. majusculus* at 25°C when fed with nymphs of *F. occidentalis* and reported a slightly longer development for both predators (17.5 and 16.7 days respectively) in comparison with our data.

Husseini *et al.* (1993) found that *O. majusculus* completed its development in 15.2 days at 25.5°C, similarly to our results when *F. occidentalis* is used as prey. On *E. kuehniella* eggs, the development of *O. majusculus* was studied at 25°C also by Fischer *et al.* (1992) and Alauzet *et al.* (1990), who both reported a similar development period (ca. 15 days), although Alauzet *et al.* (1992) recorded a much longer development time (21.3 days) at 25°C.

All species completed the development when fed with *F. occidentalis* adults. *O. majusculus* consumed significantly more thrips than *O. insidiosus* and *O. niger*. Our data support the findings of Riudavets (1995) who showed that *O. majusculus* and *O. laevigatus* can complete their development when fed only with *F. occidentalis* nymphs (total consumption rates of 62.2 and 54.1 respectively). The higher amount of prey killed

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Figure 4. Age-dependent fecundity of *Orius laevigatus* reared at three different constant temperatures.

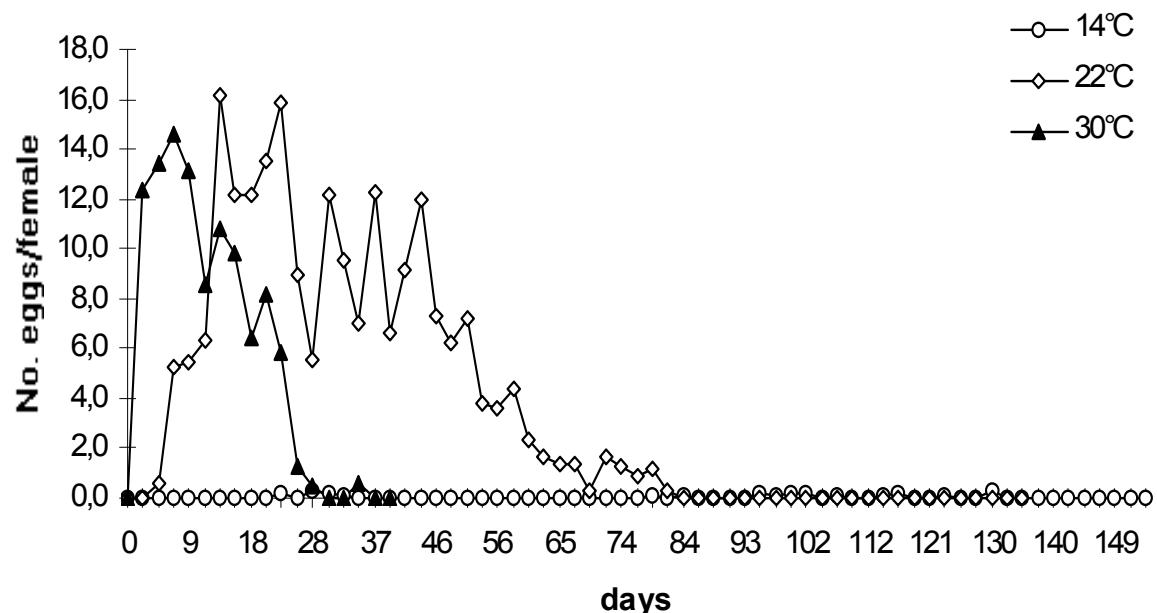
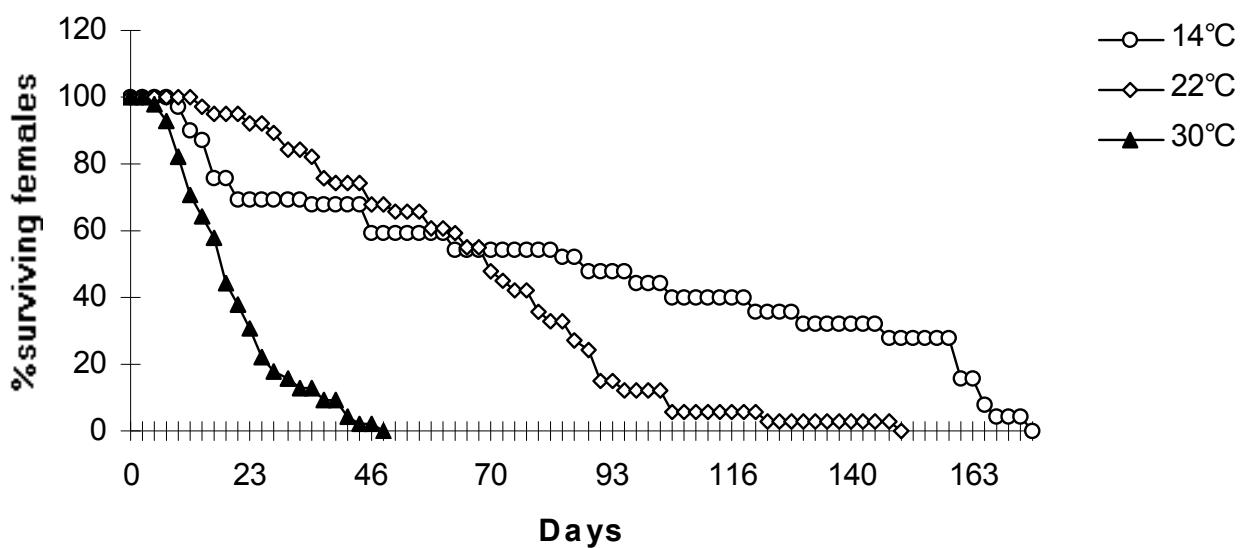


Figure 5. Survival of *Orius laevigatus* females reared at three different constant temperatures and fed with *Ephestia kuehniella* eggs.



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recorded by Riudavets (1995) in comparison with our data can be explained by both the different stage of the prey offered and the greater difficulty for *Orius* species to catch adults than nymphs (Salas-Aguillar and Ehler, 1977).

Vacante and Tropea Garzia (1993b) recorded that the last instar of *O. laevigatus* consumed a similar amount of nymphs or adults at 20°C (11.0 nymphs and 11.8 adults), but large differences have been recorded for consumption rate in the previous instars. Isenhour and Yeargan (1981c) recorded that *O. insidiosus* shows strong differences in the predation of adults or nymphs of *S. variabilis*, mostly during the young instars of the predator (4.4 larvae vs. 1.9 adult for the first instar; 10.3 larvae vs. 5.3 adults in the third instar and 14.0 larvae vs. 10.8 adults in the fifth instar). According to Husseini *et al.* (1993), *O. majusculus* showed no difference in the development time when fed with *F. occidentalis* adults (15.4±0.1 days) or with *F. occidentalis* nymphs (15.2±1.2 days).

In conclusion *Orius* nymphs can complete the development time on both *E. kuehniella* eggs and thrips, although the prey species and stage do influence *Orius* mortality and development time.

3.4.2. Adult characteristics

Pre-oviposition time, longevity and fecundity of the four *Orius* species are strongly influenced by the prey. This was earlier reported by other authors (Zaki, 1989; Tawfik and Ata, 1973a; Kiman and Yeargan, 1985; Alauzet *et al.*, 1990; Bush *et al.*, 1993).

Orius females showed better performance when fed with *E. kuehniella* eggs than with *F. occidentalis* adults, while mortality of juvenile *Orius* instars was lower when feeding on *F. occidentalis*. Pre-oviposition periods similar to our finding were recorded by Riudavets (1995) for both *O. majusculus* (3.8 days) and *O. laevigatus* (3.3 days) with *F. occidentalis* nymphs as food. *O. majusculus* showed the highest fecundity when fed with *E. kuehniella* eggs. This agrees with other authors who, on the same prey, recorded 184.7 eggs/female with ivy as oviposition substrate (Alauzet *et al.*, 1990) and 236.9 eggs on geranium leaves (Alauzet *et al.*, 1992). Our data on fecundity are similar to those found from Riudavets (1995) (176.6 eggs/female) who fed *O. majusculus* on *F. occidentalis* nymphs. Fischer *et al.* (1992) found a higher fecundity on *E. kuehniella* eggs (328.1 eggs/female).

Tavella *et al.*'s (1994) results on the fecundity of *O. laevigatus* are similar to ours when reared on *E. kuehniella* eggs (104.6 eggs/female). Others found higher fecundity when *O. laevigatus* was reared on *E. kuehniella* (Zaki (1989), 160 eggs/female; Alauzet *et al.* (1994), 158 eggs/female; Cocuzza *et al.* (1997b), 183.7 eggs/female; Vacante and Tropea Garzia (1993b), 141 eggs/female). Riudavets (1995) also recorded a higher fecundity (164 eggs/female) when *O. laevigatus* was reared on *F. occidentalis* nymphs. Both *O. laevigatus* and *O. majusculus* fed with *F. occidentalis* nymphs lived longer (45.1 and 46.1 respectively) (Riudavets, 1995) than fed with *F. occidentalis* adults, 18.5 and 18.2 days respectively.

Few data are available about the fecundity of *O. insidiosus* on the same two prey species as we used. Castañé and Zalom (1994) recorded 75.6 eggs/female with *F. occidentalis* nymphs. Kiman and Yeargan (1985) recorded 20.3 eggs/female when fed with *S. variabilis* and 103.1 eggs/female when fed with *H. virescens*. Bush *et al.* (1993) found 121.1 eggs/female when fed with *H. virescens* eggs. Barber (1936) counted 114 eggs/female with *H. obsolete* (F.) eggs as prey and Isenhour and Yeargan (1981c) found 106.4 eggs/female using *S. variabilis* (1st instar larvae) as prey.

Similar to our findings with *E. kuehniella* eggs as prey, Alauzet *et al.* (1994) found that *O. laevigatus* laid 80% of the total amount of eggs during the initial 16 days of adult life at 30°C. Also Riudavets (1995), who reared *O. laevigatus* and *O. majusculus* on *F. occidentalis*

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nymphs at 25°C recorded most egg-laying from the 7th to the 28th day. Castaño and Zalom (1994) found most oviposition from the 3rd to the 17th day for *O. insidiosus*.

Fisher *et al.* (1992) recorded a high longevity (52 days) for *O. majusculus* reared at 25°C. For *O. laevigatus*, Tavella *et al.* (1994) observed a shorter longevity (23 days) when reared under similar conditions, while Cocuzza *et al.* (1997b) found a female's longevity (41.9 days) similar to that we recorded when predator is reared on *E. kuehniella* eggs. Zaki (1989) reported a longevity of 34.5 days, Alauzet *et al.* (1994) 34 days, while Vacante and Tropea Garzia (1993b) found 40.5 days which is similar to our data. A shorter lifespan of *O. insidiosus* was recorded by Kiman and Yeargan (1985) (14.3 days) feeding the predators on the thrips *S. variabilis*. According to Tawfik and Ata (1973a) and Zaki (1989), the females of *O. laevigatus* live longer than males (32.3 and 9.9 days for females and males respectively on *A. gossypii*, 18.2 and 10.5 days on *S. littoralis* eggs, and 34.5 and 29.5 days on *E. kuehniella* eggs). As described in the previous paragraph, different results were recorded in the present study for all the four *Orius* species tested when *F. occidentalis* was used as prey.

Temperature affects the development time and lifespan of *Orius* spp. and particularly of *O. laevigatus*, which was also recorded by Alauzet *et al.* (1994), who studied *O. laevigatus* at 15, 20, 25 and 30 °C. At 30°C, development of *O. laevigatus* was fast, but its lifespan was short and fecundity lower. At temperatures of a few degrees lower the species showed its best performance. For 18, 25 and 32°C, Tavella *et al.* (1994) arrived at the same conclusions, although they recorded a lower fecundity (53.2 eggs/female at 32°C) and a longer pre-oviposition period (3.8 days at 32°C) than I did. They found a lower mortality during the pre-imaginal instars, probably due to the different methods used. Similar results were observed by Sanchez and Lacasa (2002), who studied *O. laevigatus* and *O. albidipennis* at 4 temperatures (20, 25, 30 and 35°C). They used non-linear models to explain reproduction and female survivorship in relation to temperature. For *O. laevigatus* they found the lower thermal development threshold at 11.3°C, while the upper reproductive threshold was estimated at 35.5°C.

The life-history characteristics of a natural enemy in comparison with that of the pest, are important ecological aspects to be considered in the evaluation of a potential natural enemy for biological control (van Lenteren, 1986b). Our data on four *Orius* species can provide a general basis for such a comparison with the life history of *F. occidentalis* (Table 10). These data were used to define quality control parameters, mass rearing of *Orius*, the kill rates of predators and to achieve information for biological control of thrips pest species.

O. niger was unable to develop and reproduce efficiently on *F. occidentalis*, and, in addition the rearing of *O. niger* on the factitious prey *E. kuehniella* was not successful. The three other *Orius* species showed a net reproductive rate (R_0) higher than *F. occidentalis* reared on bean leaves and cucumber, with the exclusion of *O. laevigatus* reared on *E. kuehniella*. Van den Meiracker (1994b) followed the changes in the intrinsic rate of natural increase and the net reproductive rate in a population of *O. insidiosus* reared at 25°C when fed with *E. kuehniella* eggs over several years. The intrinsic rate of natural increase (r_m) increased over time mainly due to the decrease of the development time (0.131/day after ca. 1 year from field collection and 0.169/day after 3 years). The R_0 decreased however (86.3 and 73.0, after 1 and 3 years, respectively). Van den Meiracker's values for R_0 and r_m are higher than those we recorded for the same species, but van den Meiracker reared *O. insidiosus* under different conditions and used a different method to calculate r_m (the Sekita method). The intrinsic rates of natural increase of *O. laevigatus* and *O. majusculus* given by Riudavets and Castaño (1988) are higher than the data found in the present study, but also in this case the formula used was different (presumably they did not consider pre-imaginal mortality). Also Cocuzza *et al.*,

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(1997 a) found a higher r_m (0.105) for *O. laevigatus* reared on *F. occidentalis* at 25°C than we did, and they showed that r_m was decreasing when temperature increased or decreased, $r_m = 0.051$ and 0.0099 at 35°C and 15°C, respectively. An important conclusion is that *Orius* spp. apparently change their performance over time also due to environmental conditions.

For predators, the intrinsic rate of natural increase (r_m) gives information about the speed of predator population development only. It does not tell how much prey they kill. This is quite different in parasitoids, where the r_m both provides information about the growth rate of the parasitoid population as well as its capability to reduce the pest population, because for each parasitoid egg laid, generally one pest insect is killed (van Lenteren, 1986c). Janssen and Sabelis (1992) tried to find a way to compare intrinsic rate of natural increase of predators (Phytoseiid mites) with that of their prey species (spider mites) and they concluded that predation rate is the important characteristic here to obtain an indication for the capability of biological control. However, they did not investigate the matter further. Therefore, I calculated the kill rate k_m , and based on the data obtained we can conclude that the native species *O. laevigatus* has the highest k_m . As the values for the rate of population increase do not differ a lot for *O. laevigatus* and *O. majusculus*, *O. laevigatus* is suggested to be used as natural enemy for *F. occidentalis* control because it's higher kill rate. We should realise that the searching efficiency in the field is another critical criterion for comparison of predator performance, and is not included in the kill rate.

3.5. Conclusions

All four *Orius* species are able to develop, grow and reproduce on the two prey species *F. occidentalis* and *E. kuehniella*, although the type of food influenced the development of the *Orius* species, as was observed also by other authors (Isenhour and Yeargan, 1981c; Kiman and Yeargan, 1985; Zaki, 1989; Bush *et al.*, 1993; Alvarado *et al.*, 1997).

O. niger appears to be unsuitable for biological control of *F. occidentalis*, because it is difficult to mass rear, develops slowly, has a very low r_m and has a low predation rate on *F. occidentalis*, as was also found by van Schelt (1993). *O. laevigatus* and *O. majusculus* showed similar development when fed on *F. occidentalis*. When fed on *E. kuehniella* eggs, *O. majusculus* showed a lower predation rate, higher fecundity and higher r_m than *O. laevigatus*, which are positive biological characteristics for mass production. The r_m of *O. majusculus* was lower than that of *O. insidiosus* on both prey species. However, when evaluated based on the kill rate (k_m), *O. laevigatus* and *O. insidiosus* have higher values than *O. majusculus*, so these two kill more prey per unit of time. On average, the kill rate (k_m) was highest for *O. laevigatus* and *O. insidiosus* ($k_m = 0.28$), followed by *O. majusculus* ($k_m = 0.25$) and the lowest kill rate was found for *O. niger* ($k_m = 0.23$). If we use the results obtained in this chapter for development of a practical application technique, we have to conclude that we will have to make multiple releases of *Orius*, because the development time of the predator is much longer than that of the prey.

In conclusion, the data obtained on biological characteristics and predation rate of the four *Orius* species for biological control of thrips pests, seem to indicate that *O. insidiosus*, *O. laevigatus* and *O. majusculus* are the species that best fit the criteria listed for a good natural enemy in chapter 1. It is now necessary to link these results with further information, like the presence of diapause (chapter 4) and practical field experiences (chapter 5 and 6) before drawing final conclusions about their efficiency in the field.

APPENDIX 1

Mass rearing of *O. laevigatus*

One of the main problems in the mass rearing of potentially cannibalistic predators is the provision of an adequate amount of prey. Natural prey are often difficult and expensive to rear, thus the use of factitious prey may be a solution. Based on my research it could be concluded that it is possible to easily rear *O. majusculus*, *O. laevigatus* and *O. insidiosus* on *E. kuehniella* frozen eggs. This technique is, however, economically unsuitable for *O. niger*, because of its high pre-immature mortality, long development time and low fecundity. Based on the better performance of *O. majusculus*, *O. laevigatus* and *O. insidiosus* when reared on *E. kuehniella* eggs than on *F. occidentalis*, we conclude that this factitious prey is more profitable for mass-rearing than *F. occidentalis*. It is also more simple to use and less expensive. Kiman and Yeargan (1985) studied various diets for *O. insidiosus*, and they concluded that this *Orius* species required arthropod prey to complete the development time quickly, and that mites were a more suitable diet than thrips. Vacante *et al.* (1997) and Cocuzza *et al.* (1997b) confirmed that also *O. laevigatus* can develop faster with a diet based on *E. kuehniella* rather than only on pollen.

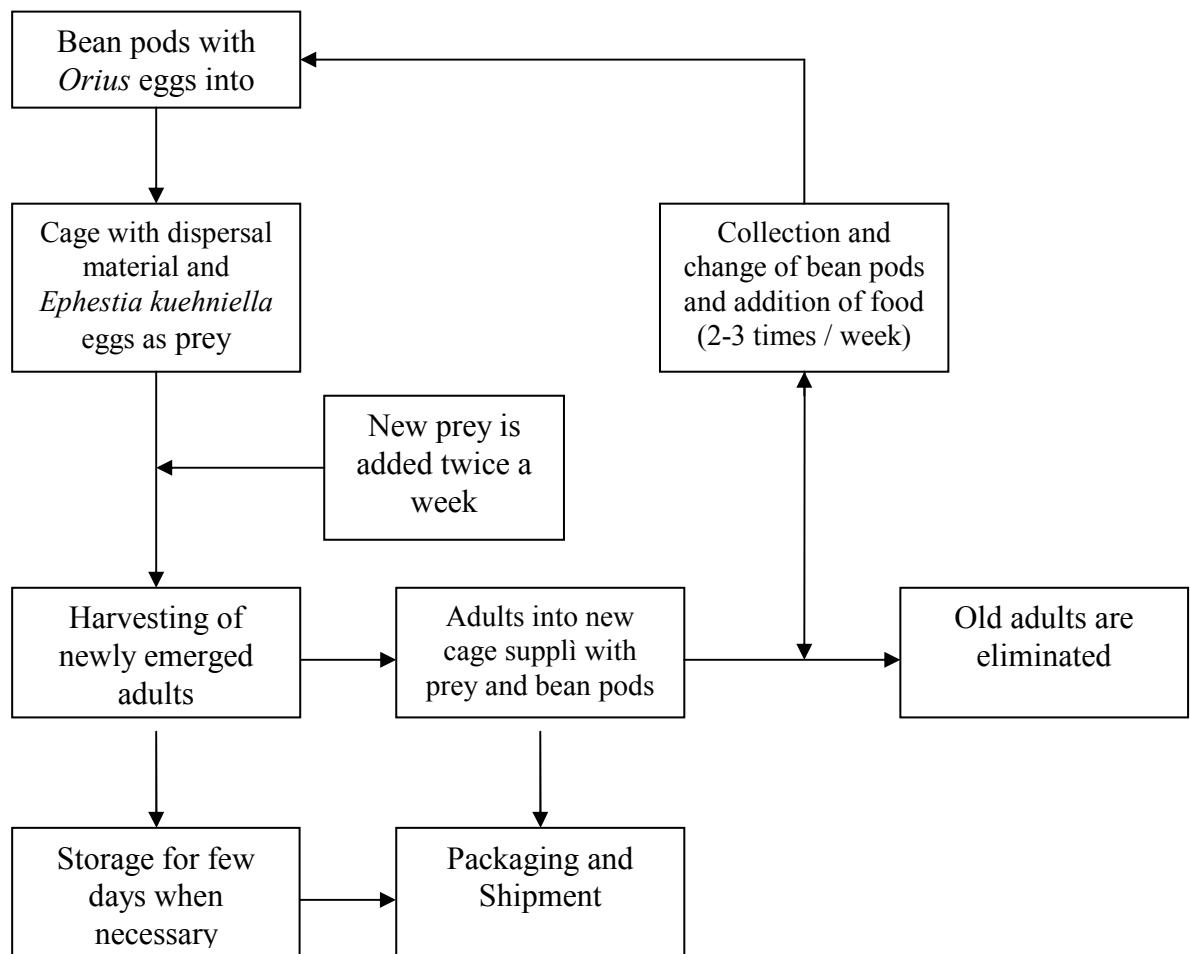
On the basis of my results, a mass rearing of *O. laevigatus* (identified by the morphological keys described in chapter 2) was set up, starting from ca. 1000 wild predators collected on Sicily (South Italy).

Environmental conditions, food and ovipositional substrate were the same as used in the pilot rearing described above. The rearing units were transparent plastic boxes (3.6 dm³ in volume), with holes for aeration closed with fine steel netting on the sides and on the top. To reduce cannibalism during the juvenile instars, a certain amount of buckwheat (ca. 1.5 dm³) was put on the bottom of each box. Each rearing unit started from ca. 1,500 eggs of *O. laevigatus* laid into French bean pods, and the whole cycle was completed in the same box. Twice a week, bean pods with eggs of the predator were collected and food and water were supplied. Adults were kept for oviposition in these boxes for ca. 4 weeks. A brief description of the rearing process is shown in figure 6. A similar rearing-method was carried out successfully for *O. laevigatus* and *O. majusculus* by Blümel (1966).

The mass-rearing of the predator has been improved in co-operation with the only Italian mass producer of natural enemies now called Bioplanet. It is now possible to produce up to 100,000 adult predators per week. They are packed in plastic bottles for release on several vegetable and ornamental crops grown in greenhouses and in open fields. The total production in 1994 was 1.5 million adult predators and increased considerably in the following years.

Quality control methods were set up both for the rearing process and for product control (van Lenteren, 1996b, 2003; Tommasini and Bolckmans, 1998).

Fig. 6. Flow-chart of rearing system of *Orius* spp.



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Chapter 4. OCCURRENCE OF DIAPAUSE IN *ORIUS LAEVIGATUS*

3

Abstract

One of the main problems in biological control of thrips in the Mediterranean area is that *Frankliniella occidentalis* (Perg.) does not undergo diapause. Therefore, finding a non-diapausing species or strain of the genus *Orius* would be very useful for seasonal inoculative releases to control this species of thrips. Both the paleartic *O. majusculus* (Reuter) and the nearctic *O. insidiosus* (Say) show a reproductive diapause that is induced by photoperiod. No data were available about the occurrence of diapause in *O. laevigatus* (Fieber). The possibility of inducing a reproductive diapause in this paleartic species was therefore investigated in the laboratory using two strains: strain N collected in northern Italy (Po Valley; ca. 44° N latitude) and strain S collected in southern Italy (Sicily; ca. 37° N latitude). The influence of photoperiod on eggs at $18\pm1^\circ\text{C}$, RH=75±10% and at several light regimes varying between 16L:8D and 8L:16D (experiment 1) and between 13L:11D and 11L:13D (experiment 2) was studied. *O. laevigatus* were fed on *Ephestia kuehniella* (Zell.) frozen eggs.

Development time, adult emergence, sex ratio, pre-oviposition period, fecundity up to day 29 of adult life, and the presence of mature oocytes were recorded. Photoperiods of 11.5L:12.5D and 12L:12D induced a longer development time, a longer pre-oviposition period and a lower oviposition rate than the other photoperiods for both populations. The percentage of egg-laying females at 18°C was higher for strain S (70%) than for strain N (44%). Termination of diapause was investigated by exposing the *Orius* strains to an higher temperature (26°C) and a longer day-length (16L:8D). The females of both strains supposedly in diapause, rapidly started to lay a high amount of eggs independently from the environmental conditions to which they were previously exposed. Next, the two strains of *O. laevigatus* were reared at five temperature regimes ($24^\circ\text{C}/12.5^\circ\text{C}$; $26^\circ\text{C}/15^\circ\text{C}$; $21.5^\circ\text{C}/6^\circ\text{C}$; $22^\circ\text{C}/12.5^\circ\text{C}$; 18°C constant) that matched the photoperiod which induced the lowest oviposition (11.5L:12.5D) in the previous experiments. The longest development time was found for both strains at $26.5^\circ\text{C}/6^\circ\text{C}$ and the shortest at $26^\circ\text{C}/15^\circ\text{C}$. A constant temperature of 18°C induced a slightly shorter development than the thermoperiod of $26.5^\circ\text{C}/6^\circ\text{C}$ in both populations. The lowest fecundity was recorded at $26.5^\circ\text{C}/6^\circ\text{C}$ and at 18°C constant for both strains, and $26^\circ\text{C}/15^\circ\text{C}$ induced the highest fecundity in the females of strain N. When the females were moved from thermoperiods of 18°C to 26°C and 16L:8D, oviposition did increase, and more than 80% of females of both strains laid eggs. In all the experiments the two strains of *O. laevigatus* gave different results.

Wild populations of *O. laevigatus* were collected in the field in August-November in Sicily and in the Po Valley and maintained in cages in the field in northern Italy (44° latitude N). During the winter, once a month females were taken from the field cages and put into a climatic chamber at $26\pm1^\circ\text{C}$, RH 75±10%. A high percentage of females laid eggs, particularly those of the Sicilian population.

³ Part of this chapter have earlier been published as: TOMMASINI M.G. & NICOLI G., 1995. Evaluation of *Orius* spp. as biological control agents of thrips pests: initial experiments on the existence of diapause in *Orius laevigatus*. Med. Fac. Landboww. Univ. Gent 60 (3a): 901-908.

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In conclusion, the two strains of *O. laevigatus* have a different way to overwinter: in the northern strain part of the population undergoes a weak reproductive diapause, while for the southern strain overwintering can be better described as quiescence.

4.1. Introduction

An important feature of insect life is their behavioural adaptation to the ubiquitous, seasonally changing environment. In many regions of the world, the biological conditions suitable for growth, development, and reproduction generally prevail only during part of the year. Many authors have studied diapause as a biological phase which occurs in many arthropods in order to survive when unfavourable seasonal conditions are present, even though not all forms of seasonal adaptations are associated with diapause (De Wilde, 1956; Mansingh, 1971; Hodek, 1973; Beck, 1980; Tauber *et al.*, 1986; Danks, 1987; Leather *et al.*, 1993). In general, the arrestment in development that enables living organisms to synchronise their life cycle with favourable environmental conditions and that avoids unfavourable conditions is called dormancy, and it can occur during all seasons. Two types of dormancy are usually distinguished in insects: quiescence and diapause. But intermediate conditions are also found and dormancy does not necessarily mean diapause.

Quiescence is a reversible state, characterised by a reduction in metabolism as a direct response to exposure to environmental extremes, such as temperature or photoperiod, and which ends immediately when favourable conditions resume. Diapause is an active response of individuals resulting in a dynamic state of low metabolic activity for adaptation to seasonal cycles, so to predictable conditions. It can be divided into three phases: diapause induction or pre-diapause (in the sensitive stage of the insect), diapause maintenance (responsive stage) and diapause termination or post-diapause. The term 'diapause syndrome', coined by De Wilde (1959), is a general term for the species-specific set of behavioural and physiological symptoms of diapause, referring initially to pre-diapause preparation for the future seasonal conditions. This concept of 'diapause syndrome' has recently been enlarged to include all pre-diapause, diapause, and post-diapause processes to seasonal changes (Tauber *et al.*, 1986). Diapause is a physiologically dynamic developmental stage and it occurs during genetically determined stage(s) of metamorphosis which are species-specific. Many factors (biotic and abiotic) can function as the token stimulus to induce diapause. In fact, the insects can translate the token stimuli in neurohormonal changes which lead to diapause (Williams, 1952). Often, the most common and reliable token stimulus is photoperiod. In many cases photoperiod and temperature interact, although other environmental factors such as food and water may also interfere (Beck, 1980; Saunders, 1982; Tauber *et al.*, 1986; Gullan and Cranston, 1994).

Beck (1980) defined four types of diapause response curves based on the photoperiod effects (Fig. 1). Type I is the long-day type of response which is typical of insects that reproduce, grow and develop under the long day conditions. Such insects go into diapause after experiencing the short days of late Summer and Autumn. Type II, the short-day type of response, is less common and is characteristic of insects that grow and reproduce under short day-length and that undergo aestival diapause. Type III is the photoperiodic response of species with both long-day and short-day responses showing two well-defined critical day-lengths. Type IV is demonstrated in only a few species, and is characterised by the absence of diapause incidence over a very restricted range of relatively long day-lengths. All other photoperiodic conditions result in a high incidence of diapause. This type of response might be termed a long-day-short-day response.

During the course of diapause, there is generally a decrease in diapause intensity and these changes can occur even if the insects are held under constant conditions. Photoperiod is one of

the major factors which acts to maintain diapause. Even the diapause termination can be dependent upon outside stimuli the insect receives, which generally are demonstrated by the return of suitable environmental conditions, such as light and temperature. Diapause intensity is generally inversely proportional to biological characteristics such as oxygen consumption, development rate, and the pre-oviposition period (Beck, 1980; Hodek and Honek, 1970). An indication of the intensity of diapause can be given by the difficulty of interrupting the diapause itself.

It is often not easy to describe the diapause syndrome of an insect species. According to many authors (e.g. Tauber *et al.*, 1986; Danks, 1987) there is no single 'correct' classification for diapause, as there is a series of cases in a continuum and adaptive responses to a variety of circumstances. A synthesis of the main diapause descriptions is shown in table 1. The classification of diapause most used in Europe is still that of Müller (1970), based chiefly on the concept of the intensity of dormancy as related to climate and geography.

Few data are available on the diapause syndrome in the predatory Heteroptera. Heteropteran predators from temperate climates generally show a seasonal activity typical of many insect species: they appear in spring or early summer and disappear in autumn (Ruberson *et al.*, 1998). All the Anthocoridae species studied overwinter as adults and those which undergo diapause in very different overwintering sites (leaf litter, organic material in wooded areas, in winter grasses or under tree bark) show reproductive diapause. Overwintering in the adult stage may provide the greatest flexibility for location of, and movement within overwintering sites, as well as movement towards food and reproductive resources in the spring.

Some *Orius* spp., such as the Nearctic species *O. insidiosus* (Iglinsky and Rainwater, 1950; Kingsley and Harrington, 1982; Ruberson *et al.*, 1991; van den Meiracker, 1994a) and *O. tristiscolor* (White) (Anderson, 1962; Askari and Stern, 1972; Gillespie and Quiring, 1993; van den Meiracker, 1994), as well as the Palearctic species *O. majusculus* (Fischer *et al.*, 1992; van den Meiracker, 1994) undergo reproductive diapause under photoperiodic stimuli (type I of diapause induction, see Fig. 1). The Palearctic *O. albidipennis* (Reuter) collected on the Canary Islands does not undergo reproductive diapause at photoperiods varying from 8:16 to 16:8 (L:D) (van den Meiracker, 1994). The Palearctic species *O. niger* Wolff is known to overwinter (Bailov, 1929), even though van de Veire and Degheele (1992) found that this species is not affected by short day-length in contrast with *O. insidiosus*, but no specific studies were carried out with this predator. Péricart (1972) recorded that the Palearctic *O. laevigatus* overwinters as an adult, but no data are available about the existence of a reproductive diapause in this species. However, Rudolf *et al.* (1993) wrote that *O. laevigatus* appears to show quiescence and not diapause, because when the individuals collected during the winter were put at favourable climatic conditions, they immediately started to lay eggs.

Differences in the response to overwintering cues among insects of the same species from different geographical areas have been found and critical photoperiods for diapause induction often appear related to latitude (Tauber *et al.*, 1986; Leather *et al.*, 1993). Two different populations of *O. tristiscolor* undergo diapause at different critical photoperiods according to their different geographical distribution in USA (Gillespie and Quiring, 1993). Parker (1975) showed genetically controlled differences in the diapause induction of two populations of another species belonging to the family Anthocoridae, *Anthocoris nemorum* (L.), collected in Scotland (56° N) and in southern England (51° N).

One of the main problems in the biological control of thrips is the synchronisation between prey and predators. In a large part of the southern Mediterranean area where temperature rarely decreases below 5-6°C during winter, *F. occidentalis* remains active in winter (Del Bene and Gargani, 1989; Lacasa, 1990; Marullo, 1991). Non-diapausing natural enemies are,

of course, more suitable for control of thrips by seasonal inoculative releases during short-day-length periods in winter. Brødsgaard (1994) studied the influence of photoperiod on *F. occidentalis* and found that this thrips species showed only slight differences in development time, longevity, and fecundity when exposed to short vs. long day-length.

The choice of methods for analysing the sensitive stage of an insect depends on the stage that enters diapause. In some species, both the sensitive stage and diapause stage occur in the same stage, but more frequently they are distinct (Tauber *et al.*, 1986). When the sensitive stage that undergoes diapause is the adult, this kind of dormancy is usually called reproductive diapause: the key arrestment in development in adults takes place in the ovaries (Beck, 19880; Saunders, 1982; Danks, 19887). From the literature it is known that the *Orius* species that show diapause, show a reproductive diapause (Péricart, 1972). The sensitive stage(s) of the Heteropterans that overwinter in diapause as adults, can comprise a large segment of the insect's lifespan (Ruberson *et al.*, 1998). Generally, the lack of juvenile hormone induces diapause in the adults (Tauber *et al.*, 1986). *O. sauteri* (Poppius) was found to undergo diapause at a short day-length (between 13 and 14 hours of light) and the sensitive stage here was the nymph (personal communication, E. Yano, 1996). In many insects that have a reproductive diapause, the sensitive stages are the last instars, *e.g.* *A. nemorum* and *Chrysoperla carnea* (Steph.) (Danks, 1987).

The aim of this study was to investigate the effect of photoperiod, as well as its interaction with temperature, on the life cycle of two strains of *O. laevigatus*, in order to determine the existence of diapause.

Figure 1. Different types of diapause incidence-day-length relationship observed among insects (modified from Beck, 1980).

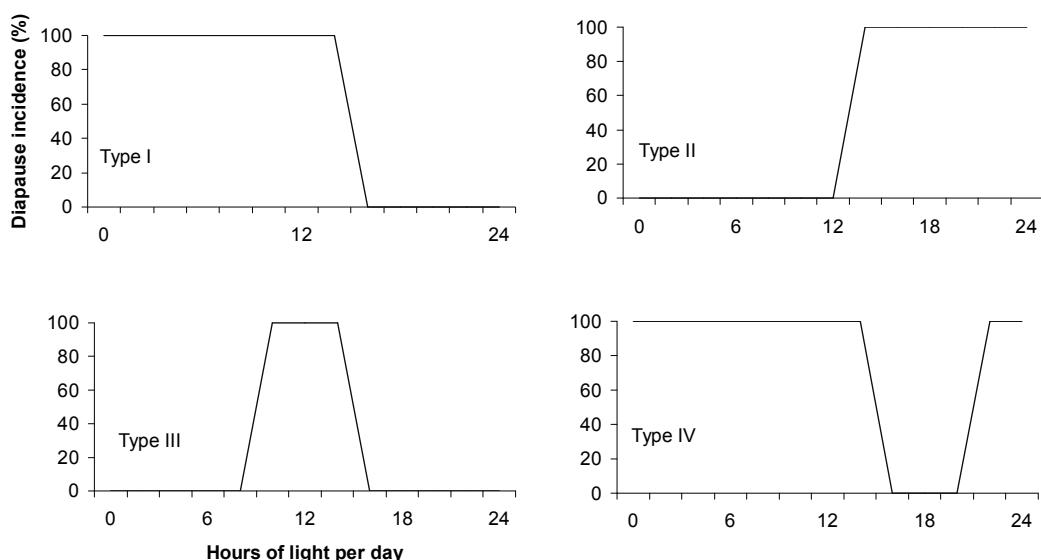


Table. 1. Summary of terminology concerning diapause and quiescence.

Terminology	Main features	Induced by	Terminated	Author
Diapause				
Parapausa	no clear induction phase	genetically fixed for univoltine species	Genetically	Müller, 1970
Diapause	long preparation before adverse situation	extreme and long-term adversity (<i>i.e.</i> photoperiod)		Mansingh, 1971
	deep and continuous diapause	extreme and long-term adversity (<i>i.e.</i> photoperiod)		Ushatnskaya, 1976
Obligatory diapause	present in every individual in each generation	regardless environmental conditions		Beck, 1980
Univoltine diapause	present in every individual in each generation	regardless environmental conditions		Tauber <i>et al.</i> , 1986
Intermediate forms of diapause				
Eudiapause	clear induction phase	facultative and due to unfavourable condition (usually photoperiod)	a different factor than the induction stimulus (for example temperature)	Müller, 1970
Oligopausa	facultative appears and ends with a delay relative to unfavourable conditions	unfavourable environmental conditions	end of unfavourable conditions	Müller, 1970
	short preparation before adversity	mild and long-term adversity	end of unfavourable conditions	Mansingh, 1971
	intermediate between quiescence and diapause	unfavourable environmental conditions	end of unfavourable conditions	Ushatnskaya, 1976
Facultative diapause	on an irregular basis in response to unpredictable exigencies	unfavourable environmental conditions	end of unfavourable conditions	Beck, 1980
Multivoltine diapause	on an irregular basis in response to unpredictable exigencies	unfavourable environmental conditions	end of unfavourable conditions	Tauber <i>et al.</i> , 1986
Quiescence				
Quiescence	immediate facultative retardation or stop of development	unfavourable conditions	end of unfavourable conditions	Müller, 1970

4.2. Material and methods

The sensitivity of *O. laevigatus* to photoperiod and temperature was tested in three laboratory and one field-laboratory experiment using two strains: strain N (northern strain, collected in northern Italy at ca. 44° N latitude (Po Valley)) and, strain S (southern strain, collected in southern Italy at ca. 37° N latitude (Sicily)). For the first three laboratory experiments, both strains were reared in the laboratory for ca. 12 generations starting from a few hundred individuals per strain. They were fed with *Ephestia kuehniella* (Zell.) frozen eggs and could oviposit on bean pods (*Phaseolus vulgaris* L.). For rearing details, see chapter 3. During all four experiments predators were fed *ad libitum* on *E. kuehniella* frozen eggs glued onto cardboard. Water was supplied by wet cotton. In the first three experiments sex ratio was determined at adult emergence. Newly-emerged adults were kept in groups during five days for mating. Pairs were then isolated into cylindrical cages (4 cm high and 4 cm diameter) and supplied with a piece of bean pod for oviposition. Dead males were regularly removed and replaced with living ones.

During all the experiments, random samples of *O. laevigatus* eggs ($n > 100/\text{exposure/strain}$) were checked for hatching. The bean pods were kept in glass tubes at 26°C (16L:8D) and hatching was checked after one week by counting the open opercules under a stereomicroscope.

At the end of each experiment, the surviving females were maintained for 24 hours without bean pods, then they were killed and dissected in order to count the number of mature oocytes. The relationship between fecundity and the number of mature oocytes per female was investigated in all experiments apart from test 1 in experiment 1.

4.2.1. Influence of photoperiod.

Experiment 1. Induction of diapause by photoperiod was tested at a fixed temperature of $18 \pm 1^\circ\text{C}$, at a light intensity of ca. 1,800 lx and RH = $75 \pm 10\%$. Bean pods with 0-6 h old *O. laevigatus* eggs were put into 5 incubators set at different photoperiods: 8L:16D, 10L:14D, 12L:12D, 14L:10D, and 16L:8D (number of eggs $> 800/\text{photoperiod}$). Eighteen degrees Celsius was chosen because it is the mean temperature in Italy during October-November in the Po Valley, and November-December in southern Italy, when potential diapause induction of *O. laevigatus* may occur. Furthermore, 18°C is the mean temperature recorded in the northern European greenhouses early in the season (van den Meiracker, 1994a). The incubators were placed in a dark chamber to prevent light interference during checks. After hatching, groups of nymphs were kept in transparent cylindrical plexiglass cages (9 cm high and 9 cm diameter) covered with gauze for aeration until adult emergence. During 24 days after isolation of adults in pairs, mortality and fecundity were checked. A period of 24 days is about 7 days longer than the estimated pre-ovipositional period of *O. laevigatus* reared at 18°C and 16L:8D (Alauzet *et al.*, 1994) and 8 times longer than the pre-oviposition period recorded at 26°C which is the optimal temperature for *O. laevigatus* (see chapter 3). Females which did not lay eggs within 29 days after emergence were excluded from the calculation of the pre-oviposition period.

In test 1 of experiment 1, only strain N was considered, and hatching and adult emergence was checked every 4 hours. The number of pairs tested ranged from 47 to 72 per photoperiod and oviposition was determined daily. In test 2 of experiment 1, both strain N and strain S were considered and adult emergence was checked twice a day. The number of pairs tested ranged from 28 to 44 per photoperiod and oviposition was recorded three times a week.

Experiment 2. Five intermediate day-lengths were set up (13L:11D; 12.5L:11.5D; 12L:12D; 11.5L:12.5D; 11L:13D) based on the results obtained during experiment 1 and close to the natural photoperiod in autumn and spring. The same procedure adopted in test 2 of experiment 1 was followed. The development time ($n = 500$ eggs) per photoperiod and the pre-oviposition period were checked daily and every two days respectively. Females which did not lay eggs within 29 days after emergence were excluded from the calculation of the pre-oviposition period. For each photoperiod survival and fecundity were checked three times a week for 24 days after isolation of pairs (44 to 50 pairs per photoperiod). After this period, pairs were moved to another climatic chamber at $26 \pm 1^\circ\text{C}$ and photoperiod 16L:8D where the same checks were continued for 24 additional days.

4.2.2. Influence of temperature.

Experiment 3. Five temperature regimes were tested ($24/12.5^\circ\text{C}$; $26/15^\circ\text{C}$; $21.5/6^\circ\text{C}$; $22/12.5^\circ\text{C}$; 18°C constant) that matched the photoperiods that induced the lowest oviposition in both strains in the previous experiments (11.5L:12.5D). The higher temperatures of the thermoperiods coincided with the photophase and the lower temperatures with the scotophase. The autumn temperatures of five years (1989-1992) and two years (1992 and 1993) recorded at several metereological cabins placed respectively in the Po Valley (ca. 44°N) and on Sicily (ca. 37°N), were analysed to choose the thermoperiods for the experiment (Table 2).

Table 2. Correspondence of thermoperiods with the seasonal periods in the Po Valley and Sicily.

Thermoperiod ($^\circ\text{C}$)	Correspondence with the seasonal period (from - to)	Mean temperature ($^\circ\text{C}$)
24 / 12.5	Po Valley: Sept. 20 - Oct. 10	18
26 / 15	Sicily: Oct. 1 - Oct. 20	20
21.5 / 6	Po Valley: Oct. 1 - Oct. 20	16.5
22 / 12.5	Sicily: Oct. 20 - Nov. 20	17
18 constant	Po Valley: Sep. - Oct. Sicily: Nov. - Dec.	18

The same procedure as in test 2 of experiment 1 was followed and more than 500 eggs per thermoperiod were used for testing. The development time and pre-oviposition period were recorded. Females which did not lay eggs within 29 days after emergence were excluded from the calculation of the pre-oviposition period. Forty-eight to 51 pairs per temperature regime were isolated five days after emergence. Female survival and fecundity were determined during 24 days after pairs were isolated, and the pairs were observed for an additional 24 days after being transferred to 26°C and 16L:8D.

4.2.3. Incidence of diapause in field collected populations

Experiment 4. The egg-laying tendency of *O. laevigatus* females collected in nature during autumn and winter at two different latitudes were measured. Wild populations of *O. laevigatus* were collected in autumn on Sicily (August-November 1994) and in the Po Valley (August-October 1994). The adults collected were phenotypically identified (for morphological keys, see chapter 2) and maintained in glass jars put in a meteorological cabin in open air in Northern Italy (ca. 44° N), with possibility to feed on *E. kuehniella* frozen eggs and with bean pods for oviposition. Absorbent paper was added as shelter and to prevent excessive humidity. New bean pods and prey were provided weekly. From August 1994 up to February 1995 some females were isolated every month in plexiglass cylinders (4 cm high, 4 cm diameter) with *E. kuehniella* frozen eggs and a piece of bean pod for oviposition in a climatic chamber at 26±1°C, RH=75±10% and photoperiod 16L:8D. Thirteen to 55 females per month per population were observed with the exclusion of September for strain S and February for strain N because an insufficient number of females was found in the field. The beginning of oviposition of each female was recorded three times a week for a maximum period of three weeks.

4.2.4. Statistical Analysis

For each condition tested in the different experiments, development time (from egg to adult emergence), pre-oviposition period, percentage of ovipositing females, fecundity, and fertility of eggs, data were statistically analysed. To obtain normal distributions, data were log transformed before analysis when necessary.

Experiment 1. Pre-imaginal development times, pre-oviposition times and female longevity during the experiment, were compared using one-way analysis of variance (ANOVA) and Tukey's test ($p<0.05$). Total oviposition was compared using the Kruskal-Wallis test followed by Dunn's procedure for multiple comparison. Percentage of emerged adults as well as the sex ratio, the percentage of egg-laying females, the percentage of females (ovipositing and non-ovipositing) with and without mature oocytes and percentages of surviving females at the end of the experiment were compared with χ^2 test ($p<0.05$). A linear correlation was established between the number of mature oocytes in the female's abdomen at day 30 and the total oviposition during the initial 29 days of adult life.

Experiment 2 and 3. Development time and fecundity were analysed by one-way analysis of variance (ANOVA), as well as for pre-oviposition time and females longevity during the experiment. When significant differences were found with ANOVA, means were separated using Tukey's test ($p<0.05$). A covariance analysis (ANCOVA) was carried out for both strains on the total fecundity (exposure 1+2), considering the fecundity during the first 29 days after emergence at different photoperiods or thermoperiods (exposure 1) as covariate. When differences were found, Tukey's test was performed ($p<0.05$). The percentages of

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hatching, of pre-imaginal mortality, the sex ratio as well as the percentages of egg-laying females, of surviving females and of fertile and infertile females with and without oocytes were compared with χ^2 test ($p<0.05$). A correlation between total fecundity and mature oocytes in the females abdomen at day 54 after emergence was calculated assuming $y = a + bx$.

Experiment 4. The percentages of the females that laid eggs after three days and three weeks was compared with χ^2 test ($p<0.05$).

4.3. Results

4.3.1. Influence of photoperiod

Experiment 1. Test 1. Table 3 reports the pre-imaginal development times of strain N of *O. laevigatus* exposed to different photoperiods. No differences were found in the sex ratio of emerged adults, so all the data were considered together. The longest development times were recorded at 12L:12D and 14L:10D. The shortest development times were recorded at the shortest day-lengths (8L:16D and 10L:14D). Differences in pre-imaginal mortality were found among all the photoperiods tested (χ^2 , $p<0.05$). The highest mortality was recorded at 14L:10D, while the lowest was at the shortest day-length. No differences among the pre-oviposition period were recorded by ANOVA, thus the photoperiod did not seem to influence strain N (Table 4). Significant differences were recorded in the number of eggs laid per female between photoperiods 12L:12D and 16L:8D (Table 5), as well as in the percentage of egg-laying females, where the lowest percentages were found at photoperiods 12L:12D (χ^2 , $p<0.05$) (Table 4). However, none of the photoperiods tested induced diapause in all females. At the photoperiods 16L:8D, 14L:10D and 12L:12D significant differences in the percentage of females with mature oocytes were found at the end of the experiment (χ^2 , $p<0.05$) (Table 5). Fig. 2 indicates that the intermediate photoperiod induced a low oviposition activity of *O. laevigatus*. At the end of the experiment no differences were recorded in numbers of surviving females among photoperiods (χ^2 , $p>0.05$).

The percentage of females with mature oocytes at day 30 from adult emergence shows significant differences (χ^2 test, $p<0.05$) among photoperiods. The highest percentage was observed at 16L:8D and the lowest one at 12L:12D, although it did not differ from that recorded at photoperiods 8L:16D and 10L:14D.

Table 3. Development time, pre-imaginal mortality and sex ratio of *Orius laevigatus* (strain N) reared at 18°C and at five photoperiods (experiment 1, test 1). Same letters indicate no significant differences by ANOVA and Tukey's test ($p < 0.05$) (Means \pm SE).

Photoperiod (L:D)	Embryonic development (days)	No. of nymphs tested	Post-embryonic development (days)	Total development (days)	% Pre- imaginal mortality	Sex ratio (% females)
8:16	8.2 \pm 0.1 a	462	22.7 \pm 0.4 a	30.9 \pm 0.3 a	51.1	43.4
10:14	8.1 \pm 0.1 a	375	23.7 \pm 0.3 a	31.8 \pm 0.3 a	59.2	51.6
12:12	9.2 \pm 0.1 b	449	28.5 \pm 0.2 c	37.7 \pm 0.2 c	64.4	45.6
14:10	9.6 \pm 0.1 b	326	28.2 \pm 0.3 c	37.8 \pm 0.3 c	69.9	58.2
16:8	8.5 \pm 0.2 a	476	25.6 \pm 0.5 b	34.1 \pm 0.3 b	60.7	47.6

Table 4. Pre-oviposition period and percentage of egg-laying females of *Orius laevigatus* (strain N) during experiment 1, test 1 (18°C and five photoperiods). No significant differences were recorded by ANOVA ($p > 0.05$) (Means \pm SD).

Photoperiod (L:D)	No. of pairs	Pre-oviposition period (days)	% Egg-laying females
8:16	38	11.1 \pm 4.9	52.8
10:14	36	13.2 \pm 5.8	58.1
12:12	19	13.3 \pm 5.1	31.7
14:10	24	11.5 \pm 4.4	48.9
16:8	46	11.3 \pm 4.1	65.7

Figure 2. Cumulative percentage of egg-laying (on the left) and surviving (on the right) females of *Orius laevigatus* (strain N) reared at different photoperiods and 18°C (Experiment 1, test 1).

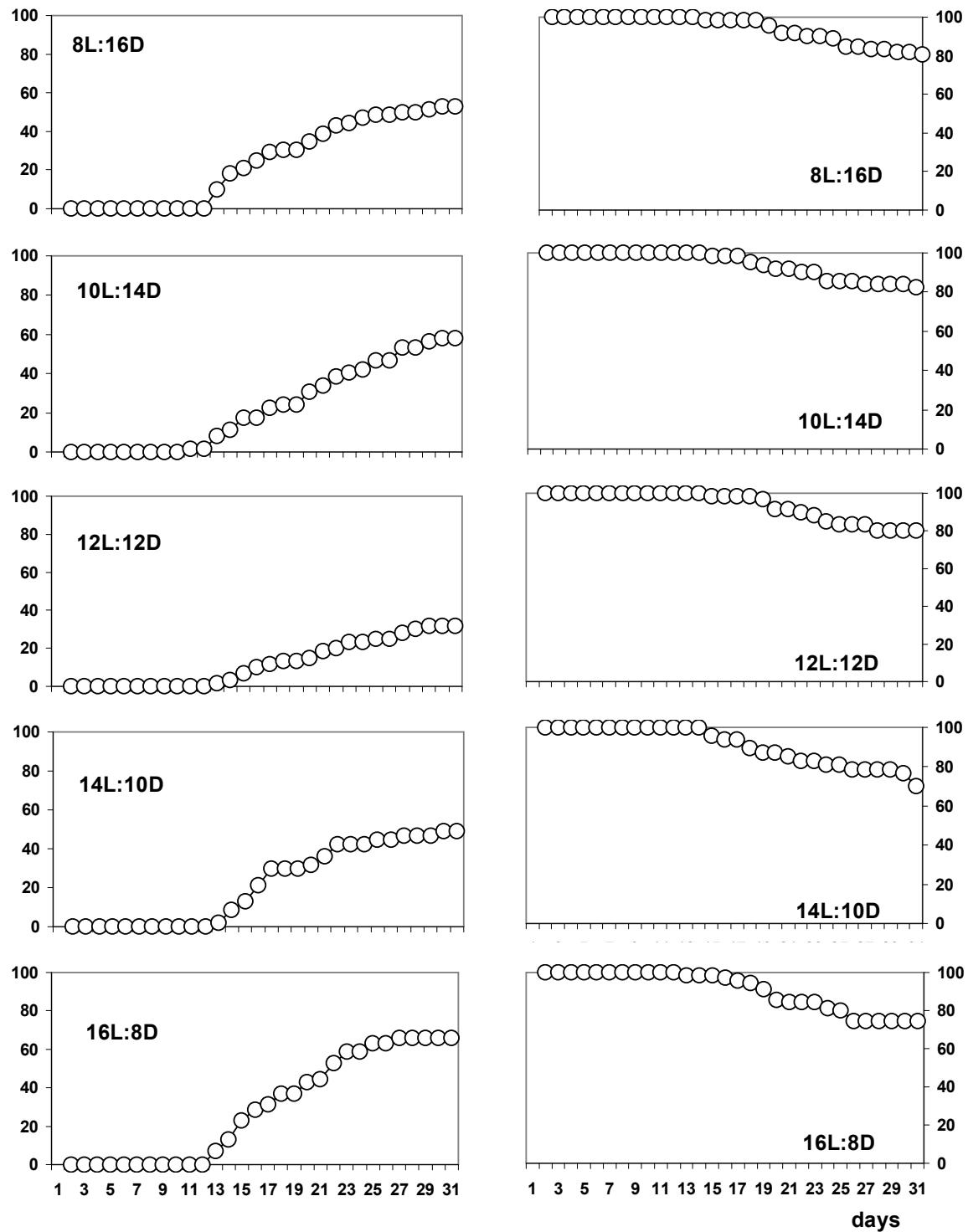


Table 5. Fecundity of females and percentage of females with mature oocytes of *Orius laevigatus* (strain N) during experiment 1, test 1 (18°C and five photoperiods). Same letters indicate no significant differences by Kruskal-Wallis test (Means \pm SD) ($p < 0.05$).

Photoperiod (L:D)	No. of pairs	No. of eggs/female	% females with mature oocytes
8:16	72	16.2 \pm 23.1 ab	56.1
10:14	62	13.1 \pm 19.3 ab	59.3
12:12	60	5.9 \pm 12.9 a	43.6
14:10	47	15.1 \pm 20.8 ab	68.9
16:8	70	21.6 \pm 23.3 b	75.8

Experiment 1. Test 2. The total development times of both strains of *O. laevigatus* are reported in table 6. No differences were found in the sex ratio of emerged adults, so both sexes were considered together for development time (χ^2 , $p > 0.05$). The longest development times were recorded at 12L:12D for both strains and 16L:8D for strain S only. Intermediate development times were recorded at 10L:14D and 14L:10D for both strains. Compared to test 1, a higher pre-imaginal mortality at all photoperiod regimes was observed and no differences were recorded among strains and regimes by the χ^2 test ($p > 0.05$).

The pre-oviposition periods showed neither differences at the five photoperiod regimes (ANOVA, $p = 0.07$), nor between strains and the interaction of strains and photoperiods. This result is strongly influenced by the limited data recorded for strain N at the photoperiod 12L:12D (Tables 7 and 8). Only one female laid eggs during exposure 1 at photoperiod 12L:12D. Therefore, to detect a possible difference, another ANOVA was carried out and all the females (egg-laying and not) were considered. For no-egg-laying females, the pre-oviposition time was taken at 29 days (the period of the experiment) (Table 7). Now, a difference was recorded among regimes. Photoperiod 12L:12D induced the longest pre-oviposition period in strain N of *O. laevigatus* (Fig. 3).

The percentage of egg-laying females is given in table 8, the number of eggs laid per female in table 9. An increase in the oviposition from day 15 to day 29 of adult life was observed (Fig. 4). Compared to test 1, strain N showed a lower oviposition rate, but the previous trend found for the oviposition activity was confirmed.

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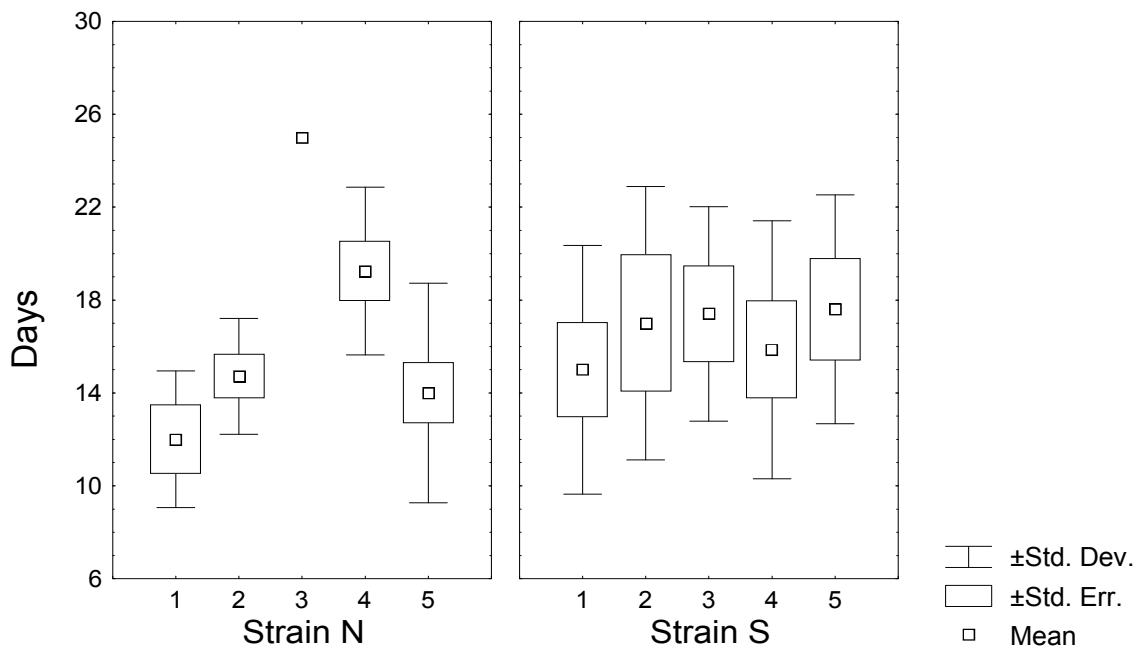
Table 6. Pre-imaginal development (egg-adult), pre-imaginal mortality and sex ratio of *Orius laevigatus* (strains S and N) at different photoperiods (experiment 1 test 2). Same letters indicate no significant differences by ANOVA and Tukey's test ($p < 0.05$) (Means \pm SE).

Photoperiod (L:D)	Strain N			Strain S		
	Total development (days)	% Pre- imaginal mortality	Sex ratio (% female)	Total development (days)	% Pre- imaginal mortality	Sex ratio (% female)
8:16	34.3 \pm 0.4 a	82.3	60.4	34.7 \pm 0.3 a	80.5	55.2
10:14	37.6 \pm 0.4 b	83.9	61.8	37.1 \pm 0.3 bc	85.3	57.3
12:12	41.7 \pm 0.4 c	87.9	61.5	38.8 \pm 0.4 d	85.0	55.8
14:10	37.5 \pm 0.3 b	85.6	49.4	36.2 \pm 0.4 b	74.2	51.9
16:8	34.2 \pm 0.3 a	77.3	54.1	38.3 \pm 0.5 cd	85.2	59.5

Table 7. ANOVA summary of the main effects on the pre-oviposition period of *Orius laevigatus* (strains N) during the exposure at five photoperiods and 18°C (experiment 1, test 1) considering only egg-laying females, and all the females respectively.

Effect	Only egg-laying females			All females	
	df	F	p-level	F	p-level
strain (1)	1	0.08	0.77	0.78	0.37
Regimes (2)	4	2.25	0.07	2.80	0.02*
Interaction (1 x 2)	4	2.03	0.10	1.98	0.09

Figure 3. Pre-oviposition period of *Orius laevigatus* (strains N and S) at different photoperiods (1, 8L:16D; 2, 10L:14D; 3, 12L:12D; 4, 14L:10D; 5, 16L:8D) and 18°C. (Experiment 1, test 2)



Presumably, the lower oviposition in test 2 is due to the reduction in the number of checks. The lower number of checks was done to keep low temperature (18°C) more constant. The number of eggs laid per female at 12L:12D was lower than that at 16L:8D, and the percentage of egg-laying females was lower at 12L:12D and at 8L:16D compared to the other photoperiods tested. In strain N, only 1 female laid eggs 23 days after emergence at 12 hours photophase. Strain S showed no differences among groups exposed to different day-lengths, indicating a lower sensitivity to influence of photoperiod than strain N, although each group showed a lower percentage of egg-laying females compared to strain N reared at 16L:8D (χ^2 test; $p<0.05$). Almost all the eggs checked during experiment 1 were fertile (hatching rate >90%).

The cumulative percentages of surviving females of the two strains of *O. laevigatus* at the five photoperiods are shown in Fig. 4. No differences in survival were recorded among photoperiods for each strain, as well as between strains for each photoperiod (χ^2 test; $p>0.05$).

The percentages of females with mature oocytes at day 30 after adult emergence, the percentages of egg-laying females and the oviposition activities, showed a similar trend for the environmental conditions tested. However, strain S showed similar results among photoperiods and no statistical differences were found (χ^2 test; $p>0.05$) (Table 10). In strain N significant differences were found in the percentage of fertile females with oocytes and among the percentage of infertile females without oocytes (χ^2 test; $p<0.05$) (Table 10). The lowest percentage of infertile females without oocytes, supposedly in diapause, was found at photoperiod 16L:8D. The highest percentage was found at photoperiods 12L:12D and 8L:16D. The percentages of diapausing (= non-egg-laying) and non-diapausing (= egg-laying)

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females with oocytes in their abdomen at the end of experiment 1, test 2, are shown in Fig. 5. It appears that a high percentage of females of both strains of *O. laevigatus* and particularly of strain N, could be considered in diapause according to the just mentioned criteria. But we have to take into account that even at 16L:8D and 18°C more than 40% of the females did not lay eggs and did not produce oocytes. Thus, at the conditions that resulted in maximal diapause, the percentage of females not laying and not producing oocytes increased with 89.7% for strain N and with 57.3% for strain S.

A slight positive correlation was found between the number of mature oocytes in the abdomen of 30 days old females (= 26 days after isolation of pairs) and the total number of eggs laid per female ($R=0.53$, $p<0.001$, $y = 0.45 + 1.3x$).

Table 8. Pre-oviposition period of *Orius laevigatus* (strains S and N) in experiment 1, test 2 (18°C and different photoperiods). No significant differences were found by ANOVA ($p>0.05$) (Means \pm SD). Percentage of egg-laying females of the entire population exposed to different photoperiods (χ^2 test; $p<0.05$).

Photoperiod (L:D)	Strain N			Strain S		
	No. of pairs	Pre-oviposition period (days)	% Egg- laying females	No. of pairs	Pre-oviposition Period (days)	% Egg- laying females
8:16	4	12.0 \pm 2.9	11.1	7	15.0 \pm 5.4	15.9
10:14	7	14.7 \pm 2.5	20.6	3	17.0 \pm 5.9	12.1
12:12	1	25.0 \pm 0.0	3.5	5	17.4 \pm 4.6	13.2
14:10	8	19.3 \pm 3.6	28.6	7	15.9 \pm 5.6	17.5
16:8	13	14.0 \pm 4.7	39.4	5	17.6 \pm 4.9	16.7

Table 9. Fecundity of *Orius laevigatus* females, during the initial 29 days of adult life at different photoperiods in experiment 1, test 2. Same letters indicate no significant differences by ANOVA and Tukey's test ($p<0.05$) (Means \pm SE).

Photoperiod (L:D)	Strain N		Strain S	
	No. of pairs	No. of eggs/female	No. of pairs	No. of eggs/female
8:16	36	3.6 \pm 2.0 ab	44	4.0 \pm 1.7 ab
10:14	34	3.2 \pm 1.3 ab	33	2.5 \pm 1.6 ab
12:12	29	0.1 \pm 0.1 a	38	2.4 \pm 1.1 ab
14:10	28	5.2 \pm 1.8 ab	40	3.4 \pm 1.7 ab
16:8	33	11.2 \pm 3.4 b	30	2.7 \pm 1.7 ab

Table 10. Percentage of fertile and infertile females with mature oocytes, and unfertile females without oocytes counted in the entire population, 24 hours after the end of test 2 of experiment 1 (day 30 after adult emergence).

Photoperiod (L:D)	Strain N			Strain S		
	No. of females	% Fertile female with oocytes	% Infertile female with oocytes	No. of females	% Fertile female with oocytes	% Infertile female with oocytes
8:16	35	11.4	11.5	77.1	37	18.9
10:14	33	18.2	30.3	51.5	31	12.9
12:12	29	0	10.3	89.7	36	11.1
14:10	28	28.6	28.6	42.9	37	16.2
16:8	29	37.9	32.1	30.0	29	17.2
χ^2 test		p<0.001	p>0.05	p<0.005		p>0.05
					p>0.05	p>0.05

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Figure 4. Cumulative percentage of egg-laying (on the left) and surviving (on the right) females of *Orius laevigatus* (strains N and S) at different photoperiods and 18°C (Experiment 1, test 2).

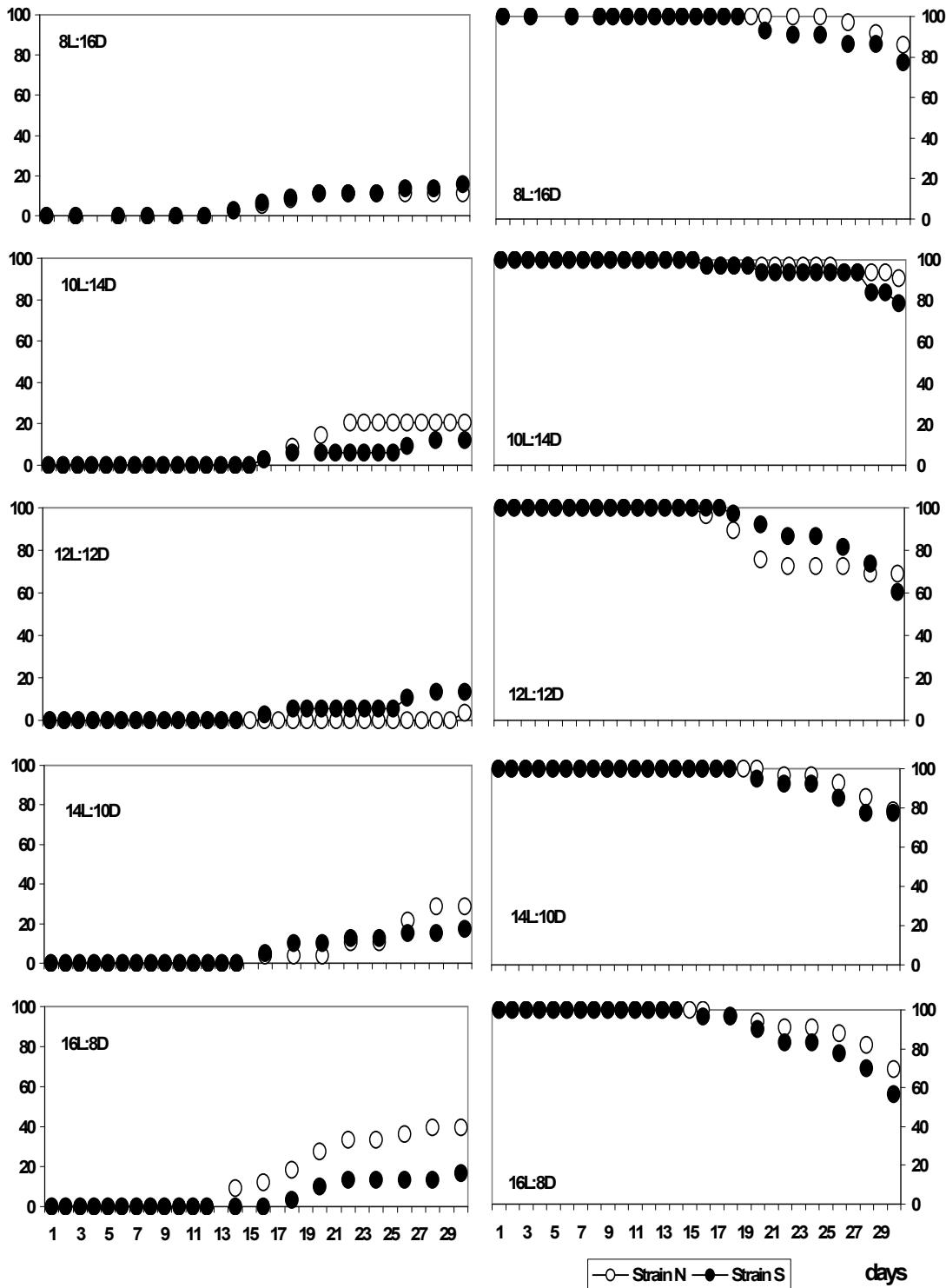
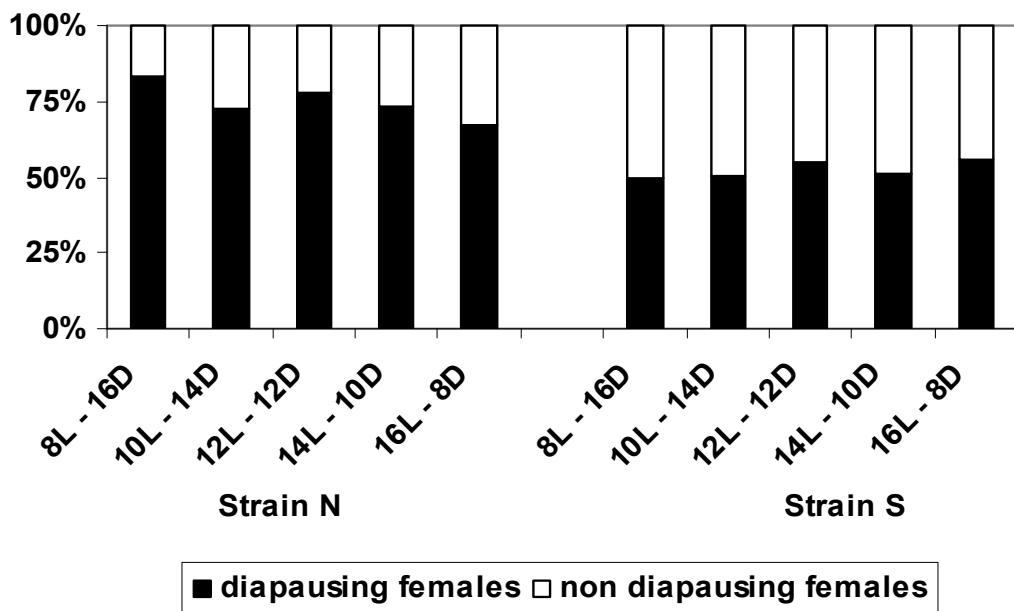


Figure 5. Percentages of egg-laying (= non-diapausing) females and non-egg-laying (= diapausing) females with oocytes at the end of the experiment (Experiment 1, test 2) at different Light – Dark periods.



Experiment 2.

The development time of the two strains of *O. laevigatus* showed no differences when reared at the same photoperiod regime and both strains showed the longest development time at 11.5L:12.5D, 12L:12D and 13L:11D (Tables 11 and 12). No differences were found in the sex ratio of emerged adults (χ^2 test), so all individuals were considered together. For the pre-oviposition period only a difference among the photoperiod regimes was recorded (Table 13). Therefore Tukey's test was carried out among the means pooled without distinguishing the strains. For both strains the pre-oviposition time was shorter at photoperiods 12.5L:11.5D and 13L:11D, when compared to that at photoperiod 11.5L:12.5D (Tables 13, 14 and 15).

Table 11. Summary of the main effects found by ANOVA on the development time of *Orius laevigatus* (strains N and S) during experiment 2.

Effect	Df	F	p-level
Strain (1)	1	4.02	0.06
Regimes (2)	4	15.28	0.001 *
Interaction (1 x 2)	4	1.07	0.41

Table 12. Development time (days) of two strains of *O. laevigatus* reared at 18°C and five photoperiods (experiment 2), starting from more than 500 eggs/strain/photoperiod. Different letters on the same line indicate a significant difference using Tukey's test on the means pooled ($p<0.05$) (Means \pm SD).

Photoperiod (L:D)	11:13	11.5:12.5	12:12	12.5:11.5	13:11
Strain N	34.5 \pm 0.7	39.5 \pm 0.7	36.5 \pm 0.7	32.0 \pm 2.6	35.7 \pm 1.5
Strain S	34.0 \pm 1.4	39.5 \pm 0.7	39.5 \pm 0.7	33.5 \pm 0.7	38.0 \pm 0.8
Means pooled	34.3 \pm 1.0 ab	39.5 \pm 0.7 c	38.0 \pm 0.7 c	32.8 \pm 1.6 a	36.9 \pm 1.1 bc

Table 13. Summary of the main effects found by ANOVA on the pre-oviposition period and on the fecundity of *Orius laevigatus* (strains N and S) when exposed to five photoperiods and 18°C (experiment 2).

Effect	Pre-oviposition period			Fecundity	
	Df	F	p-level	F	p-level
Strain (1)	1	2.24	0.13	25.72	0.001 *
Regimes (2)	4	4.23	0.05 *	5.84	0.001 *
Interaction (1 x 2)	4	0.67	0.62	3.35	0.01 *

Table 14. Comparison of pooled means of the pre-oviposition period of the two strains of *Orius laevigatus* (Tukey's test, $p<0.05$) (experiment 2).

Photoperiod (L:D)	11:13	11.5:12.5	12:12	12.5:11.5	13:11
Strains N and S	13.8 ± 4.5 ab	14.6 ± 6.0 b	14.2 ± 4.8 ab	11.5 ± 4.4 a	11.6 ± 5.2 a

During the initial 29 days of adult life at 18°C, the fecundity of the two strains of *O. laevigatus* showed differences related to both the strain and the photoperiod, as well as to the interaction of both photoperiod and strain (ANOVA, $p<0.01$) (Table 13). No differences in the fecundity were recorded among the photoperiods for strain N, while strain S showed a higher rate of oviposition at 12.5L:11.5D compared to 11.5L:12.5D, 12L:12D, and the data recorded for strain N at all the photoperiods tested (Table 16). During exposure 1, the percentage of egg-laying females increased progressively at all photoperiods and at the last day at this exposure, strain S showed a higher percentage of fertile females compared to strain N, respectively at photoperiods 11L:13D, 12.5L:11.5D and 13L:11D (χ^2 test, $p<0.001$) (Table 15). However, no differences were recorded in the percentage of egg-laying females at the end of the experiment (χ^2 test, $p>0.05$) (Table 19). The optimal climatic conditions during exposure 2, led to an increase in oviposition and in the percentage of fertile females (Fig. 7) for all groups of females, with no differences on total fecundity (exposure 1 + 2) among the five photoperiod regimes (ANCOVA, $p>0.05$) (Table 19). Because the environmental conditions were changed in exposure 2 (26°C, 16L:8D), a covariance analysis was carried out and the fecundity during exposure 1 was taken as covariate. Significant differences were recorded only between strains and their interaction with the photoperiods (ANCOVA, $p<0.05$) (Table 17).

The covariance analysis was carried out either considering the full population tested or only the egg-laying female population for both strains as shown in table 18. Similar differences were recorded for fecundity between *O. laevigatus* strains and their interaction with environmental conditions (regimes) (Tables 17 and 18) and a test of parallelism confirmed those results. The main effects found by ANCOVA on the full populations are shown in figure 6, which gives a clear idea of the behaviour of the two strains of *O. laevigatus* at the different regimes tested.

The adjusted means of the oviposition recorded during exposure 2 (when the environmental conditions were switched from 18°C and different photoperiods to 26°C and 16L:8D) show an increase compared to exposure 1 (see Fig. 7). The highest increase is found for strain N exposed to the photoperiods 11L:13D and 11.5L:12.5D (Table 19).

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Table 15. Pre-oviposition period and percentage of fertile females of two strains of *Orius laevigatus* reared at 18°C and five photoperiods (experiment 2). Different letters indicate a significant difference using ANOVA and Tukey's test ($p<0.05$) (Means \pm SD).

Photoperiod (L:D)	Strain N			Strain S		
	No. of fertile females	Pre-oviposition period (days)	% Fertile females	No. of fertile females	Pre-oviposition period (days)	% Fertile females
11:13	13	14.5 \pm 5.0 ab	31.0	30	13.0 \pm 4.0 ab	62.5
11.5:12.5	22	14.6 \pm 6.1 b	52.4	22	14.6 \pm 5.9 b	55.0
12:12	18	14.6 \pm 4.7 ab	40.9	24	13.8 \pm 5.0 ab	64.9
12.5:11.5	27	12.9 \pm 4.5 a	61.4	42	10.2 \pm 4.4 a	95.5
13:11	14	11.7 \pm 5.9 a	34.1	29	11.6 \pm 4.5 a	70.7

Table 16. Fecundity of two strains of *Orius laevigatus* reared at 18°C and five photoperiods (experiment 2). Different letters indicate a significant difference using ANOVA and Tukey's test ($p<0.05$) (Means \pm SD).

Photoperiod (L:D)	Strain N		Strain S	
	No. of pairs	No. of eggs/female	No. of pairs	No. of eggs/female
11:13	42	3.8 \pm 7.7 a	48	11.5 \pm 12.6 ab
11.5:12.5	42	7.3 \pm 10.8 a	40	5.8 \pm 7.0 a
12:12	44	3.9 \pm 7.9 a	37	8.5 \pm 10.1 a
12.5:11.5	44	8.3 \pm 10.7 a	44	19.3 \pm 16.0 b
13:11	41	3.3 \pm 7.1 a	41	12.2 \pm 13.7 ab

Table 17. Summary of the main effects found by ANCOVA on the fecundity of *Orius laevigatus* (strains N and S) during experiment 2, considering fecundity during exposure 1 as covariate; the entire female population was included.

Effect	Df	F	p-level
Strain (1)	1	12.10	0.001 *
Regimes (2)	4	1.39	0.2
Interaction (1 x 2)	4	2.85	0.02 *

Table 18. Summary of the main effects found by ANCOVA on the fecundity of *Orius laevigatus* (strains N and S) during experiment 2, considering fecundity during exposure 1 as covariate; only fertile females of the populations were included.

Test of parallelism					
Effect	Df	F	p-level	F	p-level
Strain (1)	1	14.11	0.001 *	16.44	0.001 *
Regimes (2)	4	1.60	0.1	0.94	0.44
Interaction (1 x 2)	4	2.49	0.04 *	2.20	0.02 *

When we compare fertile females with oocytes with infertile females with oocytes and with infertile females without oocytes for both strains, differences in the percentages of fertile females with oocytes and infertile females without oocytes for the various photoperiods were recorded only for strain S (χ^2 test, $p<0.05$) (Table 20).

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Table 19. Number of eggs laid per female by two strains of *Orius laevigatus* at the end of exposure 1 and at the end of the experiment 2. Only fertile females were considered. Different letters indicate significant differences found by ANCOVA and Tukey's test ($p<0.05$) (Means \pm SD).

Photoperiod (L:D)	Strain N					Strain S				
	No. of pairs	No. of eggs/fem. exposure 1	No. of eggs/fem. exposure 1+2	Adjusted means	Fertile females (%) exposure 1+2	No. of pairs	No. of eggs/fem. exposure 1	No. of eggs/fem. exposure 1+2	Adjusted means	Fertile females (%) exposure 1+2
11:13	35	4.5 \pm 8.1 a	50.5 \pm 30.4 a	58.5	91.9	39	11.2 \pm 11.9 ab	48.0 \pm 41.2 a	43.6	91.7
11.5:12.5	38	7.7 \pm 10.8 a	54.0 \pm 31.0 a	56.1	100	29	6.6 \pm 6.9 a	25.3 \pm 27.1 a	29.5	96.3
12:12	39	4.2 \pm 7.7 a	40.6 \pm 28.2 a	49.1	94.7	27	9.3 \pm 9.5 a	29.5 \pm 34.6 a	28.6	95.7
12.5:11.5	41	7.8 \pm 10.4 a	36.4 \pm 31.5 a	38.2	100	43	19.7 \pm 15.8 b	62.4 \pm 54.0 a	42.2	100
13:11	30	5.3 \pm 7.8 a	40.8 \pm 40.2 a	47.3	88.5	37	11.8 \pm 12.6 ab	44.6 \pm 42.8 a	39.1	96.8

Table 20. Percentages of fertile and infertile females with mature oocytes 24 hours after the end of the experiment 2.

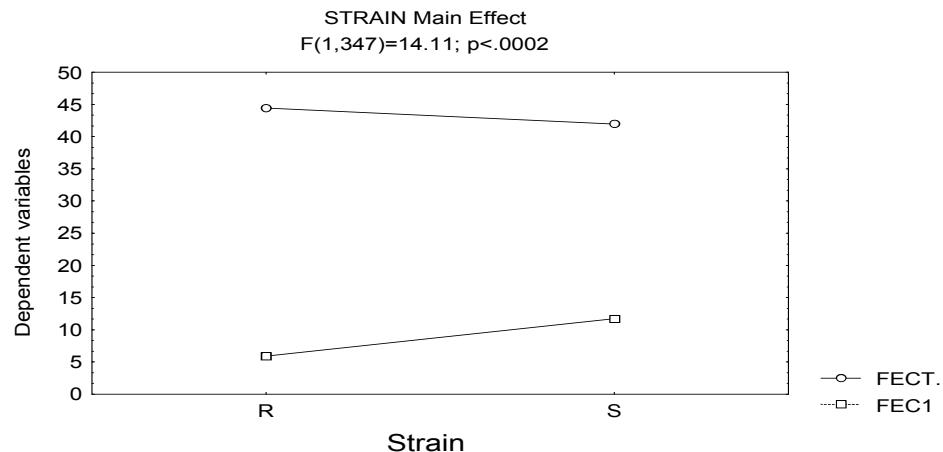
Photoperiod (L:D)	No. of females	Strain N			Strain S		
		% Fertile female with oocytes	% Infertile female with oocytes	% Infertile female without oocytes	No. of females	% Fertile female with oocytes	% Infertile female with oocytes
11:13	40	65.0	25.0	10.0	42	61.9	7.1
11.5:12.5	40	55.0	0	5.0	31	51.6	3.2
12:12	43	58.1	2.3	7.0	31	35.5	3.2
12.5:11.5	43	55.8	4.6	0	43	83.7	0
13:11	35	54.3	5.7	8.6	37	48.6	0
χ^2		p>0.05	p>0.05	p>0.05		p<0.001 *	p>0.05
							p<0.05 *

Absence of oocytes in the fertile females could be due to their old age at the end of the experiment, but absence of oocytes in the infertile females could be the result of diapause induction. In any case, only at the photoperiods 11.5L:12.5D and 12L:12D a few infertile females were found without oocytes, two and three respectively. After exposition for three weeks at 26°C and 16L:8D (exposure 2), none of the females seemed to show diapause in strain S and only a very small number in strain N (Table 20). At the end of the experiment a very low percentage of females for both strains appeared to be in diapause for each photoperiod, based on the percentages of egg-laying and non-egg-laying females with oocytes (Fig. 8).

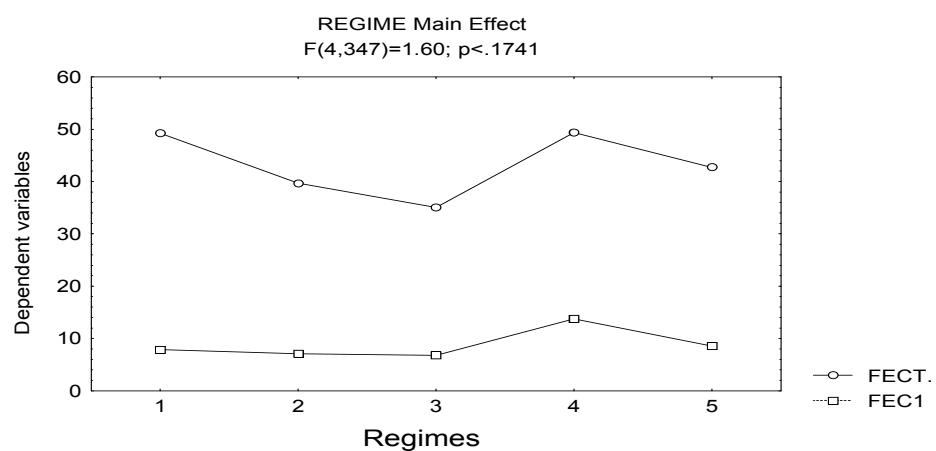
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Figure 6. Main effects - strain (A), photoperiod (B) and their interaction (C) - found in experiment 2 in the covariance analysis (ANCOVA, table 17). (R = northern strain; S = southern strain) (FECT total fecundity, FEC1 the fecundity during exposure 1 at different photoperiods used as covariate) (Regimes: 1=11L:13D; 2=11.5L:12.5D; 3=12L:12D; 4=12.5L:11.5D; 5=13L:11D)..

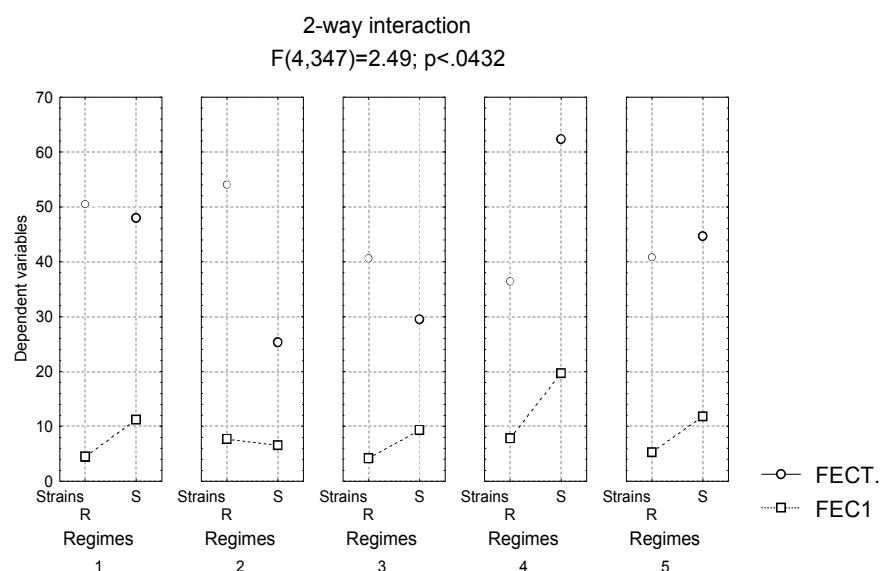
A



B



C



The cumulative percentages of egg-laying and surviving females during experiment 2 are shown in figure 7. Different effects of photoperiods were found on the percentage of surviving females for both strains at the end of exposure 1 (29th day) (Table 21) (χ^2 test, $p<0.01$). At the end of the experiment (exposure 1 and 2) a significant difference in egg-laying and survival was recorded only for strain S (χ^2 test, $p<0.01$). Furthermore, a difference in egg-laying and survival was found between the strains at photoperiod 12L:12D at the end of exposure 1, and at photoperiod 11.5L:12.5D at the end of the experiment 2 (χ^2 test, $p<0.01$) (Table 21). So, photoperiod can influence female survival.

Total fecundity (exposure 1+2) and the number of mature oocytes per female at the end of the experiment appeared to be weakly correlated ($y = 39.97 + x$; $R=0.13$, $p<0.05$).

Table 21. χ^2 test on the percentages of surviving females at various photoperiods and of the two strains at the end of exposure 1 and exposure 2.

Strain	χ^2 test (p-level) at the end of exposure 1	χ^2 test (p-level) at the end of exposure 2
N	$p<0.005$ *	$p>0.05$
S	$p<0.01$ *	$p<0.001$ *
<hr/>		
Photoperiod	(p-level)	(p-level)
11L:13D	$p>0.05$	$p>0.05$
11.5L:12.5D	$p>0.05$	$p<0.001$ *
12L:12D	$p<0.01$ *	$p>0.05$
12.5L:11.5D	$p>0.05$	$p>0.05$
13L:11D	$p>0.05$	$p>0.05$

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Figure 7. Cumulative percentages of egg-laying (on the left) and surviving (on the right) females of two strains (S=southern and N=northern) of *Orius laevigatus* reared at different photoperiods and 18°C for 29 days and then for further 24 days at 16L:8D and 26°C (Experiment 2).

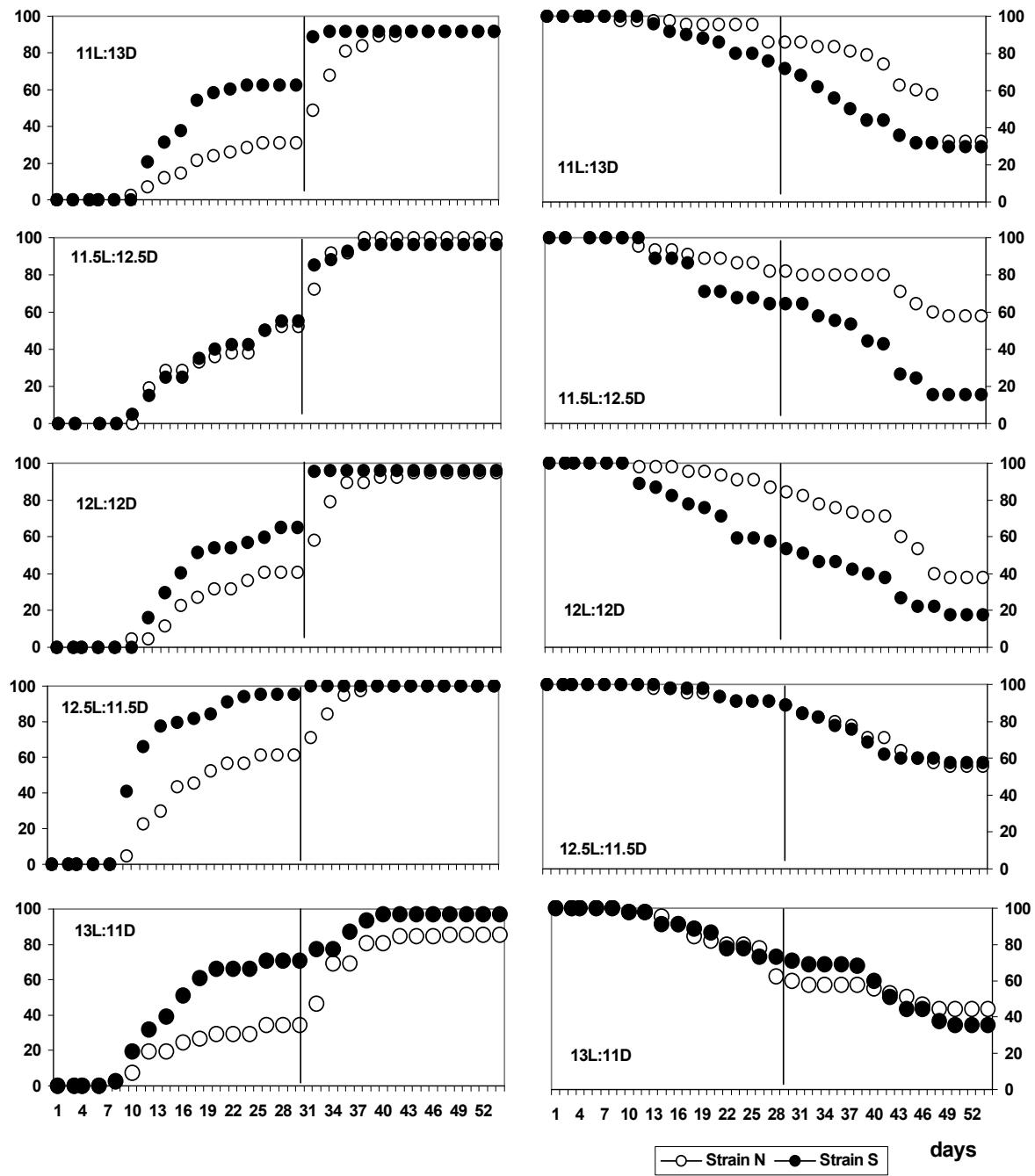
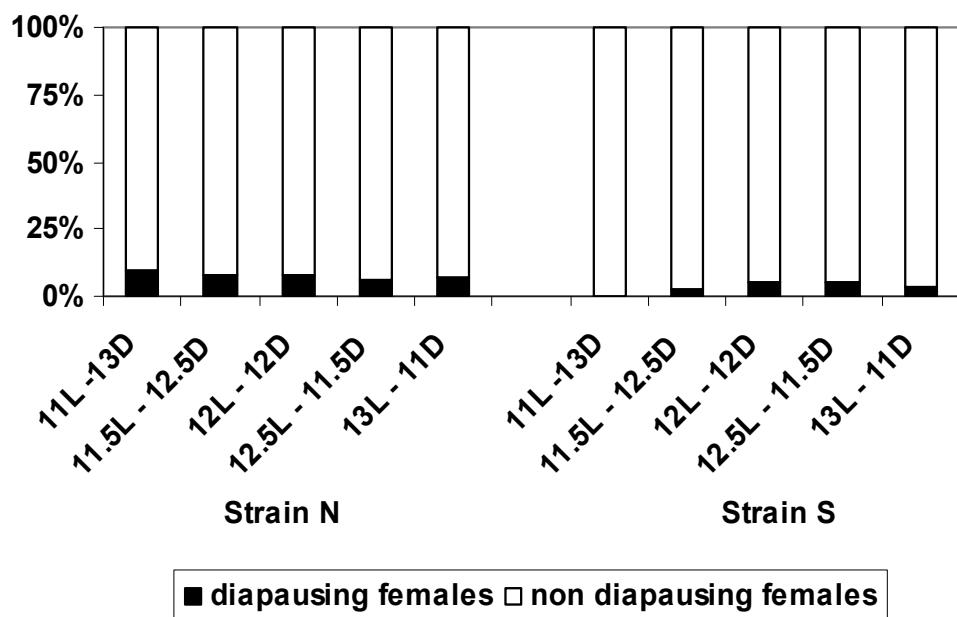


Figure 8. Percentage of egg-laying (= non-diapausing) females and non-egg-laying (= diapausing) females with oocytes at the end of the experiment 2, at different Light – Dark periods.



4.3.2. Influence of temperature

Experiment 3

This experiment was carried out to study the influence of temperature combined with a critical photoperiod (11.5L:12.5D) on diapause induction of *O. laevigatus*. The ANOVA test showed differences among the regimes of temperatures, but no differences were recorded between strains or their interaction with the regimes on the development time of *O. laevigatus* (Tables 22 and 23). The slowest embryonic development and longest development time were recorded for both *O. laevigatus* strains at a thermoperiod 21.5°C/6°C, while the fastest development was at 26°C/15°C (Table 23). Furthermore, the development time is shorter at a thermoperiod of 24°C/12.5°C with an average temperature of 18°C than at a constant temperature of 18°C. The pre-imaginal mortality was high at all the regimes tested because groups of ten nymphs were reared together in a cylinder and mortality may be a result of cannibalism. The highest mortality was recorded at 21.5°C/6°C for strain S, while the lowest mortality was observed for both strains at 26°C/15°C (χ^2 test, $p<0.05$) (Table 24). No differences were recorded for the sex ratio (χ^2 test, $p>0.05$), thus all the individuals were considered together for the calculation of the development time.

Table 22. Summary of the main effects by ANOVA on the development time of *Orius laevigatus* (strains N and S) during experiment 3.

Effect	Embryonic period			Total development	
	Df	F	p-level	F	p-level
Strain (1)	1	0.44	0.52	4.01	0.07
Regimes (2)	4	45.49	0.001 *	15.28	0.001*
Interaction (1 x 2)	4	0.23	0.92	1.06	0.41

The ANOVA (Table 25) indicated that strain N had a pre-oviposition period longer than strain S (Table 26). Differences were recorded also among the temperature regimes, although the interaction between strains and regimes was not significant. The longest pre-oviposition period was recorded for both strains at 18°C constant, but this was not significantly different from the data recorded at 21.5°C/6°C and at 22°C/12.5°C (Tables 27 and 28).

Table 23. Pooled means (\pm SD) of embryonic development time and total development time, considering together the strains N and S of *Orius laevigatus*. Different letters on the same line indicate significant differences using ANOVA ($p<0.001$) and Tukey's test ($p<0.05$) (Experiment 3).

Temperature regime (°C)	24/12.5	26/15	21.5/6	22/12.5	18 constant
Embryonic development	10.0 \pm 0 b	8.0 \pm 0 a	12.3 \pm 0.4 c	10.6 \pm 1.0 b	10.0 \pm 0 b
Total development time	32.6 \pm 0.7 b	28.3 \pm 0.9 a	51.3 \pm 1.7 d	35.0 \pm 2.2 c	36.5 \pm 1.5 c

Table 24: Embryonic development time and total development time (days \pm SD) of two strains of *Orius laevigatus* reared at five temperature regimes matched to the 11.5L:12.5D photoperiod (experiment 3). More than 500 eggs were observed per strain and temperature regime. Pre-imaginal mortality and sex ratio are shown as percentages (χ^2 test, $p<0.05$ for mortality; $p>0.05$ for sex ratio).

Temperature regime (°C)	Strain N				Strain S			
	Embryonic development (days)	Total development (days)	% Pre-imaginal mortality	Sex ratio (% fem.)	Embryonic development (days)	Total development (days)	% Pre-imaginal mortality	Sex ratio (% fem.)
24/12.5	10.0 \pm 0.0	32.4 \pm 0.5	71.2	47.0	10.0 \pm 0.0	32.7 \pm 0.8	79.7	54.0
26/15	8.0 \pm 0.0	27.0 \pm 0.0	68.9	47.0	8.0 \pm 0.0	29.6 \pm 1.7	48.9	53.8
21.5/6	12.0 \pm 0.0	52.0 \pm 0.8	83.3	47.3	12.5 \pm 0.7	50.5 \pm 2.6	88.6	54.8
22/12.5	10.5 \pm 0.7	35.5 \pm 1.3	83.7	52.3	10.7 \pm 1.2	34.5 \pm 3.1	83.9	46.2
18 const.	10.0 \pm 0.0	35.9 \pm 2.0	82.3	45.9	10.0 \pm 0.0	37.0 \pm 0.9	82.5	47.1

Table 25. Summary of the main effects found by ANOVA on the pre-oviposition period and fecundity of *Orius laevigatus* (strains N and S) during the exposure at five temperature regimes and 11.5L:12.5D (Experiment 3).

Effect	Pre-oviposition			Fecundity	
	df	F	p-level	F	p-level
Strain (1)	1	7.42	0.05 *	72.16	0.001 *
Regimes (2)	4	19.67	0.001 *	22.89	0.001 *
Interaction (1 x 2)	4	1.71	0.15	6.97	0.001 *

Table 26. Pooled means (\pm SD) of pre-oviposition periods of all the temperature regimes to which the two strains of *Orius laevigatus* were exposed. Different letters indicate significant difference by ANOVA ($p<0.05$) (Experiment 3).

	Strain N	Strain S
Pre-oviposition period (days)	13.3 ± 5.8 b	11.4 ± 5.1 a

Table 27. Pooled means (\pm SD) of pre-oviposition periods of all data of the strains N and S of *Orius laevigatus*. Different letters indicate significant differences by ANOVA and Tukey's test ($p<0.05$) (Experiment 3).

Temperature regime (°C)	24/12.5	26/15	21.5/6	22/12.5	18 constant
Pre-oviposition development (days)	8.6 ± 4.4 a	9.1 ± 4.9 a	15.1 ± 5.4 b	13.1 ± 6.2 b	15.7 ± 6.4 b

Strain S showed a higher percentage of egg-laying females than strain N, particularly at 24°C/12.5°C, 26°C/15°C and 22°C/12.5°C (χ^2 test, $p<0.05$) (Table 28). When environmental conditions were changed to 26°C and 16L:8D (exposure 2), sudden increases in the percentage of egg-laying females as well as in the number of eggs laid per female were recorded (Fig. 9 and Tables 31, 32). No differences were recorded for the percentage of fertile females at the end of the experiment, between the strains and temperature regimes (χ^2 test, $p>0.05$).

During the initial 29 days of adult life (exposure 1) strain and temperature as well as their interaction seem to have a strong influence on the fecundity of *O. laevigatus* (Table 25). The S strain showed a higher fecundity compared to the N strain. For both strains the temperature regime least suitable for oviposition appears to be 21.5°C/6°C and 18°C constant. No differences for the fecundity were observed at 24°C/12.5°C and 22°C/12.5°C for strain N. The highest fecundity for both strains was recorded at 6°C/15°C (Table 31).

Table 28. Pre-oviposition period and percentage of fertile females at 29 days after adult emergence (χ^2 test, $p<0.05$) of *Orius laevigatus* (strains N and S) reared at five temperature regimes and 11.5L:12.5D.

Temperature regime (°C)	Strain N			Strain S		
	No. of fertile females	Pre-oviposition period (days)	% Fertile females	No. of fertile females	Pre-oviposition period (days)	% Fertile females
24/12.5	21	8.6 ± 4.7	30.6	49	8.5 ± 4.0	96.1
26/15	31	11.4 ± 6.4	64.6	41	6.8 ± 3.4	85.4
21.5/6	17	15.4 ± 5.2	39.5	17	14.8 ± 5.5	43.6
22/12.5	17	14.5 ± 6.6	35.4	38	11.7 ± 5.8	80.8
18 constant	18	16.4 ± 6.0	39.1	28	15.0 ± 6.8	58.3

Table 29. Summary of the main effects found by ANCOVA on the fecundity of *Orius laevigatus* (strain N and S) considering the fecundity during exposure 1 as covariate. All populations were included (Experiment 3).

Effect	df	F	p-level	Test of parallelism	
				F	p-level
Strain (1)	1	6.40	0.01 *	4.24	0.04 *
Regimes (2)	4	6.92	0.001 *	1.16	0.33
Interaction (1 x 2)	4	1.09	0.36	1.25	0.27

Table 30. Summary of the main effects found by ANCOVA and test of parallelism on the fecundity of *Orius laevigatus* (strains N and S) considering fecundity during exposure 1 as covariate; only fertile females were included (Experiment 3).

Effect	df	F	p-level	Test of parallelism	
				F	p-level
Strain (1)	1	3.24	0.07	5.74	0.02 *
Regimes (2)	4	8.08	0.001 *	1.60	0.17
Interaction (1 x 2)	4	1.49	0.21	2.05	0.03 *

Table 31. Number of eggs laid per female at the end of exposure 1, and at the end of the experiment of the two strains of *Orius laevigatus*. All populations were considered. Different letters in column with the same description indicate significant difference by ANOVA and Tukey's test ($p<0.05$) (Means \pm SD) (Experiment 3).

Temperature regime (°C)	No. of pairs	Strain N		Strain S		
		No. of eggs/female Exposure 1	No. of eggs/female exposure 1+2	No. of pairs	No. of eggs/female Exposure 1	No. of eggs/female exposure 1+2
24/12.5	50	7.2 \pm 15.0 a	58.8 \pm 58.2 b	51	30.4 \pm 20.9 b	76.7 \pm 64.4 b
26/15	42	17.7 \pm 25.6 b	54.5 \pm 57.4 b	39	45.7 \pm 30.9 c	92.5 \pm 74.6 b
21.5/6	38	5.4 \pm 9.1 a	43.4 \pm 48.4 a	39	7.8 \pm 14.1 a	47.5 \pm 57.5 a
22/12.5	48	7.9 \pm 14.7 a	65.4 \pm 51.5 b	46	24.5 \pm 23.1 b	85.7 \pm 68.4 b
18 constant	45	5.3 \pm 10.1 a	60.6 \pm 55.0 b	47	11.6 \pm 14.5 a	68.3 \pm 57.7 b

Table 32. Number of eggs laid per female at the end of exposure 1, and at the end of the experiment of the two strains of *Orius laevigatus*. Only the fertile females were considered. The different letters given in the columns indicate significant differences by ANCOVA and Tukey's test ($p<0.05$) (Means \pm SD). Percentages of egg-laying females at the end of the experiment (χ^2 test, $p>0.05$) (Experiment 3).

Temperature regime (°C)	Strain N					Strain S				
	No. of pairs	No. of eggs/female exposure 1	No. of eggs/female Exposure 1+2	Adjusted means	% Fertile females	No. of pairs	No. of eggs/female exposure 1	No. of eggs/female exposure 1+2	Adjusted means	% Fertile females
24/12.5	37	8.8 \pm 16.2 a	71.7 \pm 56.6 ab	88.5	74.0	49	31.6 \pm 20.4 b	79.8 \pm 63.8 b	59.2	96.1
26/15	37	19.2 \pm 25.7 b	59.0 \pm 56.8 a	58.7	87.5	35	51.2 \pm 27.3 c	100.0 \pm 66.6 b	47.2	89.6
21.5/6	26	8.9 \pm 10.2 a	63.7 \pm 48.3 ab	80.3	67.5	25	12.2 \pm 16.2 a	74.1 \pm 56.4 b	85.4	64.1
22/12.5	39	9.7 \pm 15.8 a	80.5 \pm 45.1 b	95.8	81.2	42	27.0 \pm 22.6 b	95.0 \pm 65.5 b	81.8	91.1
18 constant	36	6.5 \pm 10.8 a	73.7 \pm 52.1 ab	94.3	80.4	35	15.2 \pm 14.9 a	89.2 \pm 49.6 b	95.5	75.0

Table 33. Pooled means (\pm SD) of total fecundity (exposure 1 + 2) considering all the temperature regimes to which the two strains of *Orius laevigatus* were exposed. The full populations were considered. Different letters indicate significant differences by ANCOVA ($p<0.01$) (Experiment 3).

	Strain N	Strain S
Total fecundity (exposure 1+2)	45.7 \pm 54.1 a	74.1 \pm 64.5 b

Table 34. Pooled means (\pm SD) of total fecundity (exposure 1 + 2) of all data of strains N and S of *Orius laevigatus*. Different letters indicate significant differences by ANCOVA ($p<0.05$) (Experiment 3).

Temperature regime (°C)	24/12.5	26/15	21.5/6	22/12.5	18 constant
Total fecundity (exposure 1+2)	67.7 \pm 61.3 b	73.5 \pm 66.0 b	45.4 \pm 52.9 a	75.5 \pm 59.9 b	64.4 \pm 56.3 b

Since the environmental conditions were changed in exposure 2 (26°C, 16L:8D), a covariance analysis on fecundity was carried out and the fecundity during exposure 1 was taken as covariate. A covariance analysis was done considering either all females or only fertile females (Tables 29 and 30). Differences were found in both cases among the temperature regimes tested. Only when all females were compared a difference was observed between strains ($p=0.01$), although the p -level was almost significant even when only fertile females were considered ($p=0.07$). No differences on the interaction of regimes and strains were found. Figure 10 shows the main effects of the ANCOVA undertaken on the entire population of females.

The lowest fecundity was found for *O. laevigatus* strains N previously reared at 26°C/15°C and then transferred to 26°C (exposure 2). It was, however, not significantly different from that of the females of the same strain reared before at 18°C constant, at 24°C/12.5°C and at 21.5°C/6°C (Table 32). The adjusted means showed that the smallest effects of a change in exposition were recorded respectively at the temperature regimes 26°C/15°C for strain N and 26°C/15°C and 24°C/12.5°C for strain S. This is the effect of a higher fecundity during the first exposition, which is confirmed by the test of parallelism that correlates the trend of the total fecundity with the covariate (fecundity at exposure 1)(Table 29). The total fecundity of strain S at the end of the experiment (exposure 1+2) is significantly higher than that of strain N (Table 33). The thermoperiod of 21.5°C/6°C induced the females to lay the lowest amount of eggs (Table 34).

At the end of the experiment, no differences among the percentages of fertile females and the infertile females (both groups only with mature oocytes) were recorded (χ^2 test, $p>0.05$), while a significant difference was recorded among the percentages of infertile females without mature oocytes of strain S (Table 35). The percentages of diapausing females at the end of experiment 3 were very low (Fig. 11).

The percentages of egg-laying and of surviving females are shown in figure 9. At the end of the experiment, the percentages of surviving females are similar for both strains at all temperature regimes. No differences in the percentages of surviving females were recorded either at the end of exposure 1 or at the end of exposure 2 between strains as well as among temperature regimes (χ^2 test, $p>0.05$).

The correlation between fecundity and mature oocytes per females was significant ($p<0.001$), but weak ($R = 0.44$). All females were considered together, independently from strain and the exposure ($y = 43.6 + 6.7x$).

Table 35. Percentages of fertile and infertile females with mature oocytes 24 hours after the end of the experiment 3 (and χ^2 test) (Experiment 3).

Temperature regime (°C)	Strain N				Strain S			
	No. of females	% Fertile female with oocytes	% Infertile female with oocytes	% Infertile female without oocytes	No. of females	% Fertile female with oocytes	% Infertile female with oocytes	% Infertile female without oocytes
24/12.5	48	56.3	4.2	18.8	51	52.9	0	3.9
26/15	48	56.3	4.2	8.3	48	60.4	0	10.4
21.5/6	42	47.6	2.4	28.6	38	34.2	2.6	31.6
22/12.5	48	70.8	0	18.8	47	48.9	0	8.5
18 constant	45	60.0	0	17.8	47	61.7	4.3	19.1
χ^2		p>0.05	p>0.05	p>0.05		p>0.05	p>0.05	p<0.005 *

Chapter 4

Figure 9. Cumulative percentages of egg-laying (on the left) and surviving (on the right) females of two strains of *Orius laevigatus* reared at five temperature regimes and matched photoperiod (11.5L:12.5D; exposure 1, χ^2 test, $p<0.05$) and transferred to 26°C (16L:8D) after 29 days (exposure 2, χ^2 test, $p>0.05$) (Experiment 3).

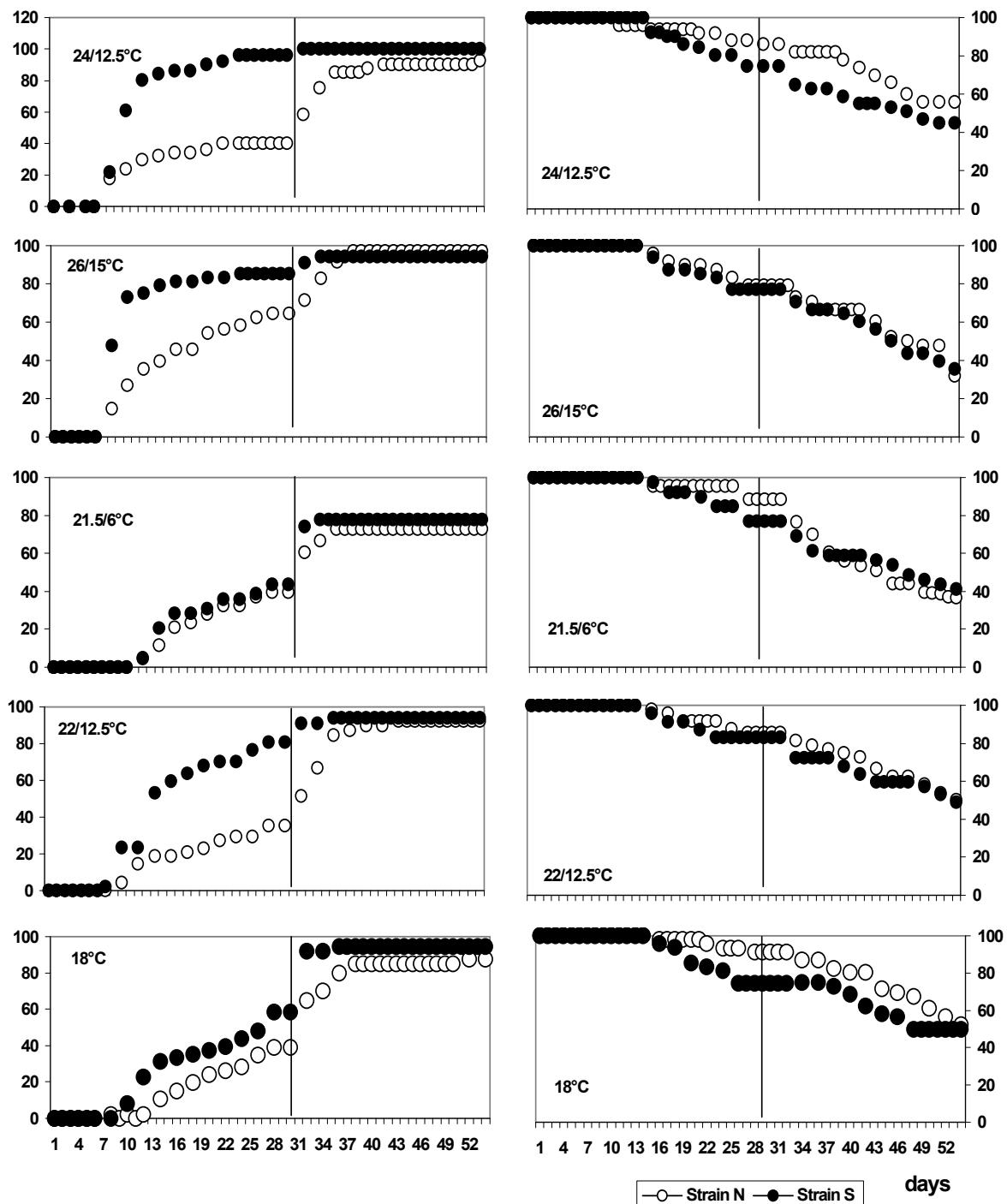
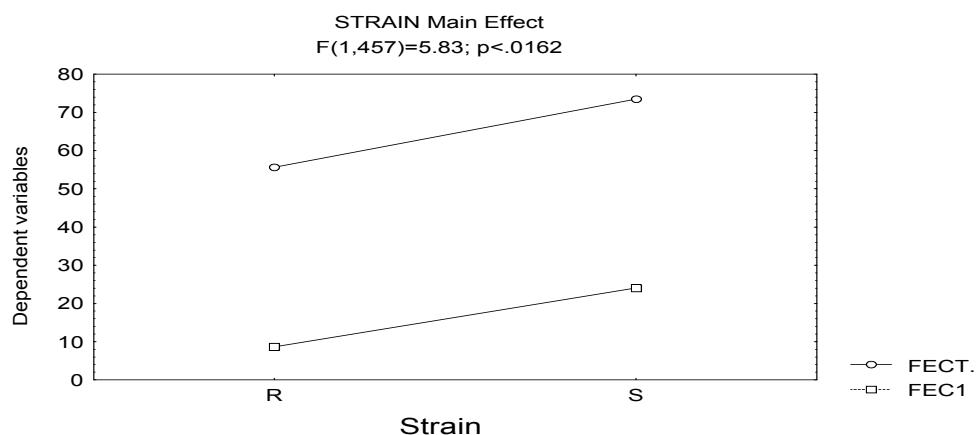
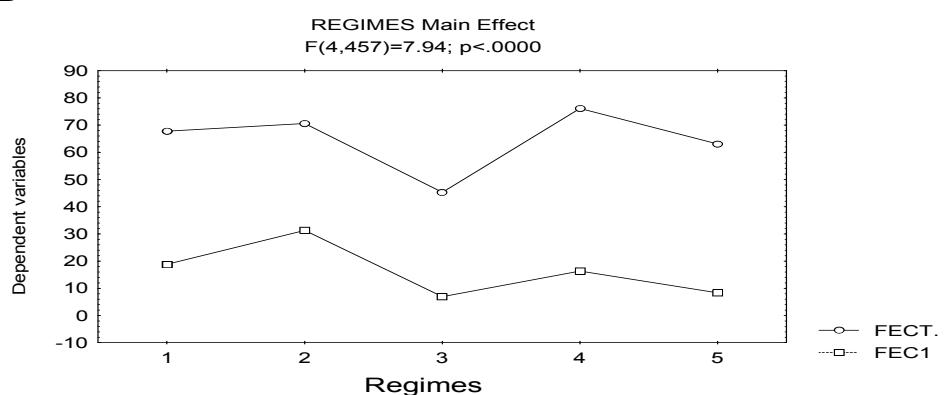


Figure 10. Main effects of strain (A), thermoperiod (B) and their interaction (C), found in experiment 3 in the covariance analysis (ANCOVA). (R = northern strain, S = southern strain)(FECT total fecundity, FEC1 fecundity during exposure 1 at different thermoperiods used as covariate) (Regimes: 1 = 24/12.5°C; 2 = 26/15°C; 3 = 21.5/6°C; 4 = 22/12.5°C; 5 = 18°C constant).

A



B



C

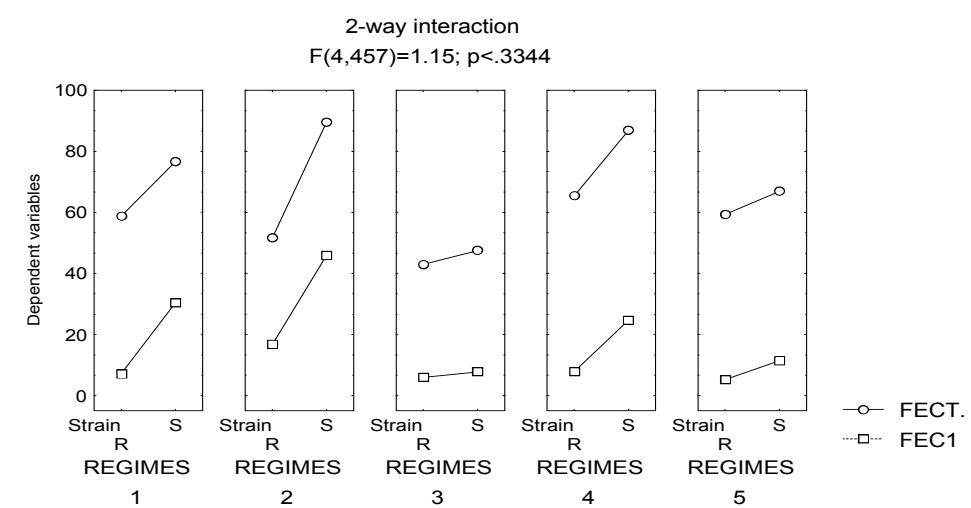
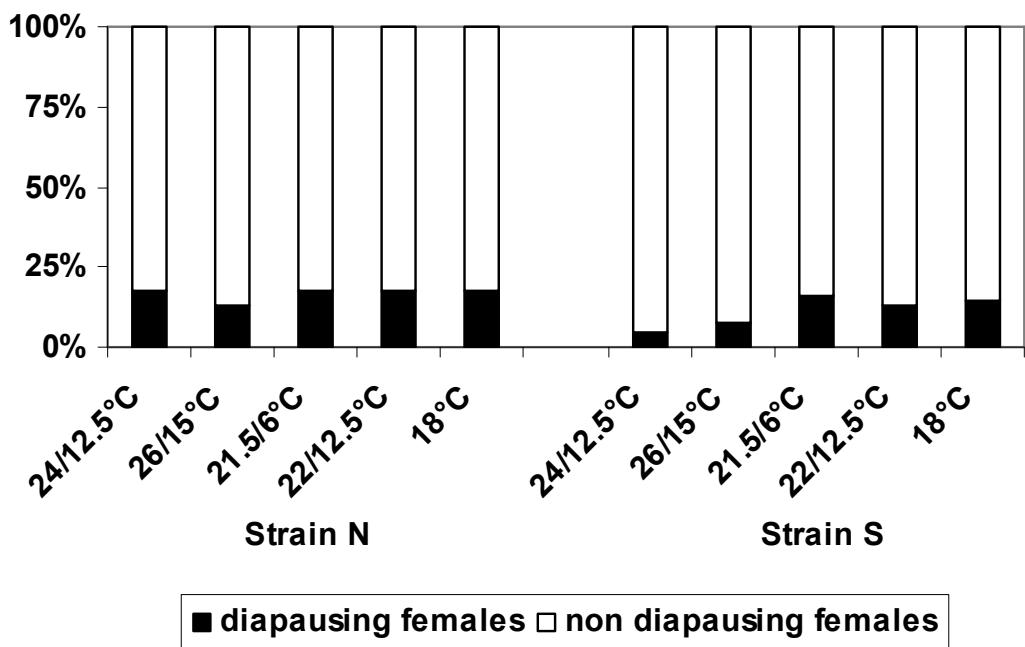


Figure 11. Percentages of egg-laying (= non-diapausing) females and non-egg-laying (= diapausing) females with oocytes at the end of the experiment (Experiment 3), at different Temperature regimes.



4.3.3. Incidence of diapause in field collected populations

Experiment 4

Adult females collected in nature and kept in a meteorological cabin continued to lay eggs up to mid-November. After that the mean daily temperature decreased to ca. 7.5°C (range 0°C-12.8°C) and many females stopped laying eggs. Some egg-laying occurred again in February when the temperature was around 10°C (range 0°C-17.6°C).

At all times, high percentages of egg-laying females were obtained within a few days after moving them from low temperature regime to optimal environmental conditions. Only in November, strain N did not exceed 48% egg-laying females within 21 days (Table 36). When females were transferred from the field to the laboratory during experiment 4, differences in the percentage of egg-laying females of both strains of *O. laevigatus* were recorded (χ^2 test; $p<0.001$ and $p<0.01$) (Table 36). The lowest percentages egg-laying females were observed during the period October-December for strain N and November-December for strain S.

Table 36. Cumulative percentage of egg-laying females of two strains of *Orius laevigatus* (N = strain N and S = strain S) collected in nature in Italy and checked monthly at different intervals in the laboratory (26°C; 75% RH; 16L:8D) (Experiment 4).

Cumulative percentage of egg-laying females after a certain number of days from isolation at 26°C and 16L:8D						
Strain	Test period	No. of females	day 3	day 7	day 10	day 12 (total %)
N	August	9	77.8	77.8	77.8	77.8
N	September	11	100	100	100	100
N	October	20	45.0	60.0	65.0	70.0
N	November	38	2.6	39.5	42.1	47.4
N	December	18	16.7	55.6	61.1	61.1
N	January	13	38.5	84.6	92.3	100
χ^2 test			p<0.001	p<0.001	p<0.001	P<0.001
						p<0.005
S	August	20	100	100	100	100
S	October	39	87.2	89.7	89.7	89.7
S	November	33	42.4	72.7	78.8	78.8
S	December	46	41.3	82.6	84.8	84.8
S	January	55	58.2	89.1	90.9	90.9
S	February	62	80.6	100	100	100
χ^2 test			p<0.001	p<0.001	P<0.01	P<0.01
						p<0.01

4.4. Discussion

Tauber *et al.* (1986) report that the successful entry into dormancy is determined by the insect's ability to reach the stage sensitive to diapause - inducing - stimuli at the appropriate time of the year. If it reaches that stage too soon, diapause will not be induced and an entire life cycle must take place before diapause can be induced. By contrast, if development is too slow, the insect may not reach the diapausing stage soon enough to avoid the effects of unfavourable conditions.

Because all the *Orius* species known to undergo diapause show a reproductive diapause, the criteria used to diagnose diapausing or non-diapausing females in the present experiments were the same as those used by other authors (Ali and Ewiess, 1977; Ruberson *et al.*, 1991; van den Meiracker, 1994). This means that if females did not start to lay eggs within 29 days after emergence, or if females did not have mature oocytes at the end of the experiment, they were considered in diapause.

4.4.1. Influence of photoperiod

Development time

For insects which are sensitive to the photoperiod, the 'critical photoperiod' is defined as the length of the day at which 50% of the sensitive stages of the insect will enter diapause (Tauber *et al.*, 1986; Danks, 1987). The critical photoperiod varies from species to species as well as within the same species for strains occurring at different geographical areas. Some insects perceive the photoperiod just as long or short-day (all or none) (Tauber and Tauber, 1976; Tauber *et al.*, 1986). Therefore, the variations in day-length below or above the critical photoperiod are not appreciated by some arthropods, as recorded for example for *Panonychus ulmi* (Koch) (Lees, 1953) and for *Wyeomyia smithii* (Coq.) (Smith and Brust, 1971; Tauber and Tauber, 1975). The contrary was observed for other arthropods such as *Chrysopa harrisii* Fitch (Tauber and Tauber, 1974) and *Adalia bipunctata* (L.) (Obrycki *et al.*, 1983). Their reaction to a critical photoperiod decreases as diapause progresses. These examples show the limits of the concept of critical photoperiod, because for some insects not only the critical photoperiod but also the gradual change in day-length can influence diapause induction and termination as observed for *Chrysoperla carnea* (Steph.) (Tauber and Tauber, 1972; 1973; Tauber *et al.*, 1986).

The influence of photoperiod on the development time and adult lifespan of insects was studied by many authors (e.g. Danilevskii, 1961; 1970; De Wilde, 1962; Tauber and Tauber, 1976; 1978; Beck, 1980; Saunders, 1982; Principi, 1992). Insects can use photoperiods to regulate their pre-diapause developmental rates, and to keep growth and development synchronous with the progression of the seasons (Tauber *et al.*, 1986). In many examples, a slow down in development occurs during the actively feeding pre-diapause stages. At the same time, accelerated feeding rates were observed resulting in storage of energy. In some species, short-day-lengths accelerate development and long-day-lengths decelerate it, but in other species it is short-day-length which causes a deceleration (Tauber *et al.*, 1986).

In the studies described in this paper, the preimaginal development time of *O. laevigatus* was shortened by short day-lengths compared to that occurring at long day-lengths. A similar relationship for preimaginal development has been observed for *O. insidiosus* (Ruberson *et al.*, 1991), but it is not always the same among Heteroptera and for *Orius* species (van den Mairacker, 1994).

O. laevigatus, as well as other *Orius* species (Ruberson *et al.*, 1991) and many other insects which enter reproductive diapause during winter, show a long-day photoperiodic response curve.

Under each experimental condition, a low percentage of *O. laevigatus* was able to complete pre-imaginal development, and the differences recorded indicate that photoperiod can influence both strains of *O. laevigatus*. In experiment 1, the longest developmental times were recorded mainly around the photoperiod 12L:12D for both strains, while the short-day photoperiod of 8L:16D induced a faster development in both strains. At a long-day photoperiod of 16L:8D, the two strains showed an opposite response: deceleration of development for strain S and acceleration for strain N. When short day-lengths were

compared in experiment 2, the intermediate photoperiods 11.5L:12.5D and 12L:12D also induced the longest development time in both strains. An acceleration of the development time induced by intermediate day-length compared to long day-length (16L:8D) was recorded for some *Orius* species which undergo hibernation (McGregor and McDonough, 1917) such as *O. insidiosus* at 10L:14D (Ruberson *et al.*, 1991) and *O. tristiscolor* at 12L:12D (Askari and Stern, 1972). This accelerating effect of the development time at short day-length was demonstrated for other Hemiptera, e.g. *Pyrrhocoris apterus* (L.) (Saunders, 1983), *Palomena angulosa* Motschulsky (Hori, 1986; 1987; 1988), *Eysarcoris lewisi* Distant (Hori and Inamura, 1991) and *Podisus maculiventris* Say (Chloridis *et al.*, 1997). However, van den Meiracker (1994) did not find a strict relationship between photoperiod and development time in the species *O. insidiosus* and *O. majusculus*. Also, there are examples of diapausing insects which show a deceleration of the development time at short day-length as *Nezara viridula* L. (Ali and Ewiess, 1977) and *Harmonia axyridis* Pall. (Ongagna and Iperti, 1994). For *O. laevigatus*, as well as for *O. insidiosus* (Ruberson *et al.*, 1991), photoperiod induced changes in development time may not necessarily be symptomatic of diapause, but rather may be used to prepare the insect for diapause. *O. laevigatus* shows an opposite behaviour which is very different from other *Orius* species that undergo diapause. At the hypothetical critical photoperiod, this species showed an increase of the development time. Experiments 1 and 2 were carried out at 18°C and this temperature was low enough to increase the development time and to induce a higher pre-imaginal mortality of *O. laevigatus* (chapter 2 and Vacante and Tropea Garzia, 1993).

Pre-oviposition and reproduction.

The pre-oviposition period is a good indicator for how an adult population reacts to external stimuli and it is often significantly influenced by photoperiod. In fertile females a great variability was recorded, mainly in experiment 1. The longest pre-oviposition periods were recorded at the intermediate photoperiod 11.5L:12.5D for both strains. The variability of the data within the same strain observed during the experiments is similar to the common intra-specific variability which occurs in other insects (Tauber *et al.*, 1986; Danks, 1987).

Photoperiod showed no influence on the oviposition activity of strain S compared to strain N in experiment 1. However, all groups of strains S and N showed a lower percentage of egg-laying females in comparison to strain N reared at 16L:8D. Photoperiod strongly affected oviposition of strain N. A photoperiod 12L:12D induced a reduction in both the number of eggs laid per female and the percentage of egg-laying females, compared with 16L:8D. Experiment 1 showed that a critical photoperiod for diapause induction could be around 12L:12D hours. This induced a long development time in both *O. laevigatus* strains and a low oviposition rate in strain N. In test 1 of experiment 1, only 31.7% of females of the strain N laid eggs and in test 2 of the same experiment only one female of the same strain laid eggs after 23 days of adult life. The low percentages of egg-laying females in strain S (all day-lengths) and in strain N (short and intermediate day-lengths) could indicate a high incidence of reproductive diapause, according to the criteria of van den Meiracker (1994). The lack of a photoperiodical response in the oviposition activity of strain S suggests, however, that in Sicily or at lower latitudes, *O. laevigatus* may overwinter in quiescence, or that only a low percentage of the population undergoes diapause.

Furthermore, a low temperature such as 18°C reduces the oviposition capability of *O. laevigatus* like in other *Orius* species (Alauzet *et al.*, 1994; Tommasini and Benuzzi, 1996) even at a long photoperiod. This decreased oviposition does not mean that diapause induction

has occurred. Short day-lengths between 8L:16D and 12L:12D strongly influenced strain N to initiate diapause, but not in strain S.

Therefore, to study the existence of diapause in strain S, further studies were needed. These studies concerned the influence of photoperiods around 12L:12D. The effect of the increase of temperature after a period at $18\pm1^{\circ}\text{C}$ (pre-imaginal development and part of adult life) were tested also for *O. majusculus* and *O. insidiosus* (van den Meiracker, 1994). In experiment 2, the critical photoperiod for strains S appeared to be between 11.5L:12.5D and 12L:12D, with a longer development time, lower fecundity and mainly lower percentage of egg-laying females during the initial 29 days of adult life. But when the environmental condition were switched to 26°C and 16L:8D, most females ($>90\%$) suddenly started to lay eggs. During adult life, the two strains of *O. laevigatus* reacted differently to the different photoperiods. In particular the fecundity of strain N seemed to be less influenced by a narrow range of photoperiods compared to that of strain S. In fact, some species of insects living in southern areas (mainly near the tropics) frequently react much more to small changes of photoperiod than the same species living in northern areas, which are exposed to a much larger variation in photoperiod during the year (Beck, 1980). Among insects reared at an intermediate photoperiod, the incidence of diapause was higher when temperature was relatively low than if it was relatively high (Danilevski, 1961; Beck, 1980).

The beginning of oviposition of hibernating females under diapause-promoting photoperiods has been considered to indicate the completion of diapause (Tauber and Tauber, 1976). The length of the pre-oviposition period could be a parameter to study the intensity of reproductive diapause in long-day conditions, as considered by Hodek and Honek (1970) for another heteropteran, *Aelia acuminata* (L.).

It is known that latitude and altitude can have an effect on the photoperiodic response of insects. Saunders (1982) and Danks (1987) report that the critical photoperiod changes to longer values with increasing latitude. The intensity of diapause was found to be greater in northern than in southern populations of several insects species (Beck, 1980).

In experiment 2 differences in fecundity were recorded between the two strains of *O. laevigatus*, but they were not caused by a difference in photoperiods. Only strain N showed differences in the percentage of fertile and infertile females with mature oocytes at the end of the experiment. It appears that for *O. laevigatus* also the geographical origin plays a specific role in the diapause induction or at least on some biological parameters. Several authors made a list of species which showed differences in critical photoperiod between populations from different latitudes (Masaki, 1961; Beck, 1980; Danks, 1987). A low incidence of diapause in more southern populations was observed in several insect species exposed to a short photoperiod (Danks, 1987). Geographical differences in the photoperiodic response at different localities at the same latitude have been investigated for a number of species. Populations of *Laodelphax stiatellus* Fallén occurring in more northern areas have evolved a geographical strain entering diapause in earlier instars compared to that of more southern regions (Kisimoto, 1989). *Mamestra brassicae* (L.) as well as *C. carnea* showed a shorter critical photoperiod at more northern than more southern latitudes (Danilevskii, 1961; Tauber and Tauber, 1972).

4.4.2. Influence of temperature

Development time and reproductive period.

The interaction between temperature and photoperiod may be important for diapause induction and intensification (Honek, 1969; Beck, 1980; Volkovich *et al.*, 1992). Kingsley and Harrington (1982) as well as van den Meiracker (1994) demonstrated this interaction also

for diapause termination of *O. insidiosus*. Temperature can influence the critical photoperiod, and a high temperature generally prevents diapause induction (Beck, 1980; Danks, 1987; Volkovich *et al.*, 1992). Under natural conditions, insects are exposed to thermoperiods in combination with photoperiods, where night-time temperatures are generally lower than daytime temperatures. For this reason, thermoperiods were used during experiment 3 instead of constant temperature used in the past by many authors to study this phenomenon. A mean temperature of 20°C (thermoperiod 26°C/15°C) combined with a short-day-length, seems enough to prevent diapause in at least 64.6% of females of strain N and in more than 85% of strain S of *O. laevigatus*. This was also found for other insects like *Corythucha cydoniae* (Fitch.) where diapause did not occur in at least 25% of the population at high temperatures and short daylength. Neal *et al.* (1992) are of the opinion that a mean temperature of about 20°C combined with a short-day-length can reduce diapause intensity. Thermal modification of photoperiod is rather common in insects.

The influence which the temperature can have on the biology of *O. laevigatus*, (mainly on strain S), is demonstrated by the high pre-imaginal mortality and low percentage of fertile females recorded at the mean temperature regime of 16.5°C. As already discussed, *Orius* spp. are rather sensitive to low temperatures independently from photoperiod. Chyzik *et al.* (1995) studied an Israeli strain of *O. albidipennis* and found that a mean temperature below 15°C leads to an interruption of oviposition irrespective to day-length until the temperature increases. High temperatures can avert diapause in long-day insects. De Wilde (1962) and Masaki (1984) reported a great variation in reaction types of diapause which can occur among different geographic populations of the same species at the same temperature stimuli. Commonly, higher environmental temperatures are required to avert diapause induction among the northern forms than among the southern forms of the same species (Beck, 1980). In fact, strain S of *O. laevigatus* showed to be less sensitive to the different temperature regimes tested with, on average, a shorter pre-oviposition period (9.4 days) than strain N (13.3 days), as well as a higher percentage of egg-laying females. In a variety of species adaptation to low latitude is related more closely to environmental temperature patterns than to day-length effects associated with differences in latitude (Beck, 1980). Low temperature did induce diapause in several species of flies close to the equator, when day-length changed by only a few minutes throughout the year and, therefore, photoperiod was not found to play a role in diapause induction (Saunders, 1982).

In *O. laevigatus* a difference in diapause reaction was recorded for both strains when tested at the temperature of 18°C constant or at thermoperiod 24°C/12.5°C with a mean temperature of 18°C. The constant temperature regime induced a pre-oviposition period almost two times longer than that at the varying temperature regime. A similar result was found by Rudolf *et al.* (1993), who observed reduced longevity and fecundity of both *O. laevigatus* and *O. majusculus* at low constant temperatures, compared to a thermoperiod with the same average. These results are not in agreement with the theory put forward by Beck (1977), in which the growth-rates produced at the thermoperiods are rather similar to those produced at comparable average temperatures.

The results of the dissection of females at the end of the third experiment made clear that the conclusion stating that females which did not lay eggs were in diapause, was incorrect. These results allow us to conclude (1) that *O. laevigatus* is influenced by short day-length and low temperature regimes to initiate diapause, (2) that only part of the population reacts to these token stimuli by entering diapause, and (3) that the northern strains are more sensitive to these stimuli than the southern strains.

4.4.3. Incidence of diapause in field collected populations.

Both strains of *O. laevigatus* used in experiment 4 were collected in the field and immediately tested in laboratory. This was done to prevent the possibility of selecting a strain where the sensitivity to a short-day-length is lost under laboratory conditions, like Hodek and Honek (1970) found for *A. acuminata*. When collecting *O. laevigatus*, only a low number of males were found (sex ratio of 1 male to 10 females), but males of *O. laevigatus* commonly live shorter than females. When collecting *O. tristicolor* and *O. insidiosus*, males were also rarely found in the field during winter (Anderson, 1962; Iglinsky and Rainwater, 1950; Kingsley and Harrington, 1982). Frequent mating was observed during our experiments at different environmental conditions. Because mating usually does not occur during diapause (Tauber *et al.*, 1986) an observation of mating could suggest the absence of diapause for at least part of the population of *O. laevigatus*. Although mating was observed also by Ruberson *et al.* (1991) for *O. insidiosus* in the laboratory under short day-length, recent studies failed to recover males of *O. insidiosus* during the late winter and early spring (Elkassabany *et al.*, 1996) and overwintering females appear to be inseminated before winter (Elkassabany, 1994).

Iglinsky and Rainwater (1950) showed that females of *O. insidiosus* collected during winter in the USA laid only ten eggs during the 45 days they were alive. More recently, Elkassabany *et al.* (1996) demonstrated that all the females of *O. insidiosus* collected in Arkansas (USA) at the beginning of November were in diapause. This confirms Ruberson *et al.*'s (1991) data, since *O. insidiosus* showed a critical photoperiod which corresponded with that of mid-October in the same area. A recent laboratory study carried out in Brasil from Argolo *et al.* (2002) showed that *O. insidiosus* did not enter in reproductive diapause at any of 6 photoperiods with ranged from 9L:15D to 14L:10D, at the constant temperature of $25\pm1^{\circ}\text{C}$ and RH $70\pm10\%$. This results can be due to the behaviour of a strain of *O. insidiosus* collected in Brasil respect those studied by other authors whom collected the predators in North America.

O. laevigatus has a different behaviour compared to that of *O. insidiosus* or other *Orius* species. In particular, the females of strain S of *O. laevigatus* collected in winter reacted quite suddenly to an increased temperature by starting to lay eggs. A quicker reaction of strain S to begin laying eggs was found during almost the entire winter compared to strain N. The geographical origin of the two strains strongly influenced the start of the oviposition. Throughout autumn and winter, at least 79% of females of strain S started to lay eggs ten days after moving the females from the field (low temperature) to the laboratory (26°C), while in strain N only about 48% of the females moved to 26°C laid eggs in November. This suggests that in nature, diapause is induced in strain N of *O. laevigatus* when day-length and temperature decrease in autumn. The differences in reaction to critical photoperiod between these strains are large enough to propose the existence of two ecotypes of *O. laevigatus*. Further, it seems reasonable to conclude that in both strains of *O. laevigatus*, only part of the population undergoes diapause and an intensive, obligatory diapause seems to lack.

It is not easy to define the overwintering behaviour of *O. laevigatus* with one of the descriptions of diapause given by different authors. However, according to Müller's classification (1970), which is used by many authors in Europe, it is possible to say that the northern strain of *O. laevigatus* shows an oligopause while the southern strain shows only a quiescence form of overwintering. Other authors prefer to describe this oligopause as ' facultative diapause' (Beck, 1980), whereas Tauber *et al.* (1986) point out that for ' non-diapause' overwintering forms the definition ' multivoltine diapause' is more reliable than ' facultative diapause'.

4.4.4. Epilogue

The presence or absence of diapause is an important criterion to select a good natural enemy, mainly when the pest can overwinter without undergoing diapause. This is true for both predatory insects and mites. For example, when diapausing strains of *Amblyseius* (= *Neoseiulus*) *cucumeris* (Oudemans) were released in winter or early in spring, they were not successful in controlling WFT (van Houten and van Stratum, 1993).

Diapause appears to be a widespread phenomenon among Heteropteran predators in temperate areas. It has an important function in enhancing survival during adverse seasons and in synchronizing the predators with prey in spring. However, when such predators are used against prey lacking diapause (*i.e.* *F. occidentalis*), the importance of understanding if a species or a strain can synchronize its behaviour with that of the target prey is very important and useful for biological control.

No specific studies were previously carried out on the influence of photoperiod and temperature on the diapause induction of strains of *O. laevigatus*. Only some information was available on a southern Italian strain (Vacante *et al.*, 1995) where photoperiod did not seem to influence fecundity.

One of the main findings of these studies is that a northern (N) and a southern strains (S) of *O. laevigatus* are different. The difference in behaviour observed allows us to distinguish two ecotypes of this species. Northern strains showed a weak diapause, while the southern population demonstrated a very low incidence of diapause and most of the individuals seem to have only a quiescence form of overwintering. However, also the southern strain of *O. laevigatus* appeared to be strongly influenced by low temperature.

Adults of *O. laevigatus* of both N and S strain, collected in nature in autumn-winter, then kept under field conditions, and eventually transferred after a certain period to controlled and optimal environmental conditions, showed that part of the females of strain N undergo reproductive diapause during November. However, their diapause could be considered rather short, because the percentage of egg-laying females increased a lot just a month later, in December.

The southern strain (strain S) collected on Sicily showed no evident response to the photoperiod, indicating that they can overwinter in quiescence or that their eventual diapause, if any, is weak. Therefore, it seems that strains collected at low latitudes can remain active also during short-day-length periods, if temperature is high enough, confirming the finding of Chambers *et al.* (1993). Moreover, the natural distribution of *O. laevigatus* in areas with marine influence (Péricart, 1972) and the good performances at high temperatures (Alauzet *et al.*, 1994) indirectly explain the effectiveness of this species also during the hot season in both the Mediterranean area and northern Europe.

The intrinsic variation among individuals that I found seems to be a characteristic of many diapause responses in other species (Danks, 1987). Commonly diapause incidence and intensity tend to increase with a higher latitude and altitude and the intrinsic features of the diapause response interact with environmental factors. Often the critical photoperiod is longer and the initiating temperature is lower for northern strains (Danks, 1987).

While an insect's diapause response is genetically based, environmental conditions determine the expression of diapause (Tauber *et al.*, 1986). Other stimuli, *e.g.* food abundance and quality or changing versus static photoperiods, can influence diapause in interaction with photoperiod and temperature (Tauber *et al.*, 1986). Low quality food can shift the critical photoperiod for predatory Heteroptera, but only slightly (Ruberson *et al.*, 1998). Because we did not compare several food resources, we do not know how food influences diapause in *O. laevigatus*. The importance of feeding for diapausing adult predators is unclear, although

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diapausing Heteropteran predators without prey did not survive better than starved non-diapausing predators. It could be that Heteropteran species must locate overwintering areas where some prey is available (Ruberson *et al.*, 1998).

To correctly describe the diapause of *O. laevigatus* is not an easy task. When I summarize the important elements of diapause given by several authors, it is possible to distinguish two main criteria to define the intermediate form of diapause that I found for *O. laevigatus*:

- presence or absence of a physiological adaptation
- degree of reaction to the environmental conditions that induce and terminate dormancy (diapause).

Interpretation of these criteria results in the conclusion that the N strain of *O. laevigatus* shows a dormancy similar to an 'oligopause' (according to Muller, 1965) or a diapause with a low intensity (according to Mansingh, 1971). For strain S we may speak of a 'quiescence' mainly influenced by temperature.

The applied importance of this diapause study in *O. laevigatus* is the following. For natural enemies used in biological control of thrips during winter and early spring, it is essential that they do not enter diapause. This resulted in a search for non-diapausing natural enemies of thrips for winter and spring when seasonal inoculative releases are necessary. The finding that southern (in this case Sicilian) strains of *O. laevigatus* do not show diapause but quiescence is an important result of this study. If this strain of *O. laevigatus* will meet the other criteria of an effective thrips predator (chapter 3), we will be able to improve biological control of thrips.

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Chapter 5. ENHANCEMENT OF THrips CONTROL IN PROTECTED SWEET PEPPER CROPS BY RELEASES OF THE PREDATOR OF *ORIUS LAEVIGATUS*.

⁴

Abstract

Key pests infesting sweet pepper in Italy, as in many other European countries, are species of thrips. During a two-year period, the efficacy of the pirate bug *Orius laevigatus* (Fieber) to control thrips on sweet pepper in protected crop was investigated in the Po Valley in Northern Italy. Two thrips species were found: *Frankliniella occidentalis* (Perg.), the most harmful one, and *Thrips tabaci* Lind. Seasonal inoculative releases of *O. laevigatus* effectively reduced the thrips infestation in sweet pepper. Interestingly, in some cases, natural control by immigrating wild *Orius* species (*O. laevigatus*, *O. niger* (Wolff) and *O. majusculus* (Reuter)), was enough to reduce the thrips population. When chemical control was applied against other pests, this resulted also in the killing of *Orius* predators and an increase of the thrips population. In these situations wild *Orius* populations entering the protected cultures later in the season were able to reduce thrips populations.

5.1. Introduction

After *Frankliniella occidentalis* (Perg.) appeared in Italy in 1987 it became one of the most serious pest species of sweet pepper (*Capsicum* spp.) both in greenhouses and in the open field, like elsewhere in Europe (Arzone *et al.*, 1989; Tavella *et al.*, 1991; Tommasini and Maini, 1995; van Driesche *et al.*, 1998). *F. occidentalis* causes the typical damage of thrips on sweet pepper: depigmentation of leaves and fruit, necrosis of attacked areas and leaf or fruit deformation. In some Italian areas like in Ligury and in the South, as well as in the south-east of Spain, Tomato Spotted Wilt Virus (TSWV) and more occasionally Impatiens Necrotic Spot Virus (INSV) which are both transmitted by *F. occidentalis* (German *et al.*, 1992; Peters *et al.*, 1996), were detected in several cultivated plant species, among which sweet pepper (Lisa *et al.*, 1990; Vaira *et al.*, 1993; Vovlas *et al.*, 1993; Sánchez *et al.*, 2000; Sanchez and Lacasa, 2002). This even increased the already serious problems due to thrips. In north-eastern Italy, where the experiments described in this paper were carried out no TSWV nor INSV were present in sweet pepper. However, the presence of INSV in ornamentals (Bellardi and Vicchi, 1998; Vicchi and Bellardi, 2000) and of TSWV in tomato (Vicchi *et al.*, 2001) and in sweet pepper crops (Vicchi, pers. com.) is known now in North-eastern Italy.

It is difficult to control *F. occidentalis* only with chemicals, because this pest is characterized by a high reproductive rate (see chapter 3), and a low sensitivity to a number of commercially available insecticides allowed on vegetable crops (Immaraju *et al.*, 1992; Brødsgaard, 1994; Robb *et al.*, 1995; Zhao *et al.*, 1995). Further, the eggs are protected from pesticides because they are laid in the plant tissue. Therefore, the development of a biological control system for thrips is of high priority. During the past decade, many studies

⁴ This chapter was earlier partially presented at the 7th International Symposium on Thysanoptera. International conference on tospovirus, Reggio Calabria (I) 2-7 July 2001. Proceeding (in press).

have been carried out in which natural enemies were tested for control of thrips (Gilkenson *et al.*, 1990; van den Meiracker and Ramakers, 1991; Chambers *et al.*, 1993; Vacante and Tropea Garzia, 1993; Bertaux, 1993; Gonzalez Zamora *et al.*, 1994; van Houten and van Stratum, 1995; Grasselly *et al.*, 1995; Loomans *et al.*, 1995; Rubin *et al.*, 1996; Tavella *et al.*, 1996; Degheele *et al.*, 1997; Mifsud, 1997; Sabelis and van Rijn, 1997; van Driesche *et al.*, 1998; Tommasini *et al.*, 2001).

Among natural enemies of *F. occidentalis*, *Orius* spp. have received a lot of attention for thrips control on sweet pepper. The following species have been studied: *O. tristis* (White) in Canada (Gilkenson *et al.*, 1990; Higgings, 1992), *O. insidiosus* (Say), *O. majusculus* (Reuter) and *O. niger* (Wolff) in Europe (van den Meiracker and Ramakers, 1991; van de Veire and Degheele, 1992; Disselveld *et al.*, 1995), *O. laevigatus* (Fieber) in Europe (Chambers *et al.*, 1993; Vacante and Tropea Garzia, 1993; Dissevelt *et al.*, 1995; Tavella *et al.*, 1996; van de Veire and Degheele, 1997; van der Blom *et al.*, 1997; van Schelt, 1999; Sánchez *et al.*, 2000) and *O. albidipennis* (Reuter) in Israel (Rubin *et al.*, 1996) and Spain (Sánchez *et al.*, 2000; Sánchez and Lacasa, 2002).

In this paper, data are presented to show that control of thrips in sweet pepper can be obtained by seasonal inoculative releases of *O. laevigatus*, or, in some cases, by natural control of immigrating wild *Orius* species.

5.2. Material and Methods

During the years 1994 and 1995, population development of thrips and *O. laevigatus* were followed in commercial unheated plastic tunnels in North-eastern Italy near Rimini, close to the Adriatic Sea coast, in a large greenhouse area. A total of 11 tunnels, ca. 300 m² each, were sampled.

In most cases, the sweet pepper cultivar Valdor was used, sometimes cultivar Bullor. The sweet peppers were planted in double rows with 50 cm plant spacing between and within rows. Hoses laying on the soil supplied water. Planting was at the end of April-early May and plants were removed at the end of August-beginning of September. Before transplanting, the soil was fumigated by methylbromide. Conventional chemical control was applied in two tunnels in 1994 and in two other tunnels in 1995 (the so-called chemical tunnels). The release of *O. laevigatus* was tested in 2 tunnels in 1994 and in 5 tunnels in 1995 (the so-called IPM tunnels). In the IPM tunnels, a blend of nymphs and adults of *O. laevigatus* (ca. 3:2 respectively) was released on the leaves, in a density of 1-3 predators per m² when thrips appeared on the plants. In some tunnels *O. laevigatus* was released once, in other tunnels twice (see Table 2 for details).

In the IPM tunnels other mass-reared natural enemies were applied to control infestations by other pest species. *Phytoseiulus persimilis* Athias-Henriot was introduced for control of *Tetranychus urticae* Koch, *Encarsia formosa* Gah. for control of whiteflies, and *Chrysoperla carnea* (Steph.), *Aphidius colemani* Viereck and *Aphidoletes aphidimyza* (Rond.) for control of aphids.

Weekly sampling was carried out during the sweet pepper cycle. Nymphs and adults of both thrips species, and *Orius* spp. were counted on 200 leaves (50% at the top and 50% at the bottom of the plants) and on 100 flowers randomly chosen from 100 plants per tunnel. Thrips and predators on the flowers were recorded by gently shaking each flower in a small transparent plastic cylinder of about 1 dl. The density of adult thrips was also sampled weekly by counting the catches on blue sticky traps (10x20 cm each) placed about 20 cm above the top of the plants. Initially 10 sticky traps were used per tunnel. As soon as more

than 10 thrips were caught per trap per week, the number of traps was reduced to two per tunnel. The index of aggregation of thrips on sweet pepper was defined by Taylor's power law (Taylor, 1961; 1984), which describes the relationship between the sample mean and variance. Taylor's parameter (intercept and slope) is estimated by regression of log (var) on log (mean), and b (slope) is the aggregation index. The regression model of Gerrard and Chiang (1970) was used to relate mean density to the proportion of infested samples.

5.3. Results and Discussion

5.3.1. Thrips species survey

Mainly two thrips species were found infesting the crop in 1994 and 1995: *Thrips tabaci* Lind. and *F. occidentalis*. The same species were recorded on eggplant during the same period and in the same area (Tommasini *et al.*, 1997; see chapter 6). Like observed on eggplant, the relative abundance of *T. tabaci* was first higher, but already in late June-early July there was an increase of *F. occidentalis* on sweet pepper, and this became the main species at the end of the crop cycle (Fig. 1). All thrips instars including pupae were found on the plants, demonstrating that under the northern Italian conditions, thrips pupate only occasionally in the soil.

The first thrips were found on the plants during the second half of May-early June in 1994 and 1995 (Figs. 2 to 12). Blue sticky traps started to catch thrips on average one week after their appearance on plants, and the catches did not always reflect the population levels of thrips on the plant, similarly to what was observed by Berlinger *et al.* (1997) in Israel.

Thrips were found on leaves occasionally, confirming that sweet pepper flowers are more attractive for adults and nymphs of thrips than leaves. Thus, flowers are suitable to sample thrips on sweet pepper. Also Berlinger *et al.* (1997) found that *F. occidentalis* is stronger attracted by flowers than leaves. Contrary to this, Higgins (1992) found in British Columbia (Canada) that more than 85% of nymphs of *F. occidentalis* were recorded on leaves of sweet pepper, while females preferred to stay within flowers (84-95%). Garcia-Mari *et al.* (1994) found that both nymphs and adults of thrips have to be monitored in order to have a good estimate of the population, and that an average of 100 flowers of a vegetable crop have to be observed to properly estimate predator populations.

A very high index of aggregation of thrips was found on sweet pepper when expressed by Taylor's power law (Taylor, 1961; 1984). With the aggregation index of Taylor and/or with the value for regression calculated with the model of Gerrard and Chiang (1970), it is possible to determine the thrips infestation level on sweet pepper just by observing how many flowers are infested (Fig. 13). Sánchez *et al.* (1997) reached similar conclusions by applying the same methodology. Based on these results, a presence-absence sampling method can be developed and an estimate of the mean population density can then be made on the basis of the proportion of non occupied organs (in this case flowers) with considerable saving of time.

5.3.2. Chemical control

Generally, the thrips infestation in chemical tunnels (Figs. 2 to 5) was higher than in IPM tunnels (Figs. 6 to 12). No insecticides were sprayed specifically for control of thrips due to a low infestation level. The peak of thrips infestation generally occurred in July. Chemicals

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were necessary to control aphids, particularly *Aphis gossypii* Glov., and *Liriomyza* leafminers. The insecticide treatments prevented wild populations of *Orius* spp. to establish in chemical tunnels. *Orius* predators appeared on the plants only late in the season and effectively reduced the thrips population. The wild *Orius* species that immigrated into the tunnels were mainly *O. laevigatus* and *O. niger*, and a few *O. majusculus*. A survey carried out in July 1994 on three vegetable crops (sweet pepper, egg-plant and cucumber) showed a different relative abundance of immigrated *Orius* species (Tab. 1). Also in other southern European countries these three *Orius* species showed to be the most common species occurring on vegetable crops (Riudavets *et al.*, 1995; Tavella *et al.*, 1996; Barbetaki *et al.*, 1999; see chapter 2).

5.3.3. Release of *Orius laevigatus*

As soon as thrips appeared on the crop, an average of 1 and 1.2 *O. laevigatus*/m² were released in 1994 and 1995, respectively. In 1995, in 4 of the 5 IPM tunnels the release was repeated one week later with the same quantity of predators. In table 2 the amount of *O. laevigatus* released in each IPM tunnel is given.

Table 1. Relative abundance (%) of immigrated *Orius* species found on three vegetables in July 1994 in north-eastern Italy.

Crop	Total number of predators sampled	<i>O. laevigatus</i>	<i>O. niger</i>	<i>O. majusculus</i>
Sweet pepper	600	64.2	30.2	5.6
Egg-plant	250	36.0	45.2	18.8
Cucumber	100	28.6	0	71.4

Soon after release, *O. laevigatus* nymphs were found in the crop, showing that the predator had established (Figs. 6 to 12). *Orius* establishment avoided outbreaks of thrips, and thrips never exceeded one individual per flower per week in IPM tunnels. At the end of the production cycle the number of *Orius* on plants was always higher than that of thrips, demonstrating the high capability of *O. laevigatus* to establish on sweet pepper in tunnels and its efficacy to control thrips. A similar results was found on sweet pepper in protected crops by Sánchez *et al.* (2000) in the South-East of Spain.

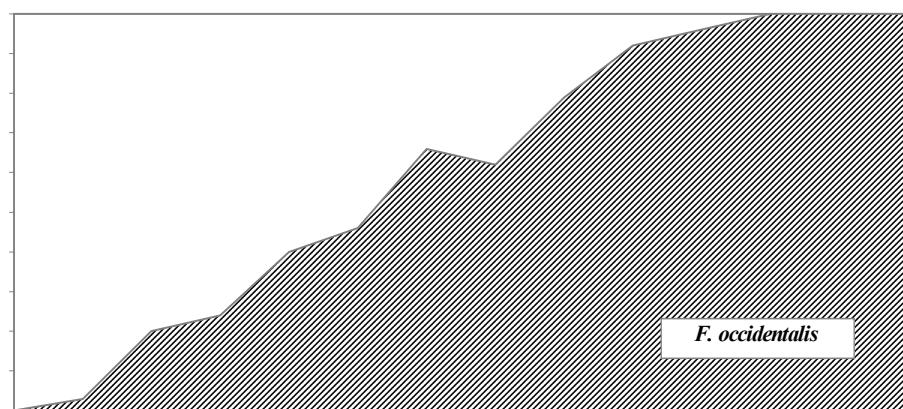
Chamber *et al.* (1993) found that releasing a total of 1-2 predators per sweet pepper plant resulted in a good thrips control over several months on sweet pepper in greenhouses in the United Kingdom. In our conditions, where thrips infestations were not high, a much lower amount of *Orius* was sufficient to obtain effective control of thrips. An average of 2 predator/m² in 1 or 2 releases (ca. 0.2 predators/plant) was enough. A similar conclusion was

reached by Sàncchez and Lacasa (2002) for control of thrips in pepper in Spain (three release rates of 0.75-0.25 *Orius*/plant). In the Netherlands, where generally much higher thrips populations occur, multiple releases of 1 *O. laevigatus*/m² combined with an *Amblyseius cucumeris* (Oud.) introduction just after transplanting, avoided thrips outbreaks in sweet pepper (van Schelt, 1999). I suppose that in my experiments immigrated natural populations of *Orius* spp. from the surrounding environment contributed to thrips control. This idea is supported by the rather high populations of *O. niger* found at the end of the growing season in all IPM tunnels. A similar result was found by van de Veire and Degheele (1992) in sweet pepper. They released the exotic species *O. insidiosus*, but later in the season they found only *O. niger* on plants. Also in Ligury (Italy) naturally occurring *O. laevigatus* together with low numbers of *O. niger* and *O. majusculus* were observed late in the growing season controlling thrips in sweet pepper greenhouses where IPM was applied (Tavella *et al.*, 1996).

Table 2. Number of *Orius laevigatus* released into sweet pepper tunnels.

IPM tunnel	Total number of <i>Orius</i> introduced/m ² (number of releases)	
1 (1994)	1	(1)
2 (1994)	1	(1)
3 (1995)	3	(2)
4 (1995)	2.5	(2)
5 (1995)	2.5	(2)
6 (1995)	2.2	(2)
7 (1995)	1.8	(1)

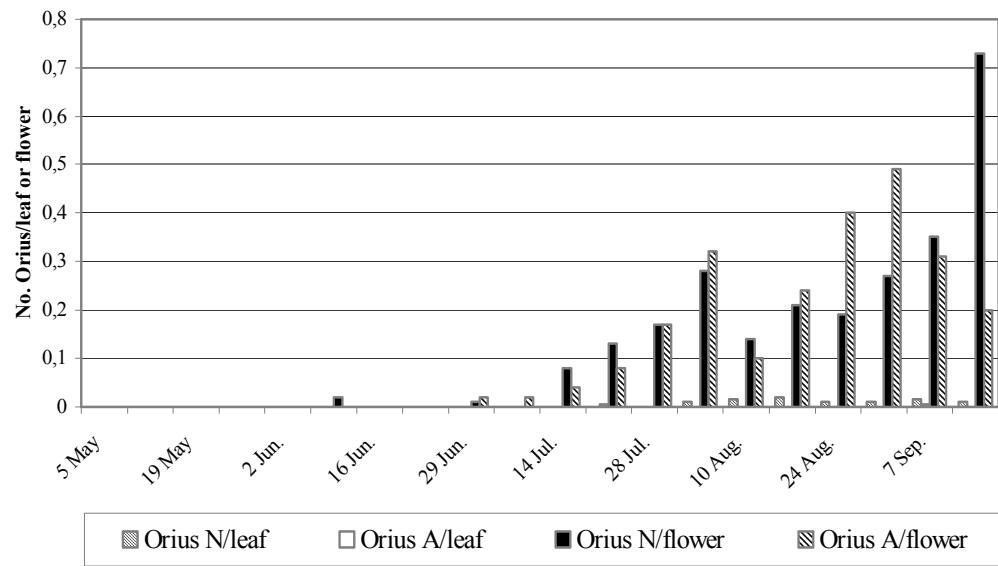
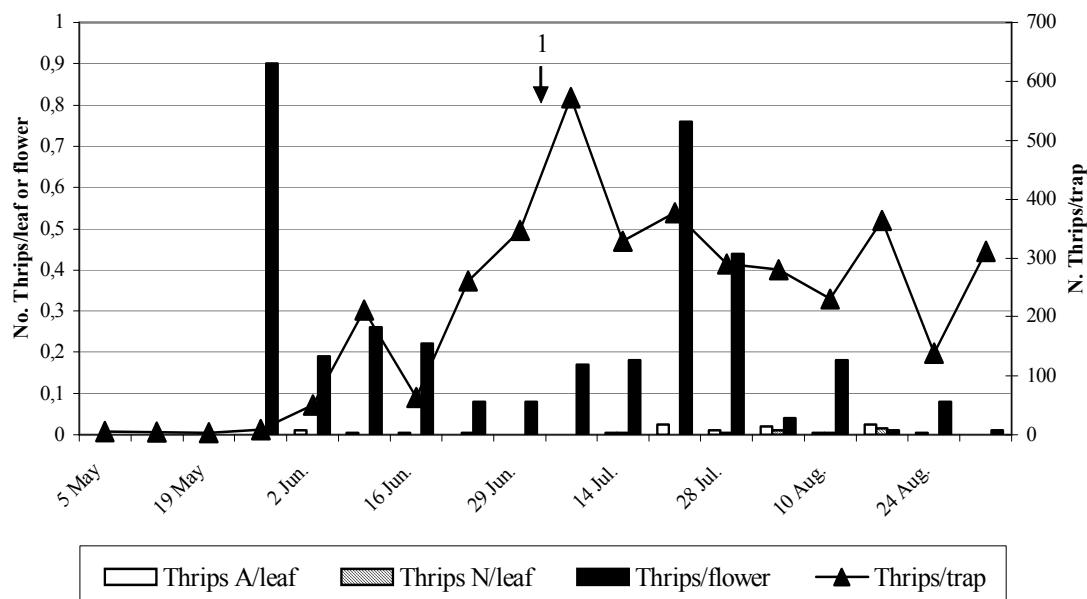
Figure 1. Ratio of *Frankliniella occidentalis* to *Thrips tabaci* in sweet pepper at intervals of ca. 10 days.



Enhancement of thrips control in protected sweet pepper crops by releases of the predator of *Orius laevigatus*.

Figure 2. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with insecticides. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina.

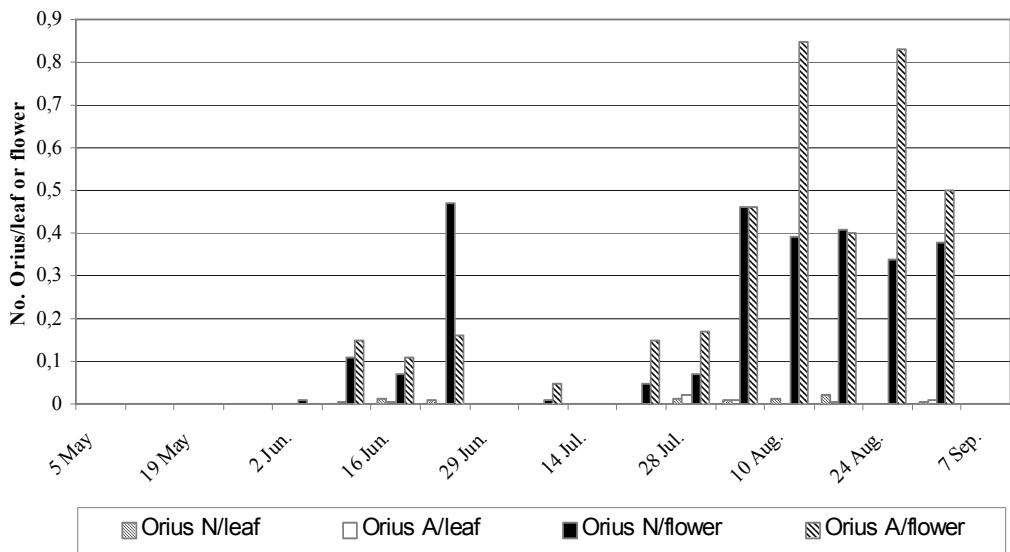
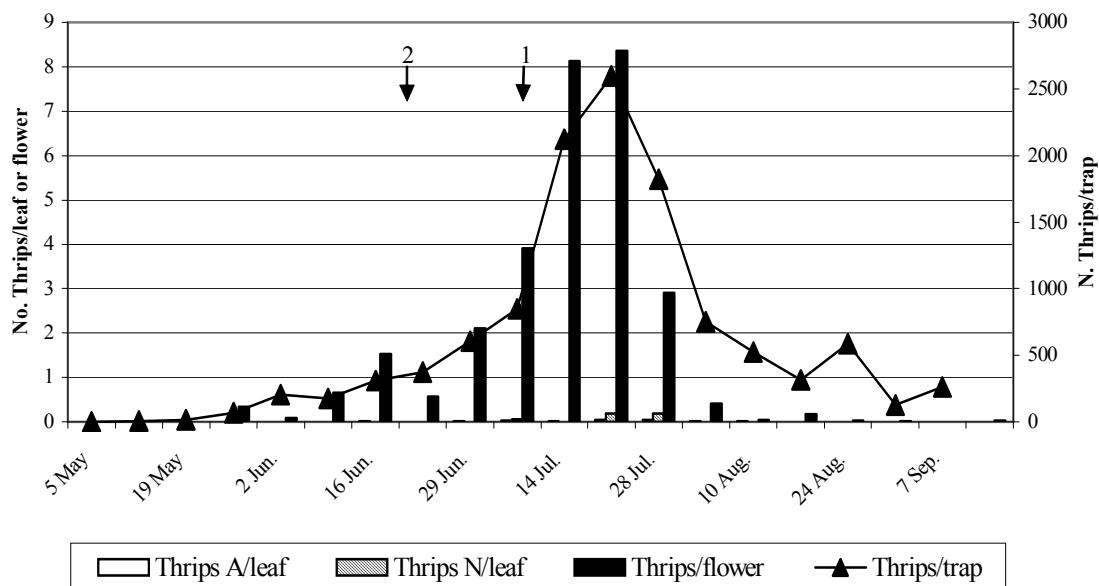
(a)



(b)

Figure 3. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with insecticides. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina.

(a)

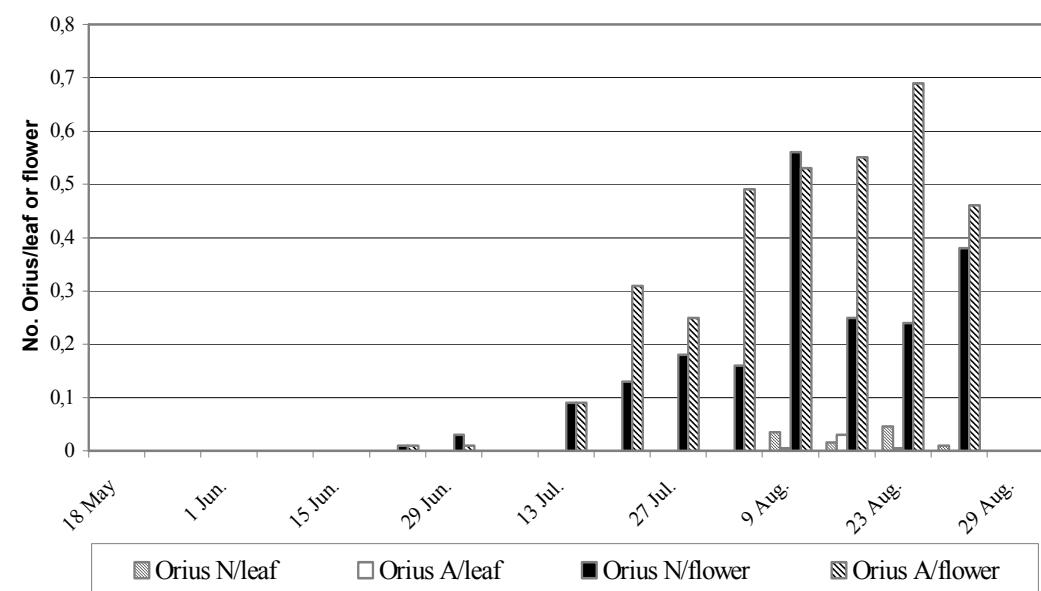
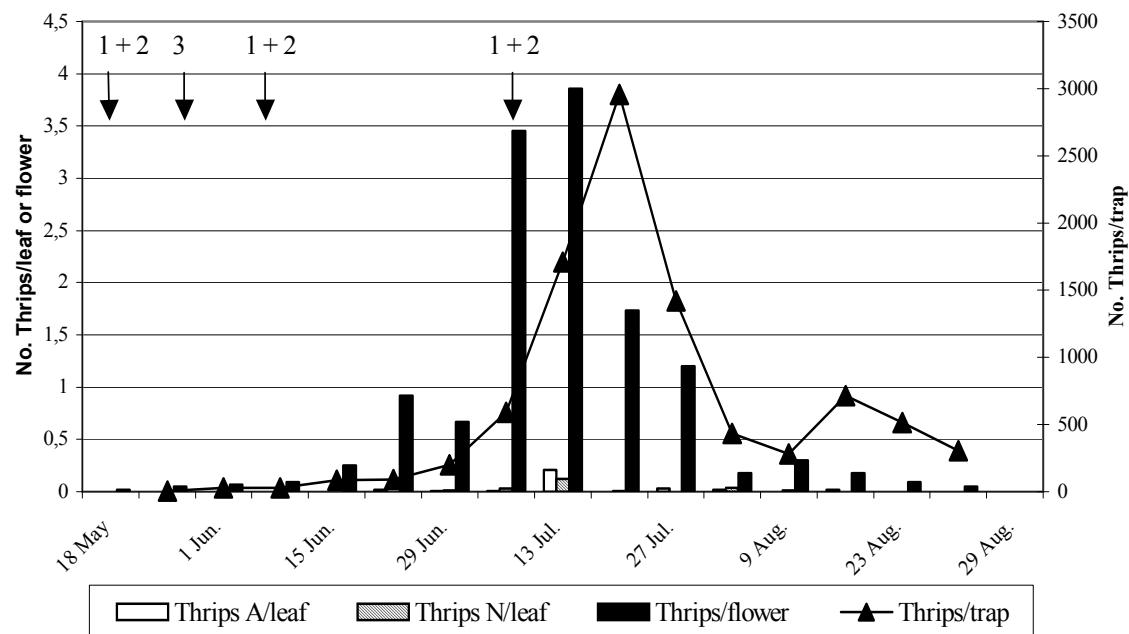


(b)

Enhancement of thrips control in protected sweet pepper crops by releases of the predator of *Orius laevigatus*.

Figure 4. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with insecticides. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina.

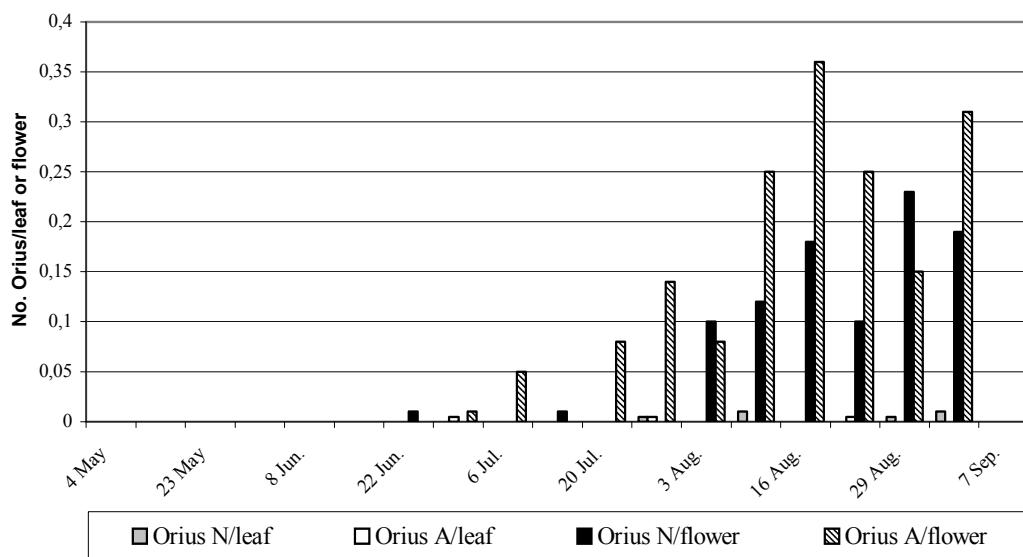
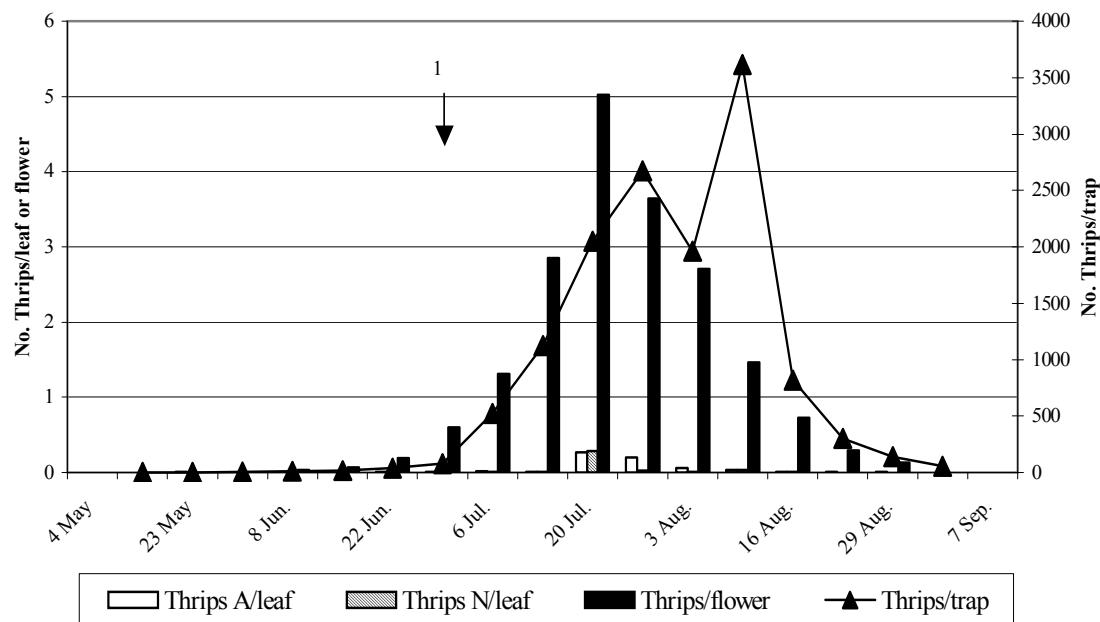
(a)



(b)

Figure 5. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with insecticides. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina.

(a)

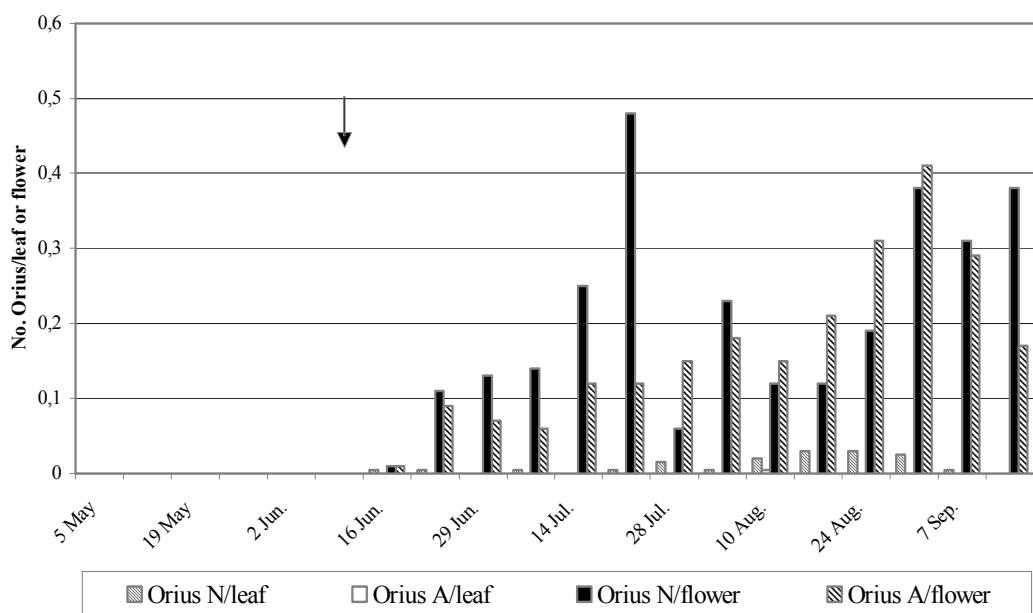
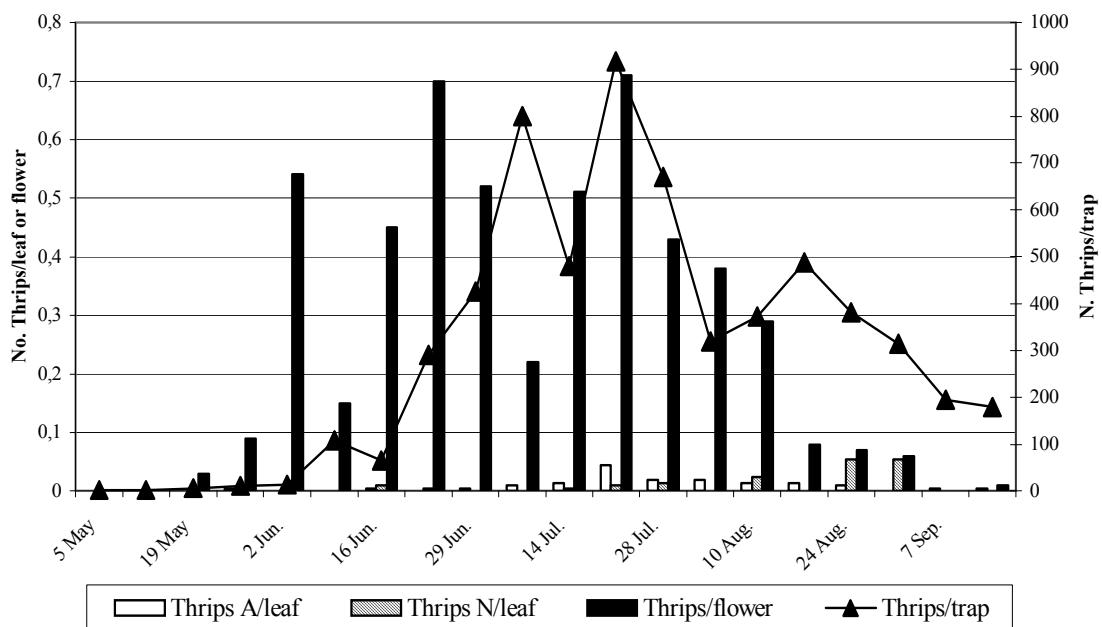


(b)

Enhancement of thrips control in protected sweet pepper crops by releases of the predator of *Orius laevigatus*.

Figure 6. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with natural enemies. Arrow indicates when *Orius laevigatus* was released (IPM tunnel 1).

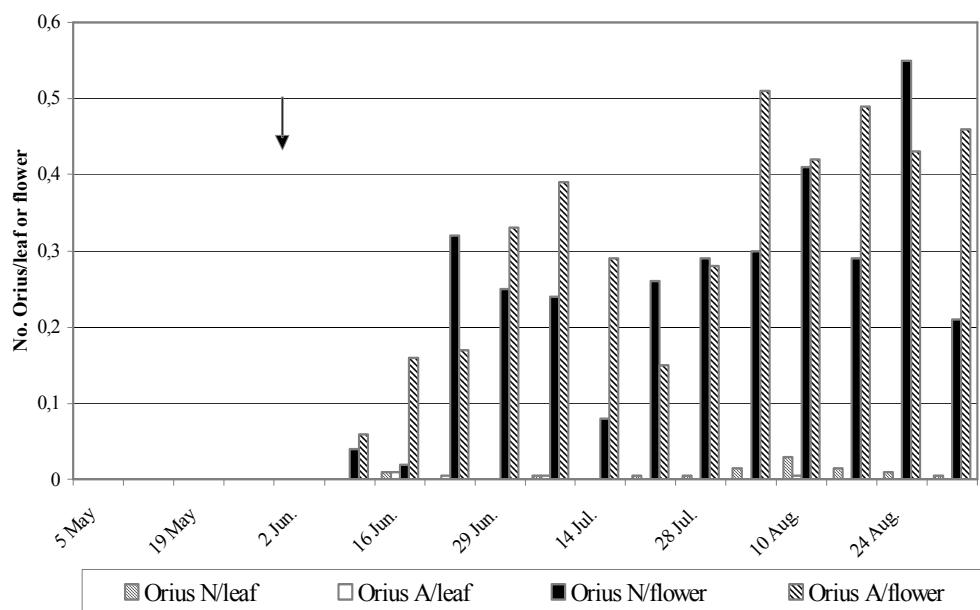
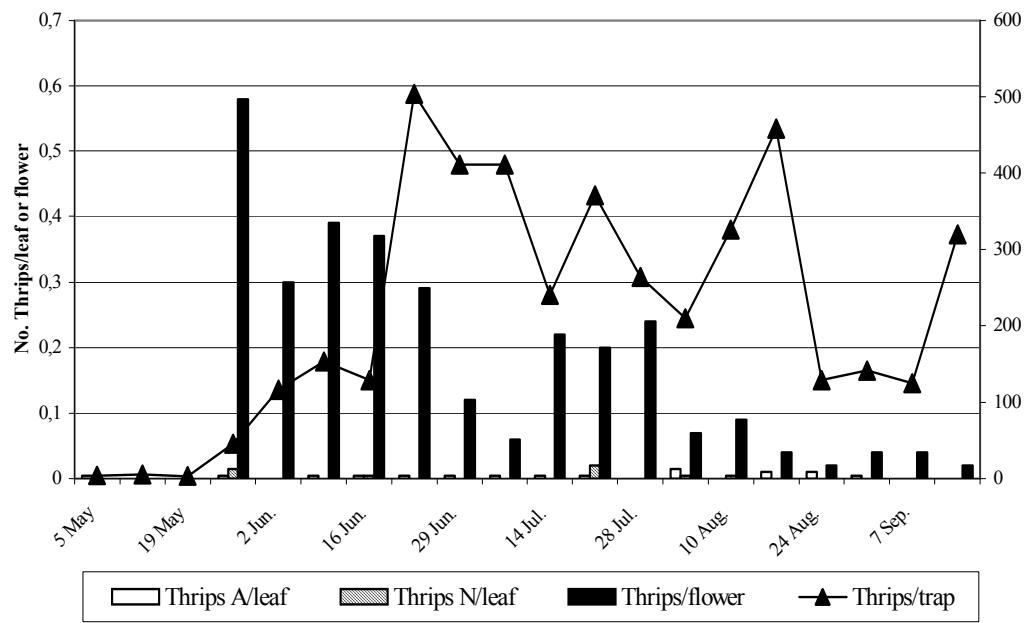
(a)



(b)

Figure 7. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with natural enemies. Arrow indicates when *Orius laevigatus* was released (IPM tunnel 2).

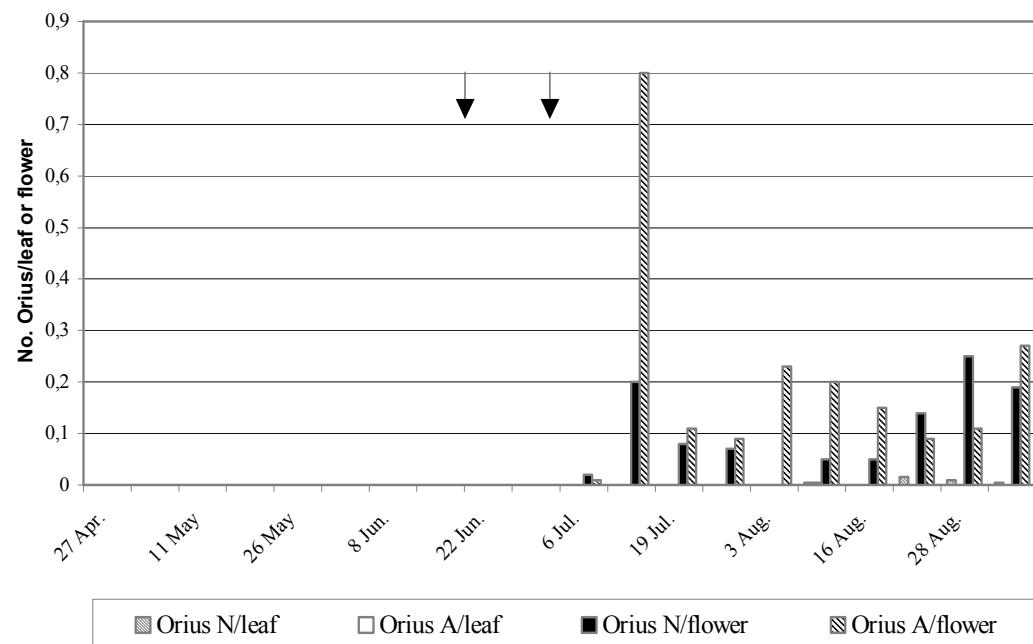
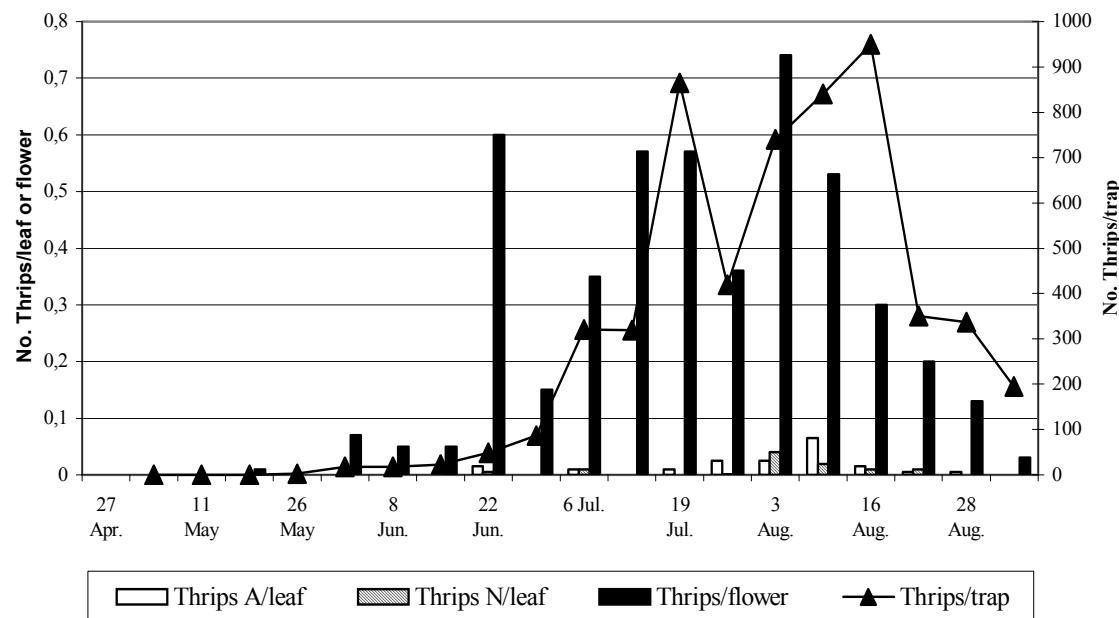
(a)



(b)

Figure 8. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with natural enemies. Arrow indicates when *Orius laevigatus* was released (IPM tunnel 3).

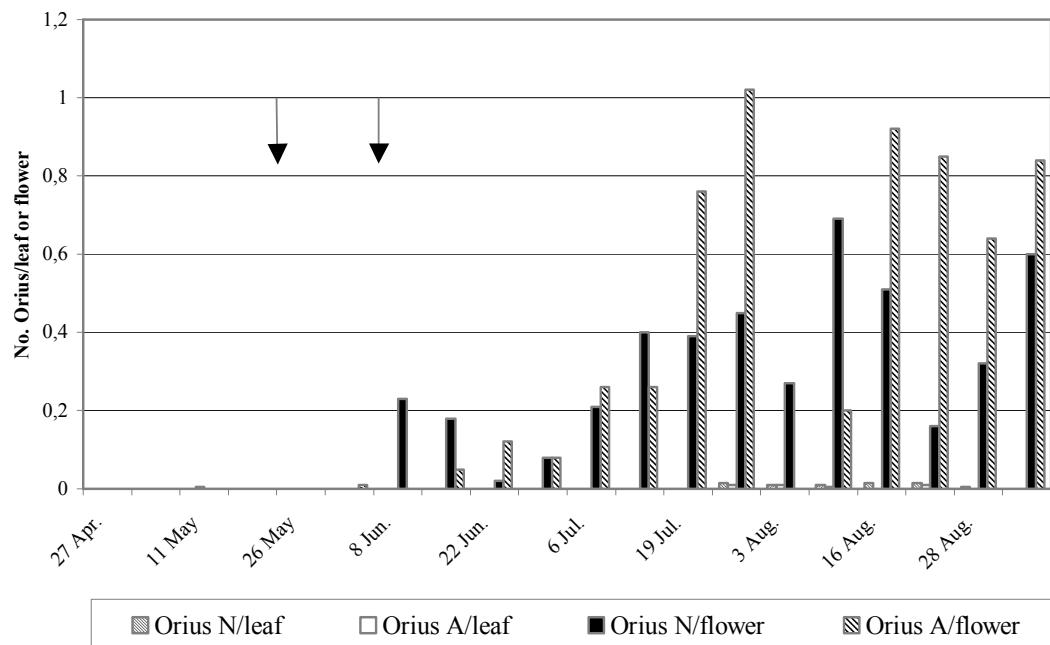
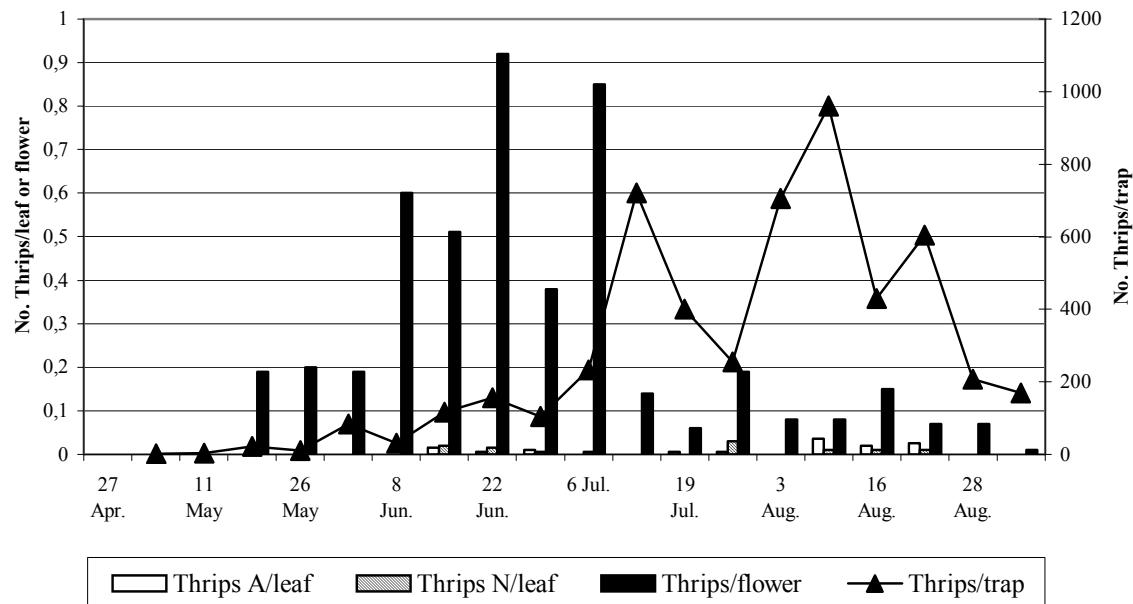
(a)



(b)

Figure 9. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with natural enemies. Arrow indicates when *Orius laevigatus* was released (IPM tunnel 4).

(a)

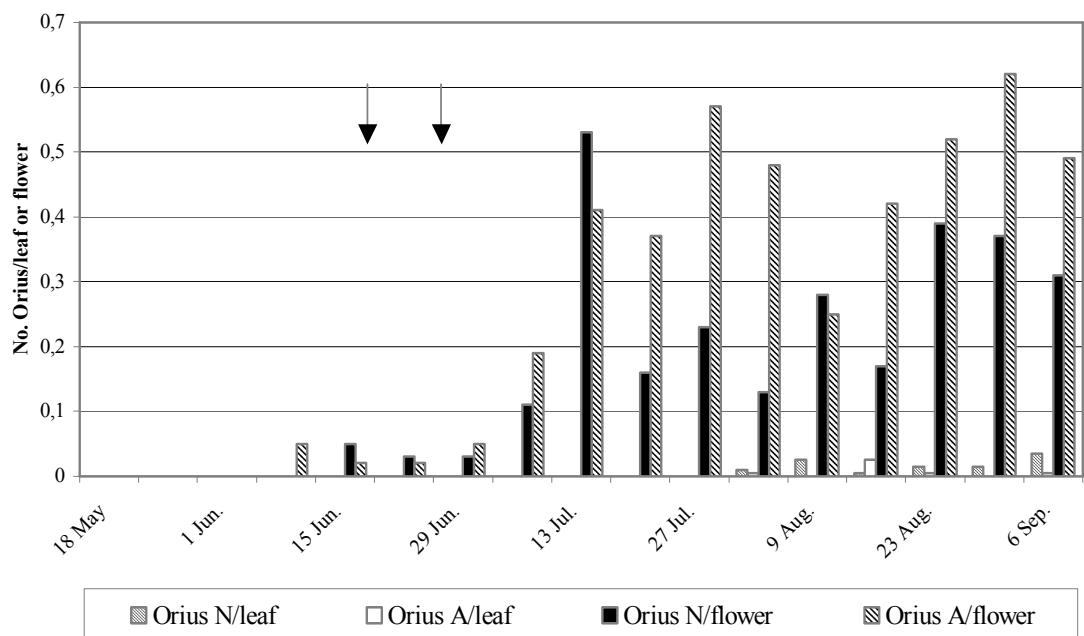
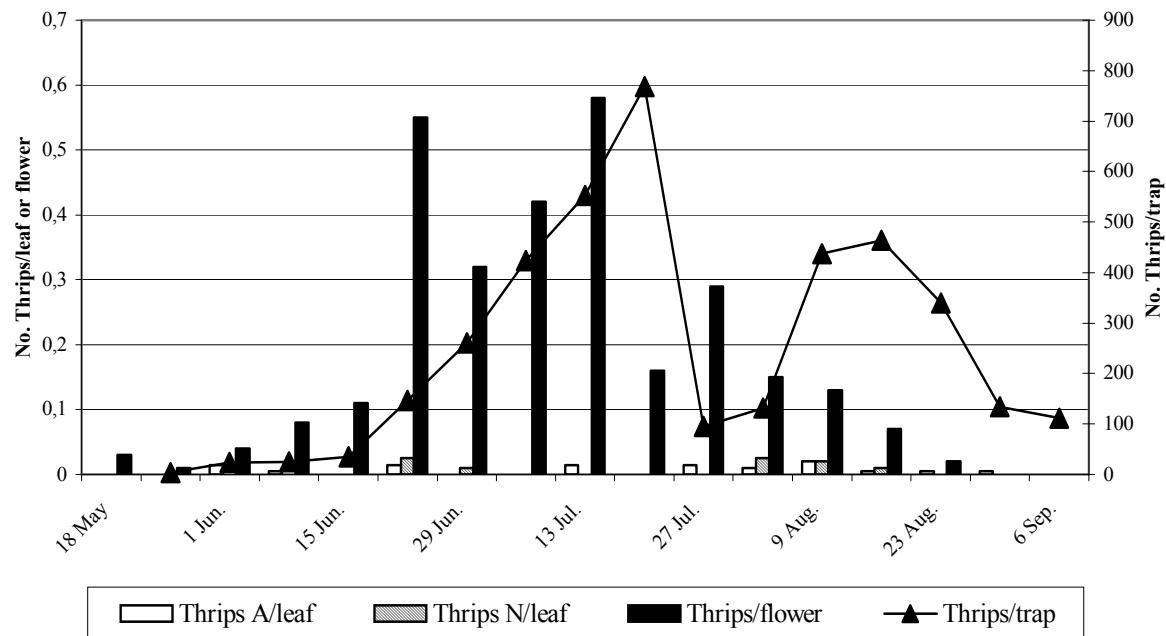


(b)

Enhancement of thrips control in protected sweet pepper crops by releases of the predator of *Orius laevigatus*.

Figure 10. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with natural enemies. Arrow indicates when *Orius laevigatus* was released (IPM tunnel 5).

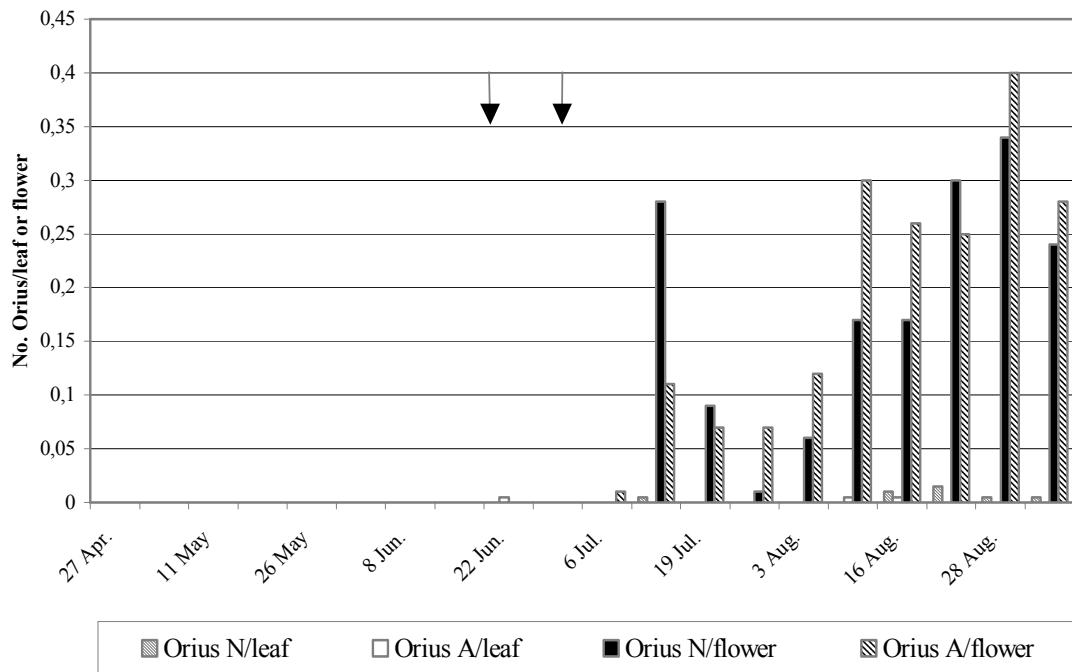
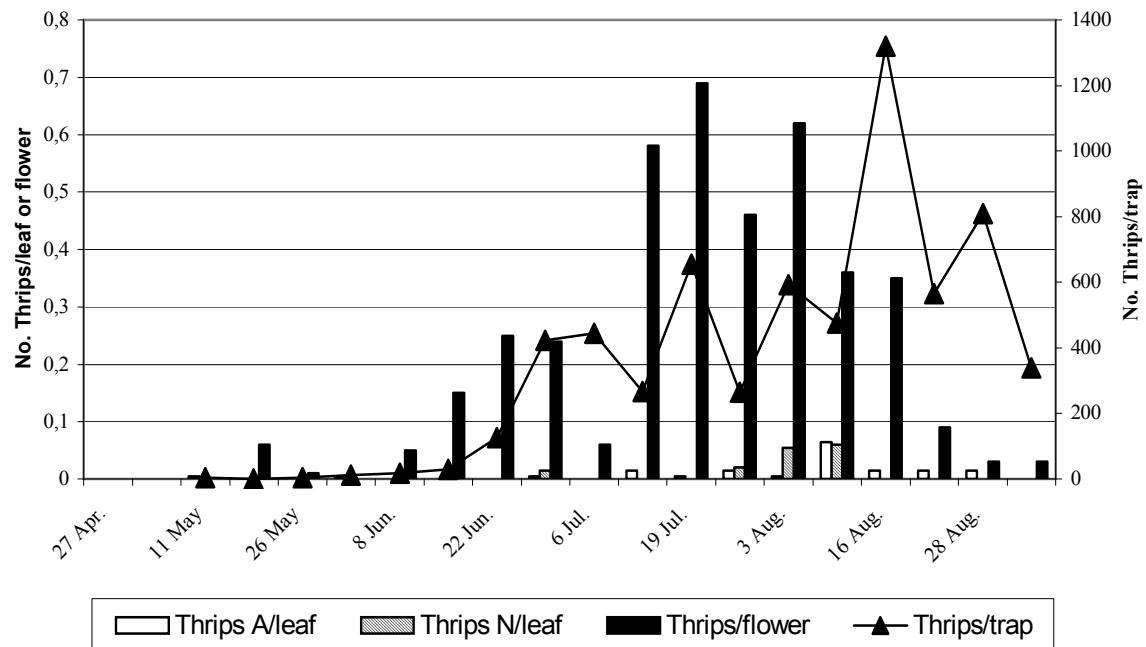
(a)



(b)

Figure 11. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with natural enemies. Arrow indicates when *Orius laevigatus* was released (IPM tunnel 6).

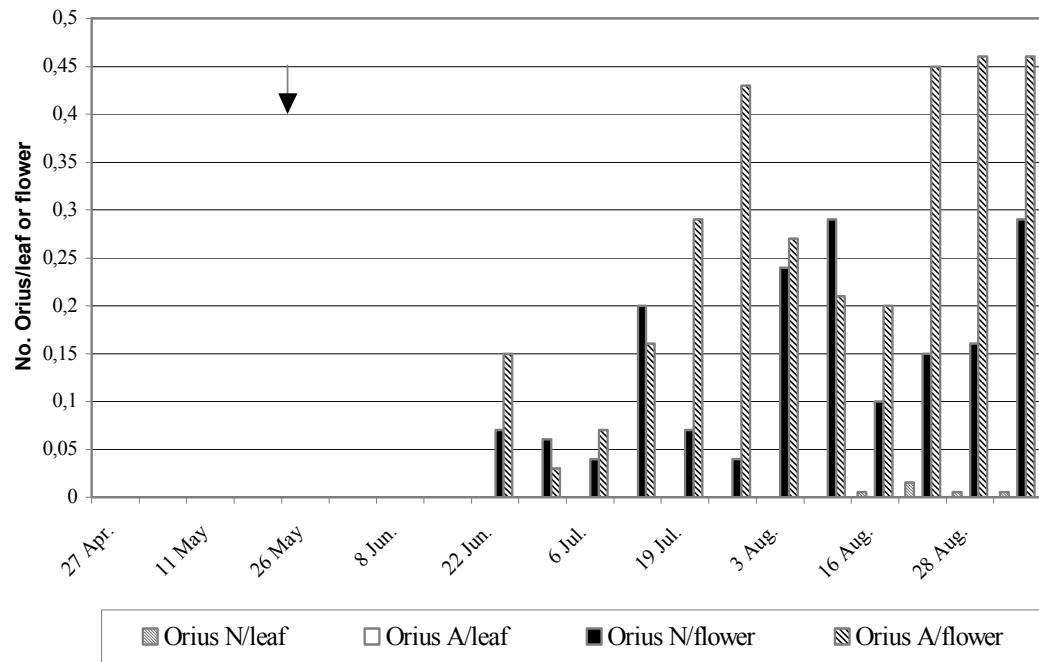
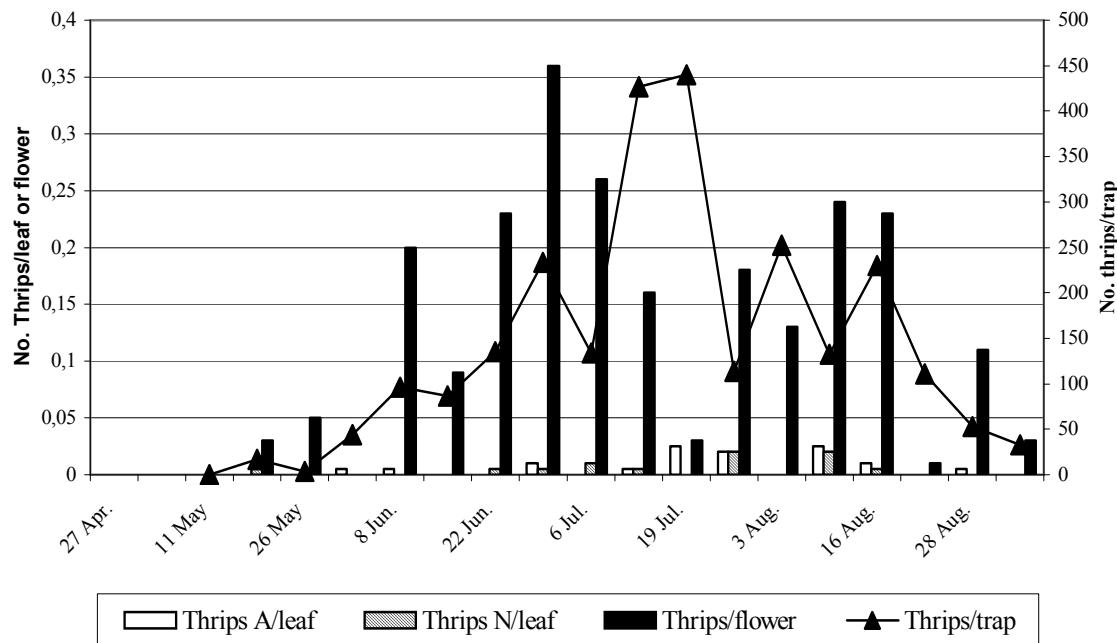
(a)



(b)

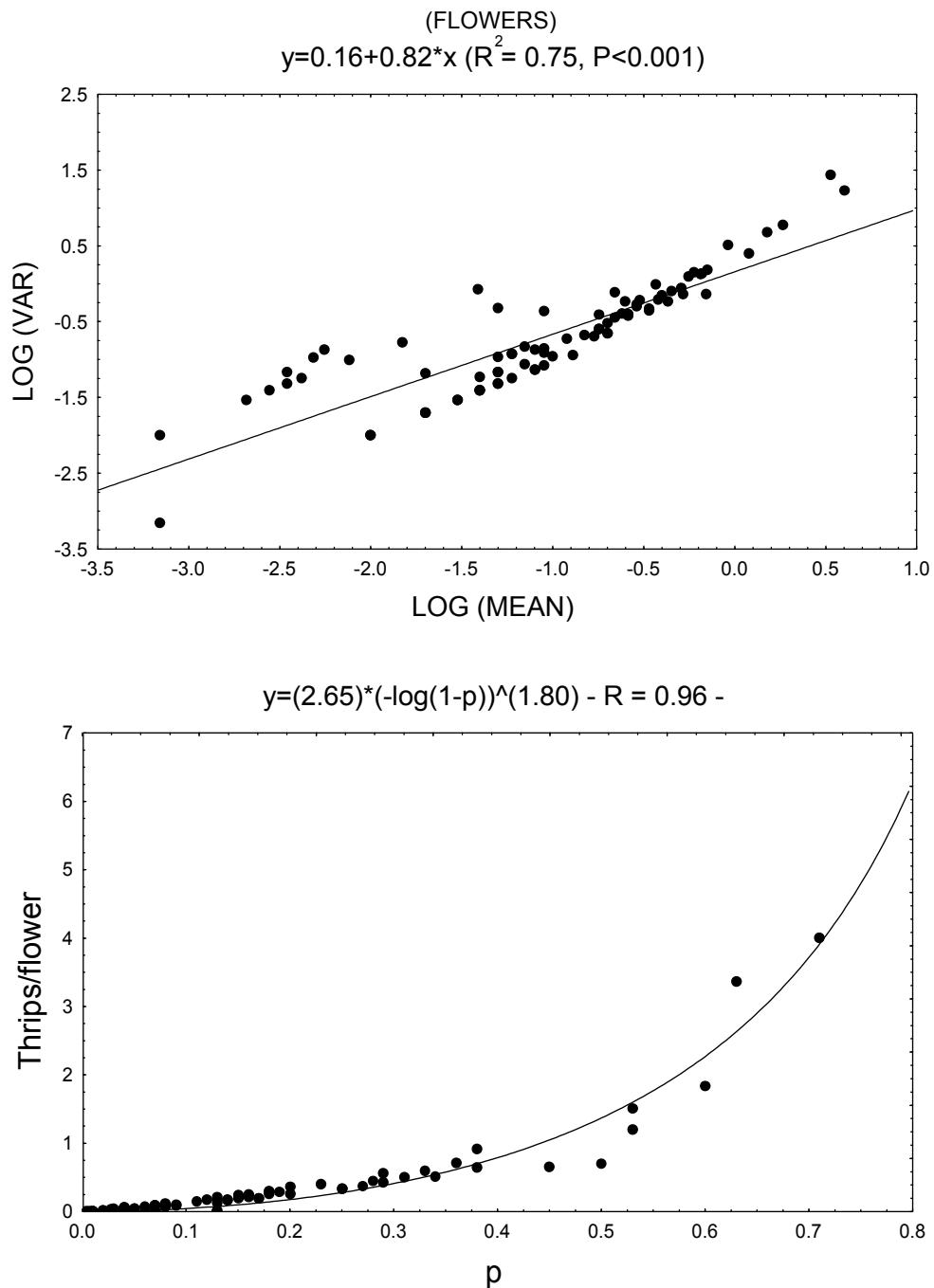
Figure 12. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with natural enemies. Arrow indicates when *Orius laevigatus* was released (IPM tunnel 7).

(a)



(b)

Figure 13. Taylor's index of aggregation (b slope) is shown in the upper graph. The parameters for intercept and slope are estimated by regression of log (var) on log (mean). Mean density related to the proportion of infested samples as calculated with the regression model of Gerrard and Chaing (1970) is shown in the bottom graph.



5.4. Conclusions

From the counts made in the crop and on the traps it appears that blue sticky traps can give an indication of thrips presence in tunnels, but that they cannot be used to reliably monitor thrips infestations in sweet pepper. Sampling flowers is a more effective and reliable method to follow development of thrips populations. Furthermore, based on the high index of aggregation of thrips found on sweet pepper (Taylor's power law (Taylor, 1961; 1984), and the Gerrard and Chaing (1970) regression calculated) it is possible to calculate the thrips infestation level on sweet pepper when the proportion of non-occupied flowers is known. The method of only counting infested flowers is also saving a lot of time, when compared with making population counts.

Early releases of *O. laevigatus* when thrips appear in flowers and on traps allow good establishment of the predators and result in effective thrips control. This was also found by van de Veire and Degheele (1997) in North Europe and Sánchez and Lacasa (2002) in Spain. When thrips infestations are not high and wide-spectrum insecticides are not used, natural control by immigrating indigenous *Orius* species is very effective and prevents thrips outbreaks. Use of wide-spectrum insecticides disrupts natural control. When chemicals are no longer applied, three natural *Orius* species (*O. laevigatus*, *O. niger* and *O. majusculus*) soon colonize the crops and control thrips. This result was recorded also on other crops such as on egg-plant (Chiappini, 1993; Tommasini *et al.*, 1997) and strawberry (González-Zamora *et al.*, 1992; 1994; Gambaro, 1995).

O. laevigatus appeared to control thrips (mainly *F. occidentalis*) effectively and is suitable to be released in combination with natural enemies used for control of other pests. This was also found by Brødsgaard and Enkegaard (1995) and Wittmann and Leather (1997).

In Israel, Rubin *et al.* (1996) found *O. laevigatus* to be less effective for control of thrips on sweet pepper compared to the phytoseid *Iphiseius (Amblyseius) degenerans* Berlese. However, in many European countries *O. laevigatus* appears to be the most suitable natural enemy for thrips control in sweet peppers (Chamber *et al.*, 1993; Dissevelt *et al.*, 1995; Tavella *et al.*, 1996; van de Veire and Degheele, 1997; Sánchez *et al.* 2000; Sánchez and Lacasa, 2002).

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CHAPTER 6. ENHANCEMENT OF THIRIPS CONTROL IN PROTECTED EGGPLANT CROPS BY RELEASES OF THE PREDATOR *ORIUS LAEVIGATUS*

5

Abstract

The implementation of IPM in eggplant produced in tunnels is difficult due to several arthropod pests that attack this crop. In a survey of two years, two thrips species were found: the very harmful *Frankliniella occidentalis* (Perg.), and the less harmful *Thrips tabaci* Lind. During three years (1993-95), the possibility to control thrips by means of releases of the pirate bug *Orius laevigatus* (Fieber) was tested in plastic tunnels with eggplants. This native predator was able to effectively control the exotic *F. occidentalis*, even despite chemical insecticides applied against *Aphis gossypii* Glov. The releases of the pirate bugs were made as soon as thrips were detected, resulting in early establishment of the predator and in an interaction between prey and predator at low population densities. When insecticides were used against other pests, the mass-reared predators were released more than once. Pure chemical control of *F. occidentalis* was also studied, but efficacy was low. Further, the application of broad-spectrum insecticides disrupted the establishment of immigrated *Orius* predators and of the released mass-reared beneficial arthropods.

6.1. Introduction

In Italy, eggplant, *Solanum melongena* L., is grown both in plastic tunnels and in the open field. Many pests attack this crop needing intensive use of wide spectrum insecticides, otherwise severe damage is the result (Maini *et al.*, 1996). Chemical control in eggplant is particularly difficult as fruits are contaminated by pesticide residues and also negative side-effects influence predators, parasitoids and pollinators released in eggplant. Further the intensive application of pesticides prevents immigration of naturally occurring beneficial insects that normally reduce pest numbers. Although the release of mass-reared arthropods and the spray of microbial insecticides can provide good results in the control of specific pests in eggplant crops, some difficulties still remain in setting up a global strategy of Integrated Pest Management (IPM) because selective control techniques were not available for two key-pests, aphids (mainly *Aphis gossypii* Glov.) and thrips. Several important eggplant pests can be successfully controlled by biological agents, like the Greenhouse whitefly, *Trialeurodes vaporariorum* (Westw.) by the release of the native predator *Macrolophus caliginosus* Wagner and the parasitoid *Encarsia formosa* Gahan, the Red spider mite, *Tetranychus urticae* Koch by introduction of the predatory mite *Phytoseiulus persimilis* Athias-Henriot (Benuzzi and Nicoli, 1989; Nicoli and Benuzzi, 1989), the exotic leafminers, *Liriomyza trifolii* (Burg.) and *L. huidobrensis* (Blanc.) by releases of the native parasitoid *Diglyphus isaea* (Walk.), and the Colorado potato beetle *Leptinotarsa decemlineata* (Say) can be controlled by spraying microbial insecticides (*Bacillus thuringiensis* Berl. subsp. *tenebrionis*; Maini *et al.*, 1994) or

⁵ This chapter is largely based on the following paper: Tommasini, M.G., Maini, S. and Nicoli, G., 1997. Advances in the integrated pest management in protected-eggplant crops by seasonal inoculative releases of *Orius laevigatus*. *Adv. Hort. Sci.*, 11: 182-188.

by application of selective insecticides (*i.e.* the synthetic insect growth regulator teflubenzuron). In addition, bumblebees, *Bombus terrestris* L., can be used for pollination (Maccagnani, 1996), which is already common in tomato crops.

In Italy, two species of thrips pests are usually found in eggplant grown in tunnels: the Onion thrips, *Thrips tabaci* Lind., and the Western Flower Thrips, *Frankliniella occidentalis* (Perg.). Before the introduction from America of *F. occidentalis* in 1987 (Rampinini, 1987), *T. tabaci* was considered an occasional pest causing only limited damage, if any, and insecticides were generally not used to control this species. After the establishment of *F. occidentalis* (Arzone *et al.*, 1989), the exotic thrips became a key pest of several vegetable and ornamental crops, including eggplant. In the past 15 years, the life cycle, the range of host plants, the direct and indirect damage caused by thrips and samplings techniques have been extensively studied (see chapter 1 and review by Tommasini and Maini, 1995). Loomans and van Lenteren (1995) and Riudavets (1995) reviewed the beneficial arthropods that can control phytophagous thrips. But at that time, the role of *Orius* spp. for control of thrips on eggplant was hardly studied (Kawai, 1995; Wang Chinling, 1995). However, in other crops in Europe the seasonal inoculative release of *Orius* spp. provided good control (Vullevieille and Millot, 1991; Van de Veire and Degheele, 1992; Chambers *et al.*, 1993; Frescata and Mexia, 1995; Vacante and Tropea Garzia, 1993; Tavella *et al.*, 1996).

Especially in the open field, but also in greenhouse, eggplant crops were regularly found to be colonised by wild populations of *Orius* species. *O. laevigatus* was the most abundant Anthocorid on vegetables grown in Central and South Italy (see chapter 2; Nicoli and Tommasini, 1996). Unfortunately, the colonisation of these predators usually occurs too late, and when thrips outbreaks have already produced serious economic damage. Therefore, the principal aim of this study was to investigate the possibility of controlling thrips by seasonal inoculative releases of *O. laevigatus*, in order to reach timely control of this pest.

6.2. Materials and methods

During a three-year period (1993-1995), populations of thrips and its predator *O. laevigatus* were checked in 8 commercial plastic tunnels of ca. 300 m² each. The unheated eggplant tunnels were located in a large greenhouse area near Rimini in North-eastern Italy, close to the Adriatic sea coast. The local cultivar 'Riminese' grafted on tomato was used, in a density of ca. 12,500 plants per hectare and water was supplied by hoses placed on the soil. The production cycle started in the middle of April and plants were usually cut between the end of August and the middle of September. Before transplanting, the soil was generally fumigated by methyl-bromide.

Conventional chemical control was applied in one tunnel in 1993 and in 1995, and in two tunnels in 1994 (the so called chemical tunnels). The release of *O. laevigatus* was tested in four, so called IPM tunnels more than 100 m away from the chemical tunnels. In the IPM tunnels, several mass-reared natural enemies and microbial control agents were applied (*M. caliginosus*, *P. persimilis* and *B. thuringiensis* subsp. *tenebrionis*) in addition to the releases of the pirate bug *O. laevigatus*. In the IPM tunnels, a blend of nymphs and adults of *O. laevigatus* (in a ratio of ca. 3:2 respectively) were released by scattering 1-2 predators per m² on the leaves when the threshold of 2 thrips per flower or 4 thrips per leaf had been exceeded. In the chemical tunnels, *O. laevigatus* was released more than once because the insecticides sprayed to control *A. gossypii* also killed the *Orius* predators. Chemical insecticides were used mainly to control *A. gossypii*, because no effective natural enemy was available at that time.

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Sampling was carried out weekly during the eggplant growing cycle. Nymphs and adults of both thrips species and *O. laevigatus* were counted on 200 leaves (50% at the top and 50% at the bottom of the plants) and in 100 flowers randomly chosen from 100 plants per tunnel. The number of thrips and predators in the flowers was recorded by gently shaking each flower in a small transparent plastic cylinder of about 1 dl. The density of adult thrips was also monitored weekly by counting the catches in blue sticky traps (10x20 cm each) placed 20 cm above the top of eggplants. Initially 10 sticky traps were used per tunnel. As soon as more than 10 thrips were caught per trap per week, the number of traps was reduced to two per tunnel. In order to determine the relative incidence of *T. tabaci* and *F. occidentalis* in 1993 and 1994, random samples of at least 30 adults were taken every fortnight.

6.3. Results and discussion

6.3.1 Thrips species survey

We confirmed that *T. tabaci* and *F. occidentalis* were the two most important thrips species attacking eggplant in protected crops in Italy. Both in 1993 and 1994 (Fig. 1), *T. tabaci* was more abundant than *F. occidentalis* during the initial part of the crop cycle, but later in the season *F. occidentalis* increased rapidly and became the most abundant species. This change in abundance might be result of a difference in resistance to insecticides of these two species. It is well known that *F. occidentalis* has a high degree of resistance to insecticides (Brødsgaard, 1994). Nevertheless, other factors like microclimate and plant quality may play a role in this nearly complete substitution.

6.3.2 Chemical control

The population trends of thrips on leaves and flowers, as well as on the blue sticky traps, showed that chemical insecticides were not sufficiently effective in the control of thrips. Control was particularly poor for *F. occidentalis*, which was the most abundant species from July to the end of the crop cycle, and severe outbreaks of this species were recorded (Figs. 2 to 5). From the end of May to the beginning of July many broad-spectrum insecticides were applied mainly to control *A. gossypii*, because the selective active ingredient available (*i.e.* pirimicarb) was ineffective in controlling this pirimicarb resistant aphid. Later in the season broad-spectrum insecticides were also sprayed to control *F. occidentalis*, but the results were only partially successful. Some acaricides had to be used for control of *T. urticae*.

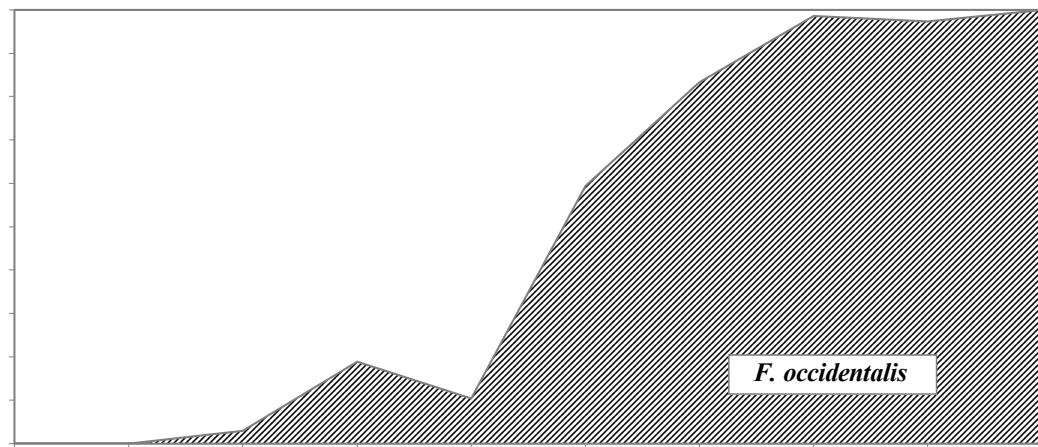
Adults of *Orius* spp. colonised the eggplant crop from outside, but application of insecticides prevented a good establishment of these wild predators, as shown by the low number of nymphs recorded, especially after the sprays with pyrethroids. Samples of adults indicated that three species of *Orius* colonised the eggplant tunnels: *O. laevigatus*, *O. majusculus* (Reuter) and *O. niger* Wolff. These species are polyphagous predators very common in all the Mediterranean basin (Riudavets, 1995; Riudavets *et al.*, 1995; see chapter 2). *O. laevigatus* and *O. majusculus* can be considered very effective natural enemies of *F. occidentalis* (Tommasini and Nicoli, 1993; 1994). Their colonisation can surely enhance the natural control of thrips and other pests particularly at the end of the crop cycle (see also the previous chapter).

6.3.3 Release of *Orius laevigatus*

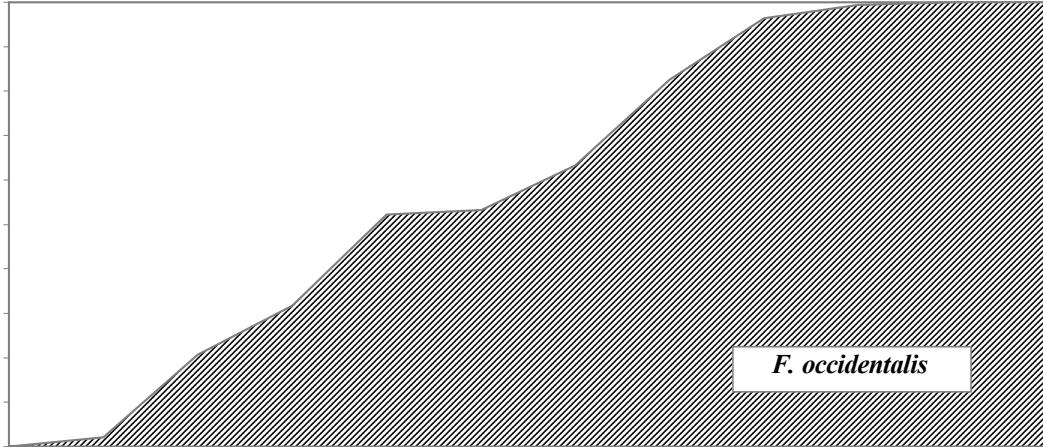
O. laevigatus was able to establish on eggplant and to reproduce well. Both adults and nymphs were usually found in the corolla of the flowers where many thrips feed and hide. Unfortunately, the very severe outbreaks of *A. gossypii* necessitated sprays with broad-spectrum insecticides, mainly methomyl. This active ingredient often killed the newly-established predators. The short persistence of the insecticide allowed us to reintroduce *O. laevigatus* in some tunnels, just a few days after the insecticide spray. The newly introduced *O. laevigatus* predators, as well as the predators surviving the chemical treatment and those colonising the tunnel from outside, were regularly able to sufficiently reduce thrips populations and resulted in good commercial fruit production. In the IPM tunnels (Figs. 6 to 9), the thrips populations appeared lower than in the chemical tunnels.

Figure 1. Ratio of *Frankliniella occidentalis* to *Thrips tabaci* in eggplant at intervals of ca. 10 days (decade) during 1993 (graphic A) and 1994 (graphic B).

A



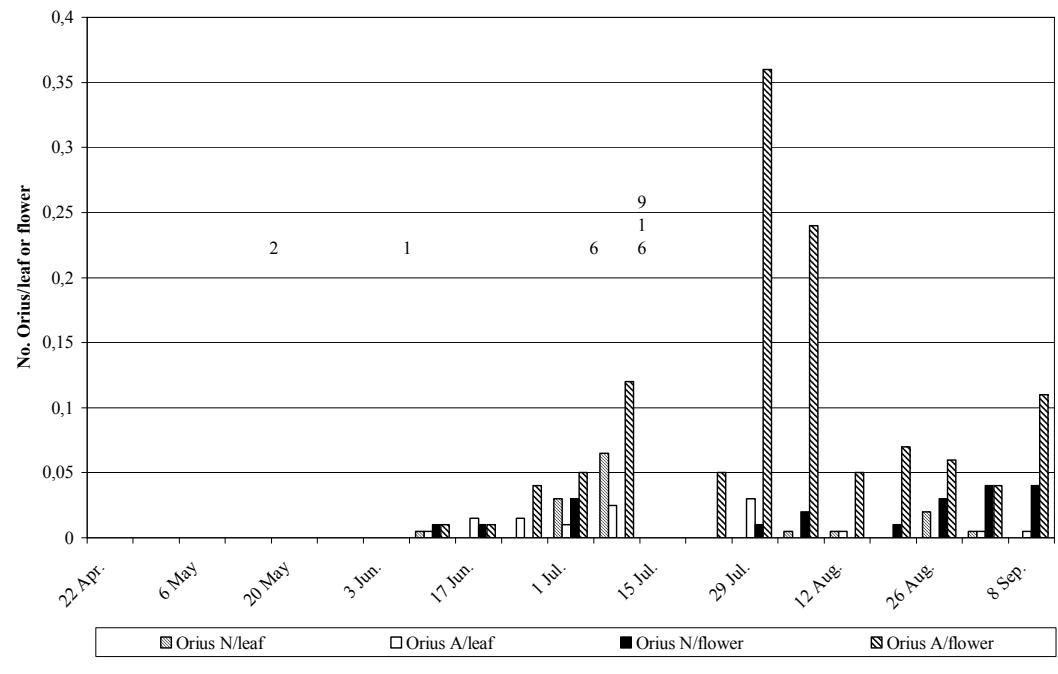
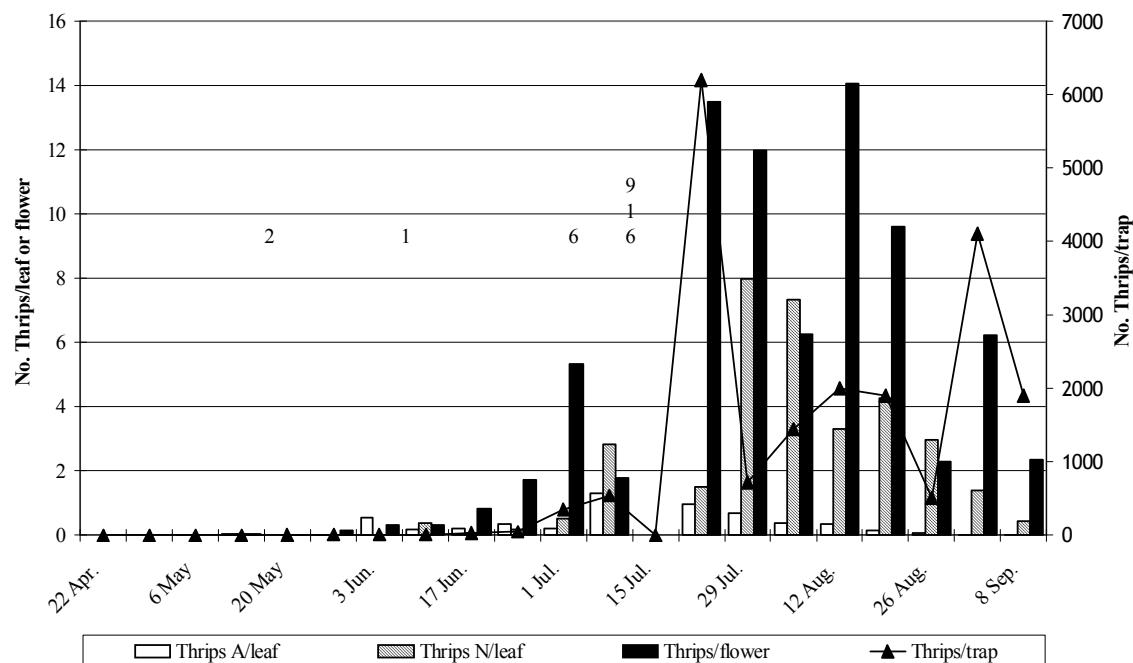
B



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Figure 2. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with insecticides. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina 1 = Methomyl; 2 = Pirimicarb; 3 = Heptenophos; 4 =Fluvalinate; 5 = Azinphos-methyl; 6 = Deltamethrin; 7 =natural pyretrum; 8 = Teflubenzuron; 9 =Azocyclotin

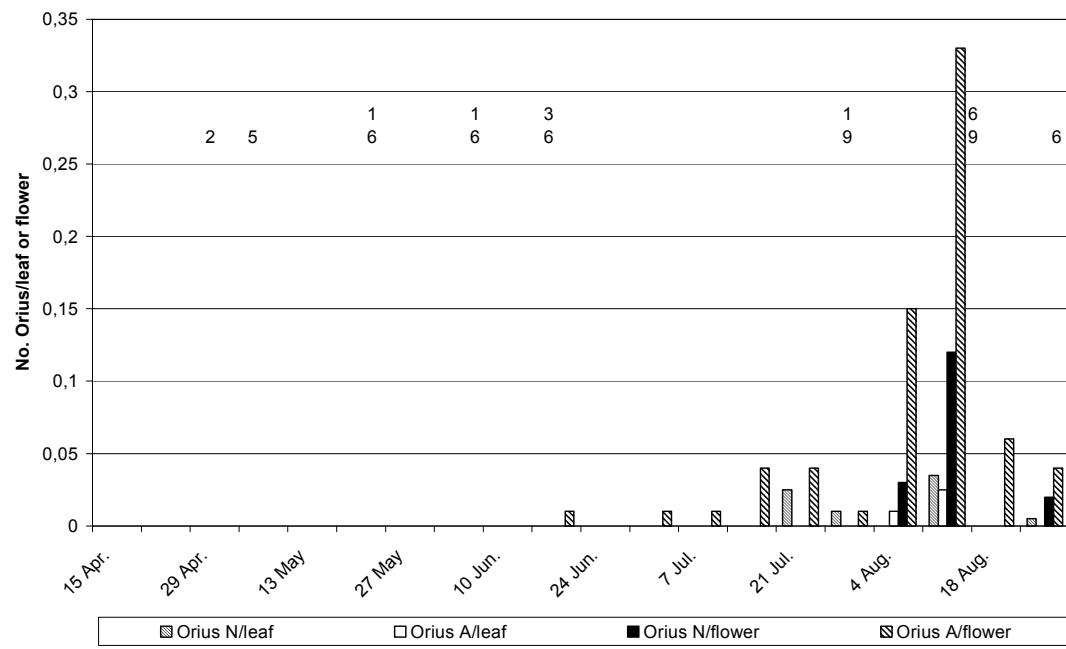
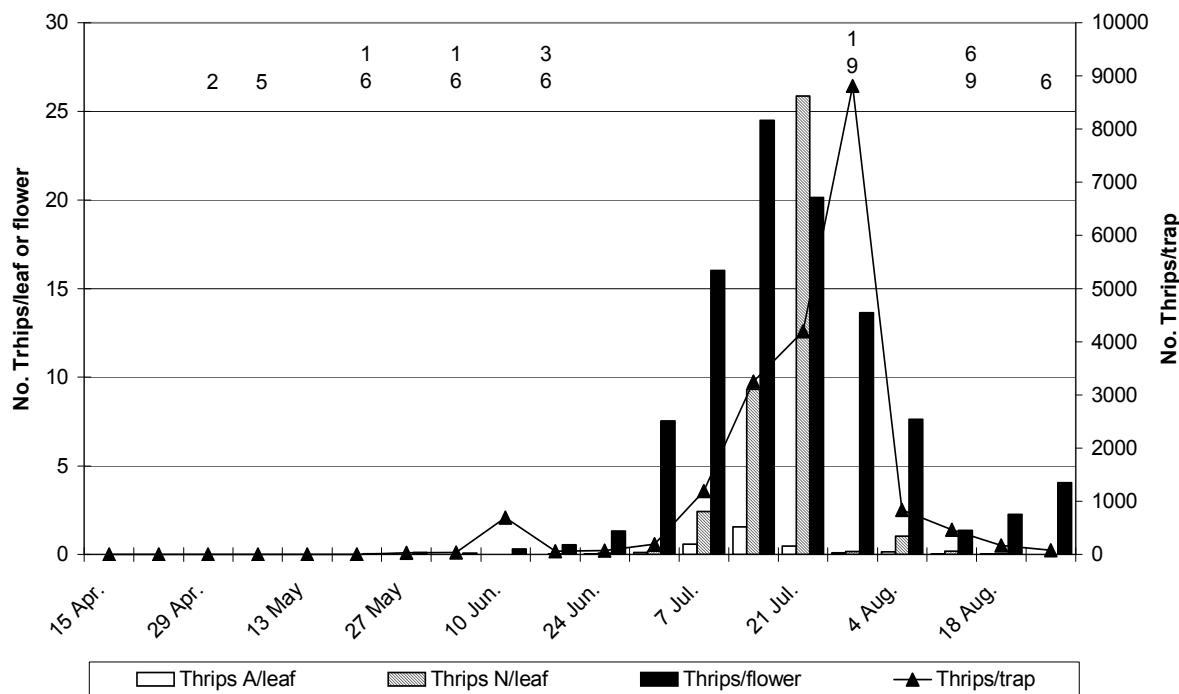
(a)



Enhancement of thrips control in protected eggplant crops by releases of the predator of *Orius laevigatus*.

Figure 3. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with insecticides. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina 1 = Methomyl; 2 = Pirimicarb; 3 = Heptenophos; 4 =Flualinate; 5 = Azinphos-methyl; 6 = Deltamethrin; 7 =natural pyretrum; 8 = Teflubenzuron; 9 =Azocyclotin

(a)

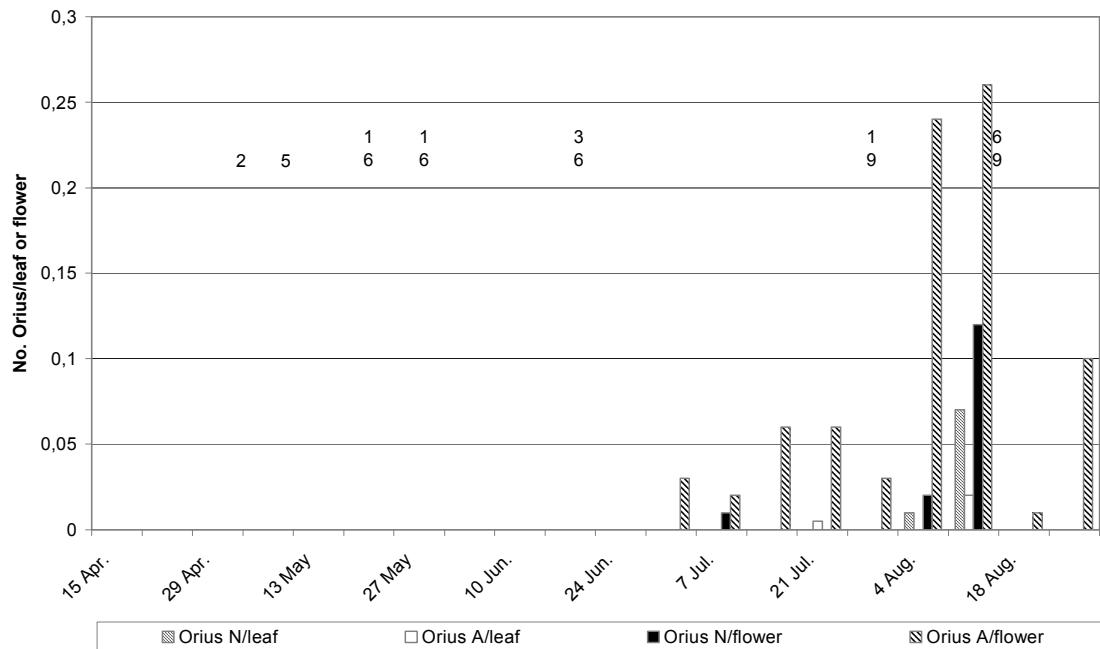
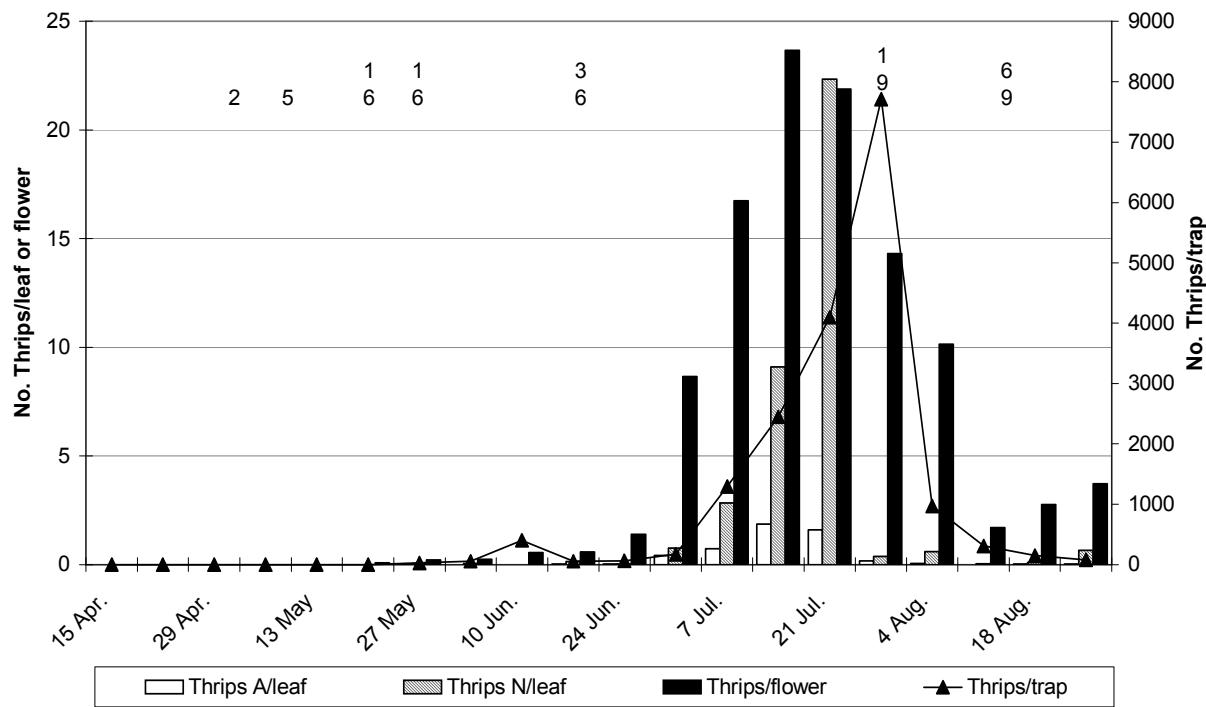


(b)

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Figure 4. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with insecticides. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina 1 = Methomyl; 2 = Pirimicarb; 3 = Heptenophos; 4 =Fluvalinate; 5 = Azinphos-methyl; 6 = Deltamethrin; 7 =natural pyretrum; 8 = Teflubenzuron; 9 =Azocyclotin

(a)

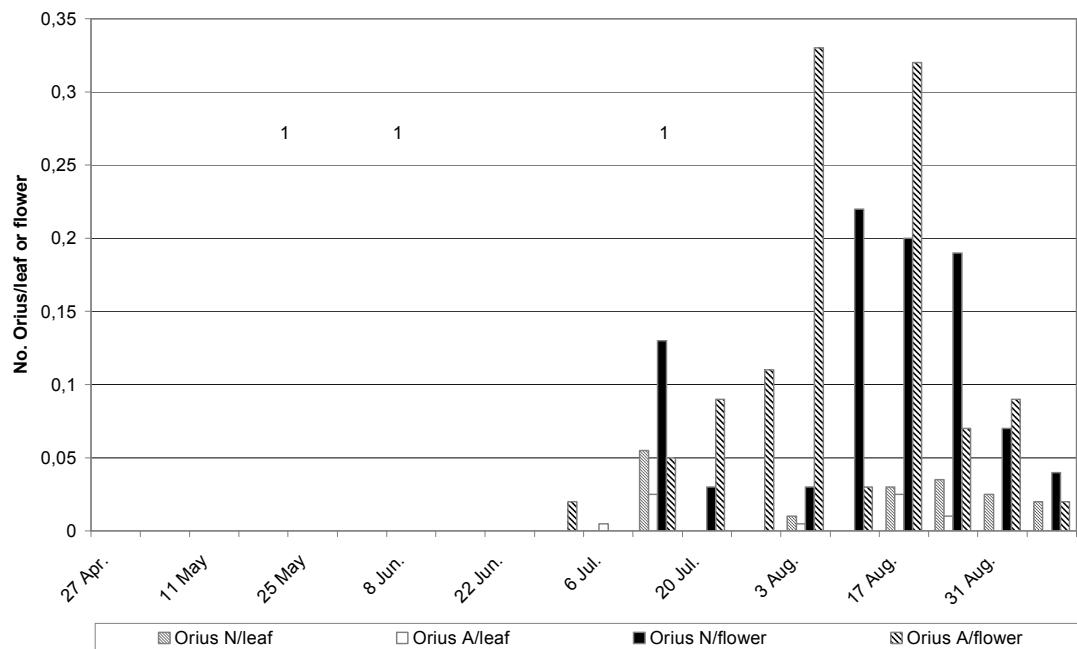
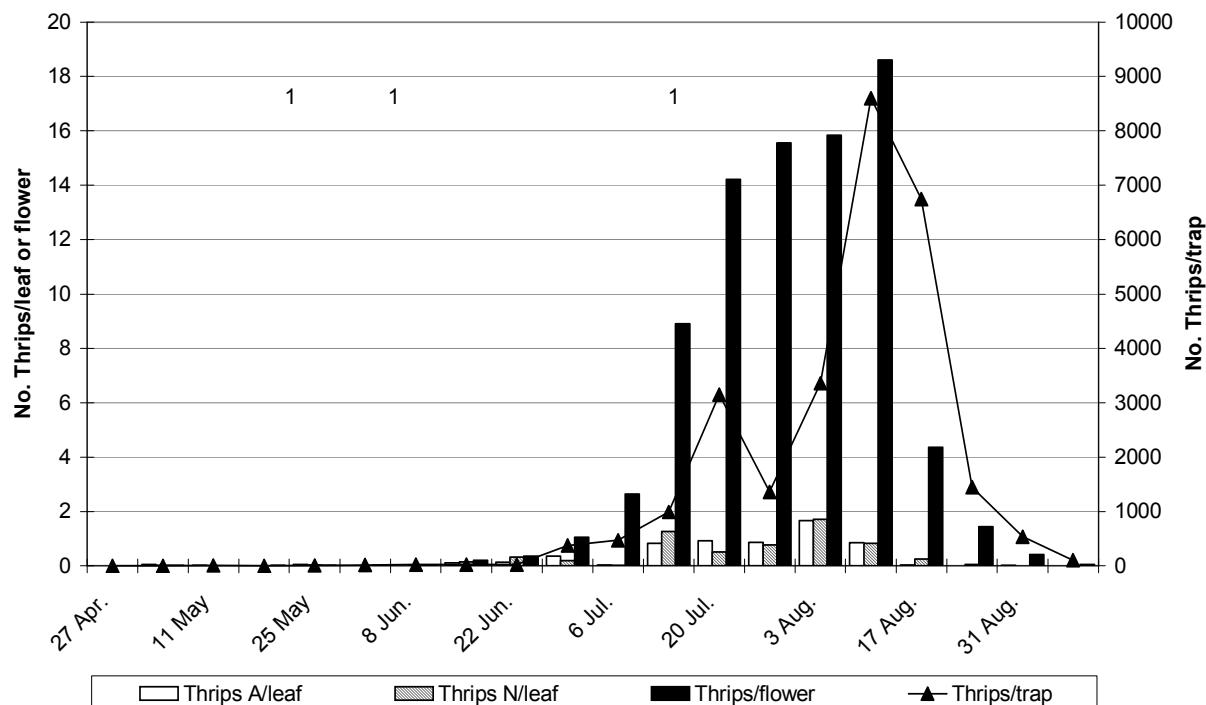


(b)

Enhancement of thrips control in protected eggplant crops by releases of the predator of *Orius laevigatus*.

Figure 5. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with insecticides. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina 1 = Methomyl; 2 = Pirimicarb; 3 = Heptenophos; 4 =Flualinate; 5 = Azinphos-methyl; 6 = Deltamethrin; 7 =natural pyretrum; 8 = Teflubenzuron; 9 =Azocyclotin

(a)

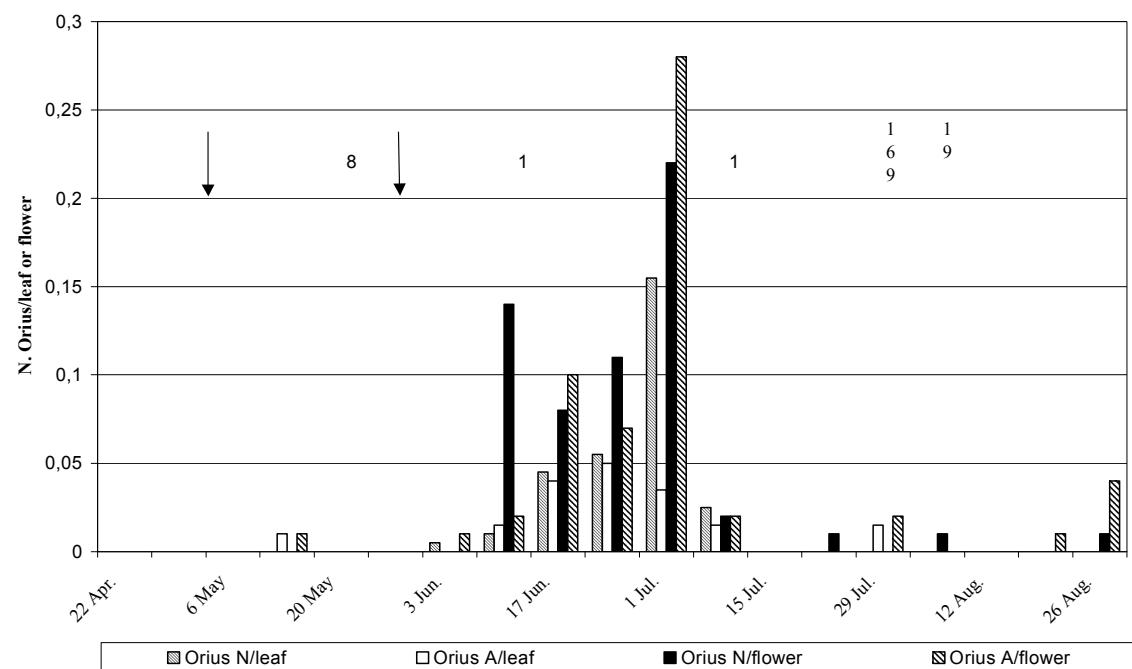
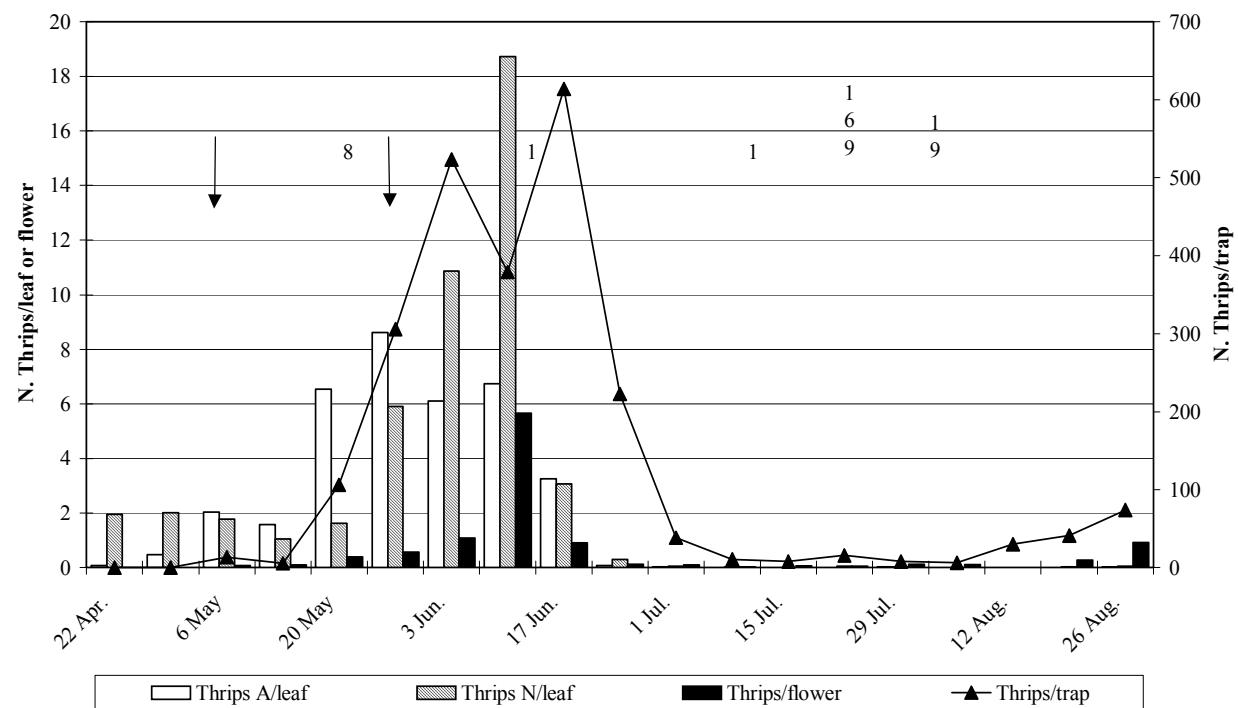


(b)

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Figure 6. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with natural enemies. Arrow indicates when *Orius laevigatus* was released. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina 1 = Methomyl; 2 = Pirimicarb; 3 = Heptenophos; 4 =Fluvalinate; 5 = Azinphos-methyl; 6 = Deltamethrin; 7 =natural pyretrum; 8 = Teflubenzuron; 9 =Azocyclotin

(a)

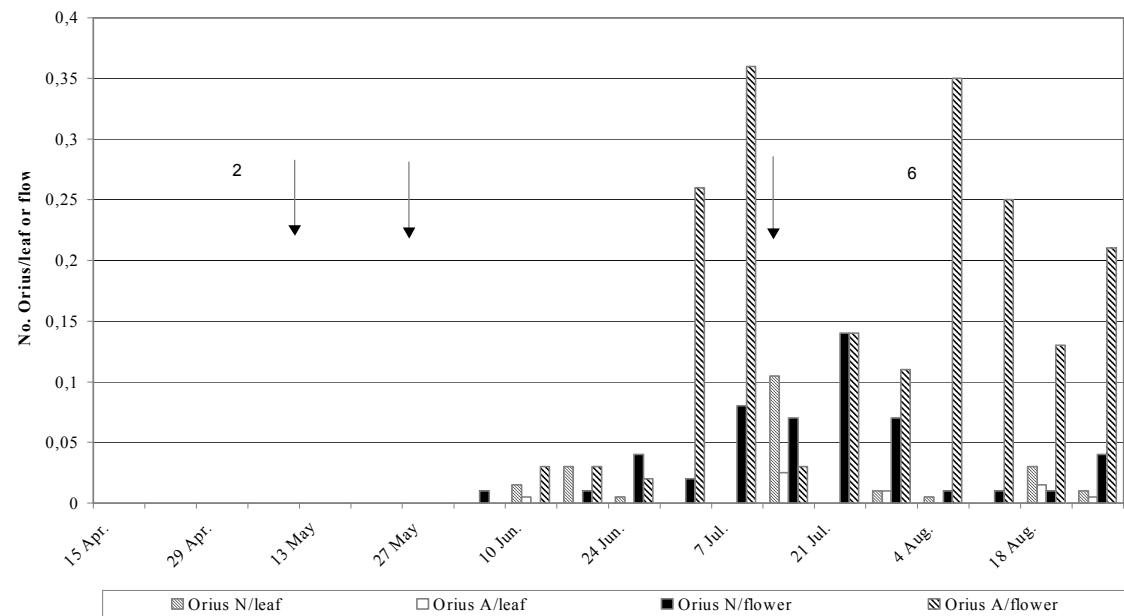
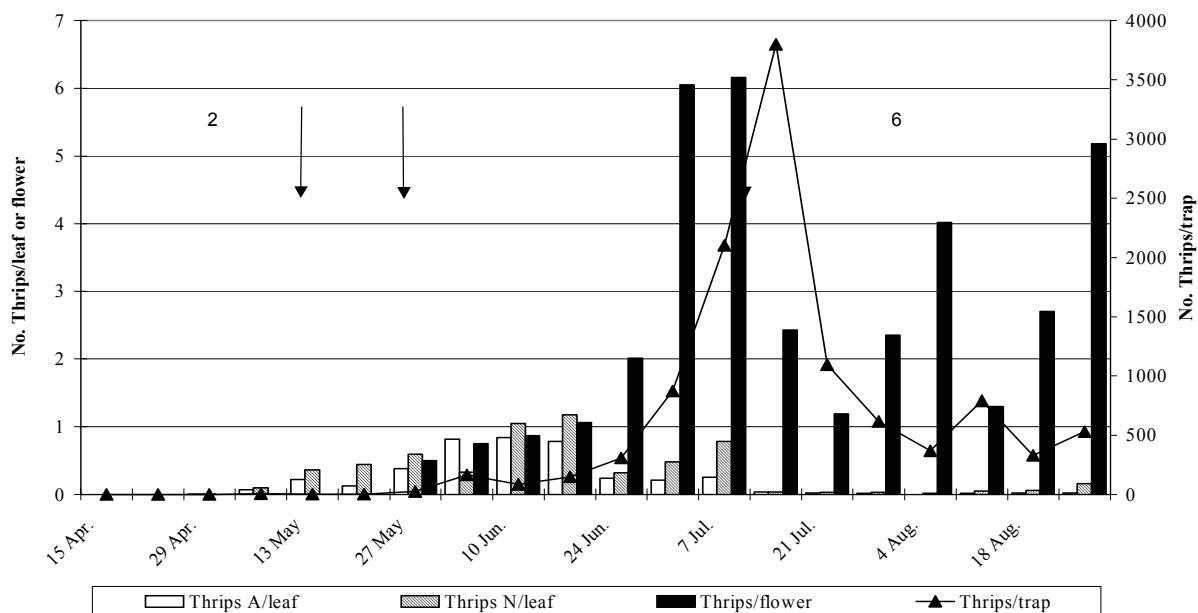


(b)

Enhancement of thrips control in protected eggplant crops by releases of the predator of *Orius laevigatus*.

Figure 7. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with natural enemies. Arrow indicates when *Orius laevigatus* was released. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina 1 = Methomyl; 2 = Pirimicarb; 3 = Heptenophos; 4 =Fluvalinate; 5 = Azinphos-methyl; 6 = Deltamethrin; 7 =natural pyretrum; 8 =Teflubenzuron; 9 =Azocyclotin

(a)

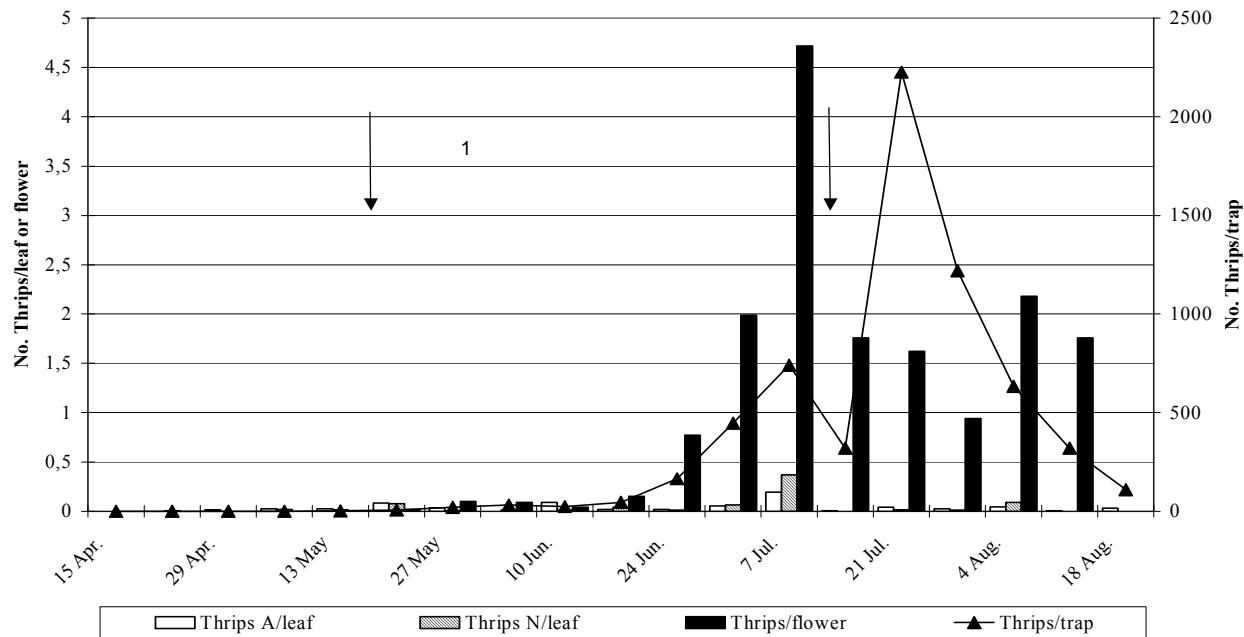


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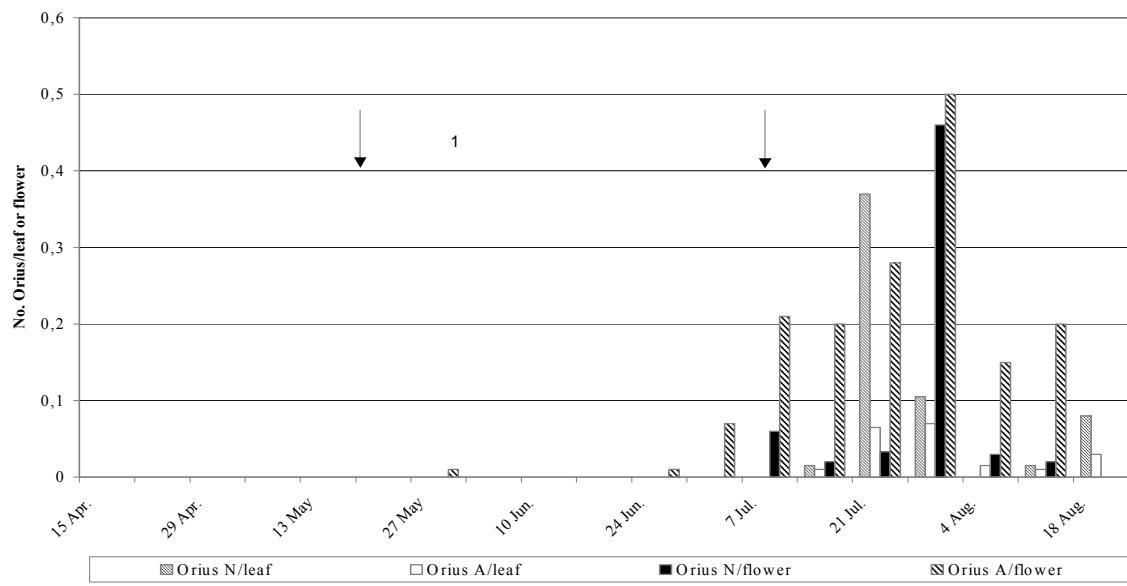
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Figure 8. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with natural enemies. Arrow indicates when *Orius laevigatus* was released. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina 1 = Methomyl; 2 = Pirimicarb; 3 = Heptenophos; 4 =Fluvalinate; 5 = Azinphos-methyl; 6 = Deltamethrin; 7 =natural pyretrum; 8 =Teflubenzuron; 9 =Azocyclotin

(a)



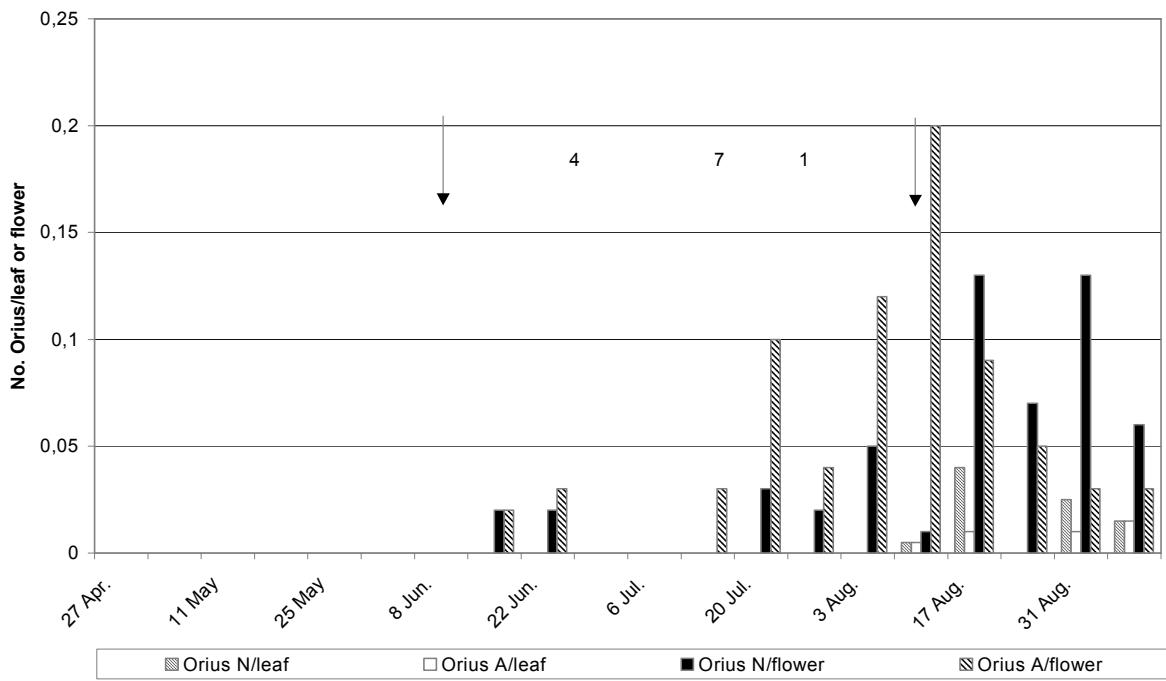
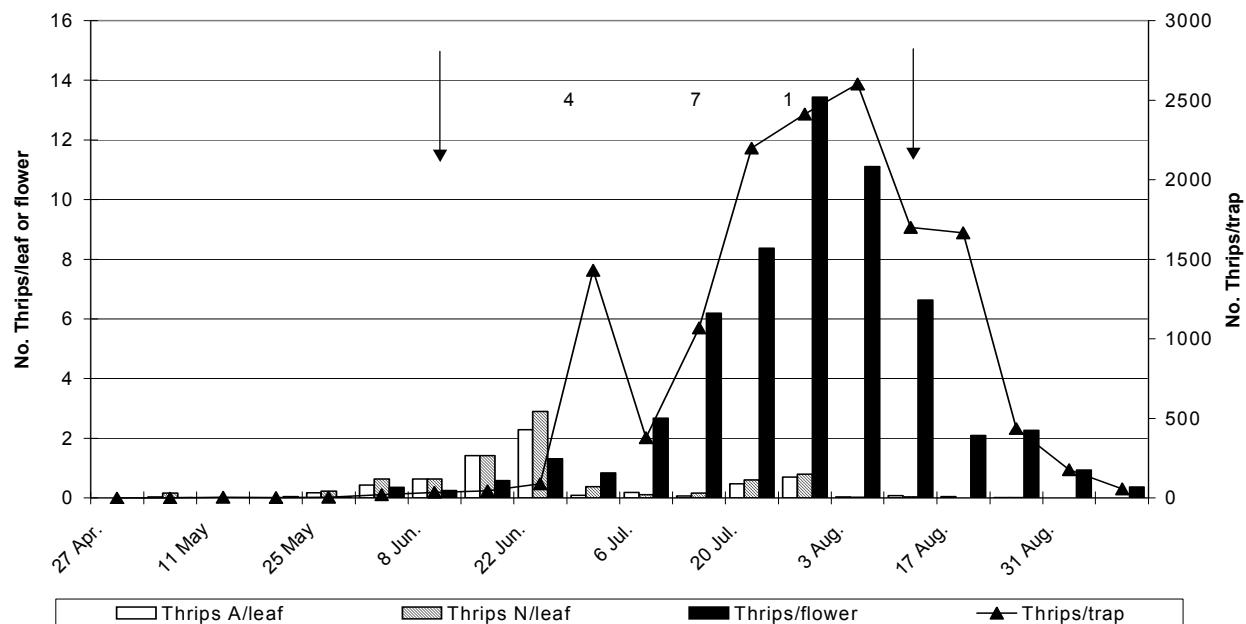
(b)



Enhancement of thrips control in protected eggplant crops by releases of the predator of *Orius laevigatus*.

Figure 9. Number of thrips per leaf/flower or trap (a) and number of *Orius* per leaf/flower (b) in tunnel where pests were controlled with natural enemies. Arrow indicates when *Orius laevigatus* was released. Legend of treatments: 1= Heptenophos; 2= Cyfluthrin; 3= Ciromazina 1 = Methomyl; 2 = Pirimicarb; 3 = Heptenophos; 4 =Fluvalinate; 5 = Azinphos-methyl; 6 = Deltamethrin; 7 =natural pyretrum; 8 =Teflubenzuron; 9 =Azocyclotin

(a)



(b)

6.4. Conclusions

At the start of the production cycle, the native *T. tabaci* was more abundant than the exotic *F. occidentalis*, but later the situation reversed in a few weeks and *F. occidentalis* became the dominant species. Part of the explanation of the strong dominance of *F. occidentalis* could be its resistance to most of the insecticides used in crop protection. Because of extensive pesticide resistance in this species, chemical control was inefficient. An additional negative effect of the frequent use of broad-spectrum insecticides is the disruption of natural control or the killing of released beneficial arthropods, including pollinators. Moreover, the continuous use of pesticides makes frequent harvest of the fruits of eggplant impossible.

As a result of the reduction in use of broad-spectrum insecticides in the IPM tunnels, adults of three species of *Orius* (*O. laevigatus*, *O. majusculus* and *O. niger*) were regularly able to colonise the tunnels, resulting in effective natural control of *F. occidentalis*. Similar results were also reported for eggplant in Italy by Chiappini (1993). Further *Orius* spp. were found to colonise open field strawberries in northern Italy, and were observed preying on *F. occidentalis* (Gambaro, 1995). González-Zamora *et al.* (1992, 1994) and Tommasini *et al.* (2001) observed that *Orius* spp. colonised protected strawberry in Spain and South Italy, respectively and Riudavets *et al.* (1995) observed *Orius* spp. colonising some vegetable crops in Spain.

The experiments with seasonal inoculative releases of mass-reared *O. laevigatus* described in this chapter show that this native predator can effectively control the exotic *F. occidentalis*. Control is particularly successful when releases start as soon as thrips are detected on the blue sticky traps or during visual checks of plants flowers, resulting in an early interaction between *Orius* and thrips at low population levels. *O. laevigatus* releases reduce the need of chemical treatments. However, the impossibility of controlling *A. gossypii* with natural enemies during these experiments, complicated the use of beneficial arthropods to control other pests. When broad-spectrum insecticides are used to control aphids, generally predators (including *O. laevigatus*) and parasitoids must be re-introduced, resulting in an increase of pest control costs. Recently effective natural enemies of the aphid *A. gossypii* have become available, the parasitoids *Lysiphlebus testaceipes* (Cresson) and *Aphidius colemani* Viereck, so a profitable IPM strategy can be adopted for eggplant crops.

Acknowledgements

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Chapter 7. SUMMARISING DISCUSSION

7.1 Introduction

The research described in this thesis was performed to develop biological control of *F. occidentalis* through the selection of an efficient beneficial arthropod. On the basis of available literature data, many arthropods were known to be natural enemies of thrips (chapter 1). They consist in general of predators, parasitoids and pathogens. Predators of thrips are mostly generalists and include Anthocoridae, Miridae, Syrphidae, Cecidomyiidae, Chrysopidae, Sphecidae, Araneida, Pseudoscorpiones and Thysanoptera (van Lenteren and Loomans, 1998). In addition to being carnivorous, some of these predators can also feed on plants and some others include in their diet some beneficial species. The best studied families of predators are the Anthocoridae and Phytoseiidae (*i.e.* *Neoseiulus* spp. and *Amblyseius* spp.), and these have shown good possibilities for thrips control. Parasitoids of thrips are specialists, and they all belong superfamily Chalcidoidea. The endoparasitoids of larvae (Eulophidae, *e.g.* *Ceranisus* spp. and *Thripobius semiluteus* Boucek) are the best studied and although they can parasitize a large amount of thrips, they are insufficient to prevent damage to a crop and the cost to mass produce them is too high to be acceptable from farmers. More than 15 species of entomopathogenic fungi have been found to infest thrips species. Among these fungi, *V. lecanii* is the best studied species and it can be used as additional control of thrips mostly in heated greenhouses, where high humidity guarantees the development of mycelium. *Steinernema* spp., *Heterorhabditis* spp. and *Thripinema* spp. are entomophilic nematods which can kill thrips, but the first two species are active only against the soil inhabiting thrips stage. *Thripinema* is not very well studied yet.

From the literature review it was concluded that predators have the best prospect for use in thrips biological control programmes. So research was directed towards the Anthocorid predators of the genus *Orius* (Rhyncota: Heteroptera), which seemed to be the most promising category of predators of *F. occidentalis*. Of the *Orius* genus, the most common species of the Mediterranean region of Europe were chosen as candidates for biological control of the exotic *F. occidentalis*. It is quite common, in fact, to find naturally occurring native natural enemies which exploit an exotic pest species (Ehler, 1990; Luck *et al.*, 1988) (Figure 7.1). Furthermore the use of native natural enemies may avoid negative effects of importation of exotic natural enemies on the native environment (Howarth, 1991). Earlier, *O. insidiosus* originating from North America was released in Europe against *F. occidentalis* in protected vegetable crops. Recently the potential risks due to its earlier introduction in Europe were evaluated, but the species had not established after release and risks were, therefore, evaluated as low (Lynch *et al.*, 2000; Tommasini *et al.*, 2003 - Erbic, EU project). It is currently considered a better procedure to first evaluate related endemic natural enemies for control of exotic pests in order to prevent risks caused by exotic biological control agents (van Lenteren *et al.*, 2003).

For evaluation of potential candidates the criteria defined by van Lenteren (1989) were used as a starting point. The criteria are:

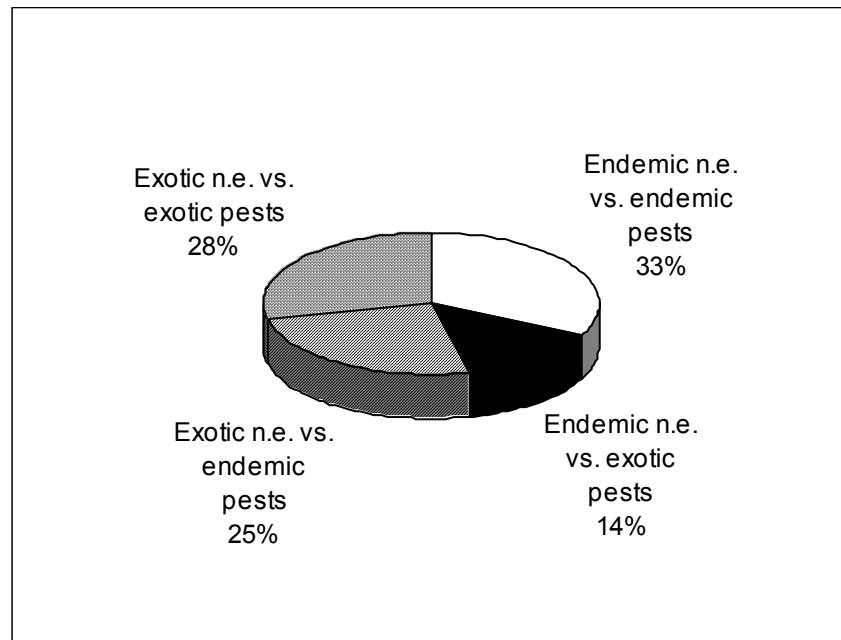
- Seasonal and internal synchronization with prey: the natural enemy has to be around when the pest occurs and the natural enemy has to be able to develop to the adult stage feeding on the pest species in order to have ongoing control;
- Climatic adaptation: the natural enemy has to be able to survive and reproduce in the climatic conditions in which it will be used for biological control;

- No negative effects: the natural enemy should not attack other beneficial organisms or non-target species;
- Good rearing procedures: this is essential for any inundative and seasonal inoculative release methods, because it determines the cost of the natural enemy and so the probability that it will be commercially applied;
- Prey specificity: it is important to introduce a natural enemy which strongly prefers to attack the pest species in order to obtain adequate pest control;
- Great prey kill potential: efficient predators should have a prey kill rate higher than the rate of population increase of the prey;
- Prey location capacity: efficient predators should be able to locate new prey patches quickly.

These general criteria were then used for developing the following specific criteria for *Orius* predators to be used in the Mediterranean situation:

- 1) is able to search effectively for thrips on different plant parts and on several economically important plant species;
- 2) can develop without entering diapause;
- 3) does not damage the plant;
- 4) has a strong preference for the pest species;
- 5) is able to survive at low prey density;
- 6) is compatible with the use of other natural enemies;
- 7) can be mass produced economically.

Fig. 7.1 Commercial biological control of endemic or exotic arthropods with endemic or exotic natural enemies (= n.e.) in Europe (modified from van Lenteren and Tommasini, 1999).



A criterion which I added to the list of van Lenteren (1989) is non-diapausing: natural enemies should preferably not show diapause during periods that the prey is still active. A specific aspect of my research was, thus, to look for predators that do not show diapause as they have to be released during winter and spring when thrips are active.

Another special aspect of this project was to develop ideas on how to evaluate the predation capacity (the prey kill rate) of all the combined predatory stages of *Orius*. For parasitoids it is relatively easy to determine the host kill rate because only adult parasitoids kill hosts. However, in *Orius* predators, both the nymphal stages and the adults are predators, but they consume very different numbers of preys.

The research findings described in the previous chapters will be summarized and discussed in the following sections.

7.2 Review on biology and pest status of thrips.

Aims of this review were (1) to obtain information on the present pest status of various thrips species in different crops in Europe, (2) to summarise thrips biology and injury and (3) to describe present thrips control methods (**chapter 1**).

The following thrips species are the most important pests in Europe: *F. occidentalis*, *T. tabaci*, *H. haemorrhoidalis*, *P. dracaenae*, *T. simplex*, *T. meridionalis*. The most serious problems are caused in vegetable and ornamental crops, although there is increasing damage recorded from fruit trees (e.g. table grape and nectarine). Thrips biology can be characterized as having a short developmental time (ca. 17.5 days at 25°C for *F. occidentalis*), a high reproduction (ca. 106 eggs/female and an r_m of 0.187 for *F. occidentalis*), and a wide host plant range (e.g. more than 240 host plants for *F. occidentalis*). Furthermore, some thrips species like *F. occidentalis* do not show diapause in mild and warm climates, and start to cause damage on plants early in the season. Thrips injury consists of direct and indirect damage. Direct damage is caused by feeding and oviposition. Thrips often prefer the younger parts of the plant for feeding e.g. flowers and sprouts. Many thrips species are vectors of harmful viruses thus causing indirect damage (i.e. *F. occidentalis* and *T. tabaci* transmit TSWV and INSV which are very harmful to vegetable and ornamental crops, respectively).

Control of thrips is still mainly with insecticides, but quick development of resistance and pesticide residues on the fruits are becoming a large obstacle to continue with this chemical control. Biological control of thrips seems well possible and good results have already been obtained with predatory mites and heteropteran bugs (i.e. *O. insidiosus* and *O. tristis* in the USA, and more recently, with indigenous *Orius* species in Europe).

One of the main difficulties of thrips control with natural enemies is the capability of thrips to transmit viruses. Despite this, a good natural enemy will be able to keep the thrips infestation at a low level, and thus to reduce the risk of virus transmission. Biological control will, however, only be acceptable in areas with low or no incidence of virus.

An extensive literature review of natural enemies of thrips indicated that *Orius* species might be good candidates for future biological control of thrips. In the following sections I describe the evaluation of *Orius* species as biological control agents of thrips.

7.3 Distribution of *Orius* species in Italy.

Extensive sampling of *Orius* species took place to determine which species were abundant on herbaceous plants, and on vegetable and ornamental crops in Italy (chapter 2). The host plant range of *F. occidentalis* in Europe found in literature is very large and includes both vegetable, ornamental and wild plants.

A collection of *Orius* spp. as potential candidates for biological control of WFT, was carried out in many Italian regions, including greenhouse crops and open field crops infested by *F. occidentalis*. Samples of *Orius* species were collected along all Italy in the main areas where vegetable and ornamental crops are cultivated. All the specimens collected were eventually reared and then identified in laboratory. Predators belonging to the genus *Orius* were collected in Italy on 18 species of vegetable crops, 10 species of ornamental crops, tobacco, prickly pear and 6 species of wild plants. During a four years survey, 518 samples were collected and 4,931 adults were identified, which comprised 6 *Orius* species, *O. laevigatus*, *O. majusculus*, *O. niger* and less common *O. horvathi*, *O. vicinus* and *O. pallidicornis* which is a phytophagous species.

Similar collection studies were carried out along the North-eastern coast of Spain by Goula *et al.* (1993) and Riudavets and Castañé (1994). A general survey on *Orius* spp. distribution in Europe was first described by Péricart (1972). Many authors provided information on *Orius* distribution in specific areas in South Europe (González Zamora *et al.*, 1992; Gargani, 1993; Vacante and Tropea Garzia, 1993; Vacante, 1993; Chambers *et al.*, 1993; Frescata and Mexia, 1993; Tavella *et al.*, 1994; Ivancich Gambaro, 1995; Barbetaki *et al.*, 1999).

Orius species were rarely found on tomato, but also *F. occidentalis* does not occur on high densities on this plant, as was observed as well in Spain (Riudavetes and Castañé, 1994). *O. laevigatus* showed to be the most abundant species in Italy (57.9% of the predatory *Orius* species collected) and a similar result was obtained in Spain and Greece (Riudavetes and Castañé, 1994; Lycourressis and Perdikis, 1997; Barbetaki *et al.*, 1999), indicating a dominance of *O. laevigatus* in the Mediterranean basin.

The sampled *Orius* species showed different geographic areas of occurrence: *O. niger* was very common in all the Italian regions; *O. laevigatus* was frequently found in central and southern regions (in Ligury and Sicily it was the most abundant), but it was rarely found in the northern regions; *O. majusculus* decreased in relative abundance from northern to central Italy, and was absent below 38° N latitude. The distribution map of predators (see chapter 2) indicates that *O. laevigatus* is the predominant species in the warmest areas, *O. majusculus* in the coldest areas, while *O. niger* appears to be able to develop well under all Italian climatic conditions.

Despite the fact that some releases of *O. insidiosus* from commercial insectaries were carried out in South Italy in the early nineties, *O. insidiosus* was never found during my recent sampling. However, another predator that was commercially released during the early nineties, *O. albifrons*, was found back (ca. 20% of a sample of ca. 2000 individuals) during my sampling in Sicily.

The survey indicates that among the indigenous species, *O. niger* and *O. laevigatus* are well adapted to the Mediterranean area which may make them good candidates for biological control of thrips.

7.4 Measurement and comparison of biological parameters of several *Orius* species.

The next phase of the PhD project consisted of studying the main biological characteristics of four *Orius* species (*O. majusculus*, *O. laevigatus*, *O. niger* and *O. insidiosus*) and their predatory capacity on two prey species (*F. occidentalis* adults and *Ephestia kuehniella* eggs) (chapter 3).

All *Orius* species were able to develop and reproduce on both prey species, although predators showed greater longevity and higher reproduction on *E. kuehniella* than on *F. occidentalis*. *O. niger* was difficult to rear, confirming results of van Schelt (1993). It showed high nymphal mortality, a high consumption of *E. kuehniella* eggs, a low predation of *F. occidentalis* adults, a long development time, a low fecundity and a low r_m on both preys. *O. majusculus* and *O. laevigatus* showed a similar development time when feeding on *F. occidentalis*. The predation on *E. kuehniella* eggs was higher for immature stages of *O. laevigatus* than for *O. majusculus* (174.6 vs. 99.4). Fecundity of *O. laevigatus* was lower than that of *O. majusculus* on the factitious prey (118.6 vs. 174.0 eggs/female), but no differences were found when both species were fed *F. occidentalis* adults. The exotic *O. insidiosus* showed similar results as *O. laevigatus* and *O. majusculus*. The species of prey used as food influenced the biology of the predator a lot, and this is confirmed by many authors (e.g. Isenhour and Yeargan, 1981; Kiman and Yeargan, 1985; Zaki, 1989; Bush *et al.*, 1993; Alvarado *et al.*, 1997): the development time of *Orius* species was, for example, much faster on *F. occidentalis* than on *E. kuehniella*.

The main biological traits studied (development time, mortality, sex ratio, female lifespan, fecundity and predation of *F. occidentalis* by each *Orius* species) were used to determine the intrinsic rate of natural increase (r_m) and the kill rate (k_m) of each species. For r_m I used Southwood's (1966) formula: $r_m = \ln R_0/T$, where R_0 is the net reproductive rate and T is the generation time. For the kill rate (k_m) I developed the formula $k_m = \ln K_0/T_k$, where K_0 is the number of prey killed during both the nymphal and adult stages and T_k is the generation time. The results are summarised in table 7.1.

Table 7.1 Intrinsic rate of natural increase (r_m) and the kill rate (k_m) of four *Orius* species on two prey species (adults of *F. occidentalis* and *E. kuehniella* frozen eggs).

	r_m		k_m
	<i>F. occidentalis</i>	<i>E. kuehniella</i>	<i>F. occidentalis</i>
<i>O. laevigatus</i>	0.094	0.068	0.23
<i>O. majusculus</i>	0.097	0.080	0.21
<i>O. niger</i>	0.035	-0.003	0.19
<i>O. insidiosus</i>	0.116	0.101	0.25

The data obtained indicate that *O. insidiosus*, *O. laevigatus* and *O. majusculus* are the species that better fit some of the criteria listed for a good natural enemy than *O. niger*. But these characteristics were recorded under laboratory conditions and it is also important to

observe how these predators perform in the field, before drawing final conclusions about their efficiency.

The data in table 7.1 indicate that *O. insidiosus* might be the most efficient thrips predator because of its high value for the kill rate. However, currently exotic polyphagous species of natural enemies are no longer preferred for import and release, because of their potentially negative effects on non-target species (van Lenteren *et al.*, 2003). Therefore, we choose to evaluate the effectiveness of the indigenous species *O. laevigatus* for control of *F. occidentalis*.

7.5 Determination of the existence of diapause in *O. laevigatus*.

The effect of photoperiod, as well as its interaction with temperature on the life cycle of *O. laevigatus* was studied, in order to determine the existence of diapause in this species (**chapter 4**). Diapause is a biological phase which occurs in many arthropods in order to survive when unfavourable seasonal conditions are present, even though not all forms of seasonal adaptations are associated with diapause (Mansingh, 1971; Hodek, 1973; Beck, 1980; Tauber *et al.*, 1986; Danks, 1987; Leather *et al.*, 1993). The phenomenon of diapause was earlier studied for several *Orius* species, *e.g.* *O. insidiosus*, *O. majusculus*, *O. tristiscolor*, *O. albipennis*, *O. sauteri* and *O. tantillus* (Motschulsky) (Ruberson *et al.*, 1991 and 1998; Gillespie and Quiring, 1993; van den Mairacker, 1994; Yano, 1996; Nakashima and Hirose, 1997). All Anthocoridae species studied overwinter as adult. The species which undergo diapause (*O. insidiosus*, *O. tristiscolor* and *O. majusculus*) show reproductive diapause as a result of photoperiodic stimuli. Since a considerable variability in diapause responses was observed in *Orius* species, it may provide an excellent source of material for selecting non-diapausing strain.

Few data were available from existing literature on the presence of diapause in *O. laevigatus*. The presence of reproductive diapause in this palearctic species was therefore investigated in the laboratory using two strains: strain N collected in northern Italy (Po Valley; ca. 44° N latitude) and strain S collected in southern Italy (Sicily; ca. 37° N latitude). The influence of photoperiod on eggs at 18±1°C, RH=75±10% and at several light regimes varying between 16L:8D and 8L:16D, and later between 13L:11D and 11L:13D was studied. Further, *O. laevigatus* was reared at five temperature regimes (24°C/12.5°C; 26°C/15°C; 21.5°C/6°C; 22°C/12.5°C; 18°C constant) that matched the photoperiod which induced the lowest oviposition (11.5L:12.5D). To confirm the laboratory data, wild populations of *O. laevigatus* were collected in the field in August-November on Sicily and in the Po Valley. Both wild populations were maintained in cages in the field in northern Italy (44° latitude N). During the winter, once a month some females were taken from the field cages and put into a climatic chamber at 26±1°C, RH 75±10%, for checking fertility.

Developmental time, adult emergence, sex ratio, pre-ovideposition period, fecundity were recorded. Photoperiods of 11.5L:12.5D and 12L:12D induced a longer development time, a longer pre-oviposition period and a lower oviposition rate than the other photoperiods for both populations. The percentage of egg-laying females at 18°C was higher for strain S (70%) than for strain N (44%). Termination of diapause was investigated by an increase in temperature and day-length (26°C, 16L:8D). The result was that females of both strains supposedly in diapause, rapidly started to lay a high amount of eggs independently from the environmental conditions to which they were previously exposed.

When the influence of thermoperiods on *O. laevigatus* were analyzed, the longest development time was found for both strains at 26.5°C/6°C and the shortest at 26°C/15°C. A constant temperature of 18°C induced a slightly shorter development than the thermoperiod of 26.5°C/6°C in both populations. The lowest fecundity was recorded at 26.5°C/6°C and at 18°C constant for both strains, and 26°C/15°C induced the highest fecundity in the females of strain N. When the females were moved from different thermoperiods and short-day photoperiod to 26°C and 16L:8D, oviposition did increase, and more than 80% of females of both strains laid eggs. In all the experiments the two populations of *O. laevigatus* gave, in general, different results.

One of the main results observed are the differences recorded between the northern and the southern strains of *O. laevigatus*, allowing to define them as different ecotypes or strains. The northern strain showed a high intraspecific variability in response to the same environmental conditions

In the experiment carried out with wild populations of *O. laevigatus*, a high percentage of females laid eggs, particularly of the Sicilian population, while part of the females of strain N where in reproductive diapause during November. However, their diapause could be considered rather short because the percentage of egg-laying females increased a lot just a month later. The southern strain showed no evident response to the photoperiod, indicating that predators can overwinter in quiescence or in weak diapause (Tommasini and Nicoli, 1995; 1996). Therefore, it seems that strains collected at low latitudes can remain active also during the short-daylength period, if temperature is high enough (Chambers *et al.*, 1993). Moreover, the natural distribution of *O. laevigatus* in areas with marine influence (Péricart, 1972) and the good performance at high temperatures (Alauzet *et al.*, 1994) partly explains the effectiveness of this species also during the hot season in both the Mediterranean area and North Europe.

In conclusion, the two strains of *O. laevigatus* have a different way to overwinter: part of the northern population undergoes a weak reproductive diapause, while the southern strain overwinters in quiescence.

The presence or lack of diapause is an important criterion to select a good natural enemy, mainly when the pest can overwinter without undergoing diapause. This is true for both predatory insects and mites. For example, when diapausing strains of *Amblyseius* (= *Neoseiulus*) *cucumeris* (Oudemans) were released in winter or early in spring, they were not successful in controlling WFT (van Houten and van Stratum, 1993). The current project shows that strain S of *O. laevigatus* could be used effectively in autumn, winter or early in spring against *F. occidentalis*, because it starts to develop and reproduce at similar environmental conditions at which the pest species is active.

7.6 Evaluation of the efficacy of *O. laevigatus* against thrips pests under practical conditions.

The efficacy of the pirate bug *O. laevigatus* to control thrips was investigated in the Po Valley in northern Italy in two protected crops, sweet pepper and eggplant (**chapter 5 and 6**). Seasonal inoculative releases of *O. laevigatus* were carried out in 7 IPM (Integrated Pest Management) sweet pepper tunnels during two years and in 4 IPM eggplant tunnels during three years. During the experiments, 4 tunnels where chemical control was applied were sampled and served as control. In the IPM tunnels, a blend of nymphs and adults of *O. laevigatus* in a ratio of about 3:2, were released by scattering 1-3 predators per m² on the

leaves when the threshold of 2 thrips per flower or 4 thrips per leaf was exceeded on eggplant, and when thrips were seen on sweet pepper. Sampling was carried out by blue sticky traps and by visual counting of thrips on flowers and leaves. In both crops, blue sticky traps gave useful information about thrips presence and helped to determine the start of release of predators. They are, however not a reliable monitoring system for thrips during the whole production cycle of these crops. Thrips were rarely found on leaves of sweet pepper, while on egg-plant thrips are present on both leaves and flowers. Sampling on flowers is the best method to follow development of thrips populations. However, sampling on flowers is a rather laborious method, so a simpler but still reliable method was developed for sweet pepper. Because of the high index of aggregation of thrips found on sweet pepper (Taylor's power law (Taylor, 1961; 1984) and the Gerrard and Chaing (1970) regression) it is possible to calculate the thrips infestation level on sweet pepper, based on the proportion of non-occupied flowers. This presence-absence method of thrips sampling in flowers is more practical and saving a lot of time, compared to counting thrips.

On both vegetable crops two thrips species were found: *F. occidentalis* and *T. tabaci*. At the beginning of the production cycle in May, the native *T. tabaci* was more abundant than the exotic *F. occidentalis*, but later the situation reversed and *F. occidentalis* became the dominant species in August. Early releases of *O. laevigatus* after thrips appear on flowers and/or on traps, resulted in a good establishment of the predators and showed that this native predator can effectively control the exotic *F. occidentalis*.

On both sweet pepper and eggplant crops, natural control by immigrating wild *Orius* species (*O. laevigatus*, *O. niger* and *O. majusculus*) was in some cases enough to reduce the thrips population. Implementation of IPM on eggplant is difficult due to several other arthropod pests that attack this crop. The main problem was to control *Aphis gossypii* where chemical control was applied because no efficient natural enemies were available at the time of these experiments. This resulted also in the killing of *Orius* predators, and in an increase of the thrips population. In these situations additional releases of *O. laevigatus* were necessary, resulting in increasing costs of pest control. Wild *Orius* populations entering the protected crops later in the season were still able to sufficiently reduce thrips populations. When thrips infestations are not high and wide-spectrum insecticides are not used, natural control by immigrating indigenous *Orius* species is very effective and prevents thrips outbreaks. Use of wide-spectrum insecticides disrupts natural control. This result was recorded also by Chiappini (1993) on egg-plant, and by Gonzàles-Zamora *et al.* (1992; 1994) and Gambaro (1995) on strawberry.

That *O. laevigatus* appears to control thrips effectively and is suitable to be released in combination with natural enemies used for control of other pests, was confirmed also by other authors (Brødsgaard and Enkegaard, 1995; Wittmann and Leather, 1997). Rubin *et al.* (1996) found *O. laevigatus* to be less effective to control thrips on sweet pepper in Israel compared to the phytoseid *Iphiseius (Amblyseius) degenerans* Berlese. However, in many European countries *O. laevigatus* appears the most suitable natural enemy for thrips control on many vegetable crops (Chambers *et al.*, 1993; Dissevelt *et al.*, 1995; Tavella *et al.*, 1991, 1994, 1996; van de Veire and Degheele, 1997; Sàncchez *et al.* 2000; Tommasini *et al.*, 2001).

For successful thrips control by *O. laevigatus*, sampling and precise timing of releases is most important. Early releases of the pirate bugs as soon as thrips are detected, is resulting in early establishment of the predator and in a good interaction between prey and predator at low population densities. *O. laevigatus* is able to develop over a large range of temperature, but, when the average temperature is below 14°C, its efficacy is low.

7.7 The future of thrips control by *O. laevigatus*.

The conclusion that *O. laevigatus* is currently the best natural enemy for biological control of thrips on vegetable crops in Europe is based on the following reasons:

- indigenous origin of the species;
- good natural distribution in the main areas in which vegetable crops are cultivated and where *F. occidentalis* is a major risk;
- feasibility to be economically mass-reared under artificial conditions;
- high kill rate (k_m) compared to that of other indigenous *Orius* species;
- presence of a non-diapausing strain that can be released on crops also early in spring;
- proven efficiency of thrips control in protected crops at low prey density;
- does not damage the plant;
- is compatible with the use of other natural enemies.

Thrips are still a big problem on many crops. For protected crops, biological control is possible using *O. laevigatus*, but control remains a problem in open field vegetables and fruit crops. The use of *Orius* on vegetable crops in the field is generally too expensive. In this case thrips control might be more feasible with microbials like fungi. For fruit crops the problem is even more difficult to solve, because of the following variables: the period of the infestation, the plant organs attacked, and the thrips species which causes the damage. *O. laevigatus* is a species that typically occurs on herbaceous plants, so its use on fruit trees seems unfeasible. *Orius* species with a preference for (fruit) trees have not yet been studied. Furthermore some fruit crops are attacked very early in the season, e.g. nectarine during blooming, when hardly any *Orius* are available in nature under Italian conditions.

Due to the resistance of many thrips species to pesticides, chemical control of these pests is always difficult on fruit crops, and particularly on organically grown nectarine, plum and grape crops. For this reason it is very important to focus the attention of future research on a solution of biological control of thrips on fruit crops, by studying predators of thrips that occur on trees.

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Summary

The overall aim of this research was to develop a biological control programme for *F. occidentalis* through the selection of an efficient beneficial arthropod.

First, a general review of the literature about thrips pest species in Europe and in particular of *Frankliniella occidentalis* (Perg.) (Western Flower Thrips) was made. Information regarding the biology, distribution, host plants of thrips and damage induced by this pest species were discussed and summarized. The main candidates as natural enemies for control of thrips emerging from this literature study and from an evaluation of all present data, were Anthocoridae, and, thus, further research was directed towards Anthocorid predators of the genus *Orius* (Rhyncota: Heteroptera) (**chapter 1**).

Next, of the genus *Orius*, the most common species of the Mediterranean regions of Europe were chosen as candidates for biological control of *F. occidentalis*. *Orius* predators were collected in several areas in Italy on 36 plant species infested by thrips. The most common species were *O. niger* Wolff, *O. laevigatus* (Fieber) and *O. majusculus* (Reuter). No clear host-plant preferences of these *Orius* species were recorded (**chapter 2**).

Consequently, biological characteristics and predation activity of four *Orius* species (the paleartic *O. majusculus*, *O. laevigatus* and *O. niger* and the neartic *O. insidiosus*, an exotic species that was earlier released in Italy) were determined by laboratory experiments using two prey species: *Ephestia kuehniella* (Zell.) eggs and *Frankliniella occidentalis* adults. Preimaginal mortality, development time, sex-ratio, pre-oviposition period, longevity, fecundity, and predation during the instar stages and the adult stage were measured. The intrinsic rates of natural increase (r_m) and the kill rates ($k_m = \ln k_0/t_k$) for all four *Orius* species was determined. The k_m was 0.23 for *O. laevigatus*, 0.21 for *O. majusculus*, 0.25 for *O. insidiosus*, 0.19 for *O. niger*, respectively. In all species, the females that fed on *E. kuehniella* showed greater longevity and higher reproduction than those fed on *F. occidentalis*. Most data for the neartic *O. insidiosus* were similar to those of *O. laevigatus* and *O. majusculus*. Mass rearings of *O. insidiosus*, *O. laevigatus* and *O. majusculus* were successfully developed, while *O. niger* appeared difficult to rear. Based on these data, it was concluded that *O. laevigatus* might be the best candidate for control of thrips (**chapter 3**).

No data were available about the occurrence of diapause in *O. laevigatus*. As thrips pest occur early in the season, it is important to use natural enemies that do not go into diapause. The possibility of inducing a reproductive diapause in this palearctic species was therefore investigated in the laboratory using two strains: strain N collected in northern Italy (Po Valley) and strain S collected in southern Italy (Sicily). The influence of photoperiod on *Orius* eggs was studied. Development time, adult emergence, sex ratio, pre-oviposition period, fecundity, and the presence of mature oocytes were recorded.

The two strains of *O. laevigatus* showed to have a different way of overwintering: in the northern strain part of the population undergoes a weak reproductive diapause, while for the southern strain overwintering could best be described as quiescence (**chapter 4**).

Finally, the capacity of *O. laevigatus* to control thrips pests (*F. occidentalis* and *T. tabaci*) was studied by releases of this predator in two vegetable crops in commercial greenhouses, sweet pepper and eggplant. The releases of the pirate bugs were made as soon as thrips were detected, resulted in early establishment of the predator, in an interaction between prey and predator at low population densities and often in sufficient control of the pest (**chapter 5 and 6**).

In conclusion, the southern Italian strain of *O. laevigatus* showed to be an efficient natural enemy of thrips and *F. occidentalis*. This natural enemy is currently produced and

commercially used on large scale in Europe to control thrips species in vegetable and ornamental crops, mostly in protected crops (**chapter 7**).

Riassunto

Lo scopo principale di questa ricerca è stato lo sviluppo del controllo biologico di *Frankliniella occidentalis* attraverso la selezione di un efficiente entomofago.

Nel **capitolo 1**, viene descritto quanto rilevato dalla letteratura esistente sui tripidi fitofagi in Europa e particolarmente su *Frankliniella occidentalis* (Perg.) (Western Flower Thrips). Le informazioni riassunte riguardano gli aspetti biologici dei tripidi, la loro distribuzione, le piante ospiti ed i danni indotti da questi fitofagi. Dalla ricerca bibliografica eseguita e da una attenta valutazione di questa, emerge che i principali nemici naturali dei tripidi sono i predatori Anthocoridi. Conseguentemente le successive ricerche sono state mirate sugli Anthocoridi del genere *Orius* (Rhyncota: Heteroptera).

Sono state quindi scelte come candidate per il controllo di *F. occidentalis* le specie più comuni del genere *Orius* presenti nelle regioni mediterranee europee. La raccolta dei predatori è stata eseguita in quasi tutte le regioni italiane su 36 specie vegetali infestate dai tripidi. Le specie più comuni sono risultate *O. niger* Wolff, *O. laevigatus* (Fieber) e *O. majusculus* (Reuter). Non è stata individuata nessuna particolare preferenza fra pianta e ospite (*host-plant*) ossia *Orius* spp. (**capitolo 2**).

Successivamente sono state studiate in laboratorio le caratteristiche biologiche e di predazione di 4 specie di *Orius* (le paleartiche *O. majusculus*, *O. laevigatus* e *O. niger* e la neartica *O. insidiosus*, una specie esotica rilasciata precedentemente in Italia). Due prede sono state impiegate a confronto: uova congelate di *Ephestia kuehniella* (Zell.) e adulti vivi di *F. occidentalis*. Sono stati rilevati i dati sulla mortalità preimmaginale, i tempi di sviluppo, la sex-ratio, la pre-ovideposizione, la longevità, la fecondità e la predazione sia degli stadi giovanili che degli adulti su entrambe le prede. E' stato inoltre calcolato il tasso intrinseco di crescita (intrinsic rates of natural increase) (r_m) ed il tasso di predazione (kill rate) ($k_m = \ln k_0/t_k$) per tutte e 4 le specie di *Orius*. Il k_m è risultato pari a 0.23 per *O. laevigatus*, 0.21 per *O. majusculus*, 0.25 per *O. insidiosus* e 0.19 per *O. niger*. In generale tutte le femmine alimentate con *E. kuehniella* hanno mostrato una maggior longevità e fecondità rispetto a quelle alimentate con *F. occidentalis*. *O. insidiosus* ha mostrato di essere simile biologicamente a *O. laevigatus* e *O. majusculus*. E' stato anche sviluppato l'allevamento massale delle specie *O. insidiosus*, *O. laevigatus* e *O. majusculus*, mentre l'allevamento di *O. niger* è risultato difficile. Sulla base dei dati raccolti si è concluso che *O. laevigatus* poteva essere la miglior specie candidata per il controllo dei tripidi (**capitolo 3**).

Siccome i tripidi compaiono precocemente in primavera, è importante impiegare nemici naturali che non presentino diapausa. A seguito dell'assenza di informazioni sulla presenza di diapause nella specie *O. laevigatus*, si è ritenuto opportuno indagare su questo aspetto, valutando la possibilità di indurre diapause riproduttiva su questa specie paleartica attraverso esperimenti di laboratorio. A tal fine sono stati studiati 2 ceppi di *O. laevigatus*: il ceppo N, raccolto in Nord Italia (Valle del Po) ed il ceppo S, raccolto in Sud Italia (Sicilia). L'influenza del fotoperiodo è stata studiata a partire dalle uova di *Orius*. Nelle varie condizioni sperimentali sono stati rilevati i dati sui tempi di sviluppo, sulla percentuale di sfarfallamento, sulla sex ratio, sul periodo di pre-ovideposizione, sulla fecondità e sulla presenza di oociti maturi nell'addome delle femmine. I due ceppi di *O. laevigatus* hanno mostrato di svernare in due modi distinti: nel ceppo del Nord parte della popolazione sverna in una lieve diapause riproduttiva, mentre il ceppo S sverna in quiescenza (**capitolo 4**).

Infine è stata valutata la capacità di *O. laevigatus* di controllare i tripidi (*F. occidentalis* e *T. tabaci*) attraverso il lancio di questi predatori in serre commerciali su due specie orticole, peperone e melanzana. Il lancio dei predatori è stato eseguito non appena i tripidi sono stati

rilevati sulla vegetazione e gli *Orius* si sono prontamente insediati sulle colture, mostrando una efficiente interazione con i tripidi anche a basse densità del fitofago, ed il controllo degli stessi (**capitoli 5 e 6**).

In conclusione il ceppo del Sud Italia di *O. laevigatus* ha mostrato di essere un efficiente nemico naturale dei tripidi e di *F. occidentalis*. Attualmente è prodotto e impiegato commercialmente su larga scala in Europa per il controllo dei tripidi su orticole e ornamentali in coltura protetta (**capitolo 7**).

Samenvatting

De algemene doelstelling van mijn onderzoek was het ontwikkelen van een biologisch bestrijdingsprogramma voor Californische trips, *Frankliniella occidentalis* (Pergande). Selectie van een efficiënte natuurlijke vijand is daarbij van groot belang. Allereerst is met behulp van de bestaande literatuur een literatuuroverzicht gemaakt van economisch belangrijke tripssoorten in Europa, en *F. occidentalis* in het bijzonder. Informatie over de biologie, verspreiding, waardplanten en schade veroorzaakt door trips worden daarin besproken en samengevat. Uit de literatuur en praktijk kwamen Anthocoridae (bloemwantsen) als belangrijkste kandidaten naar voren, met name predatoren binnen het geslacht *Orius* (Rhynchota: Heteroptera) (**hoofdstuk 1**). Als volgende stap werden die *Orius* soorten geselecteerd die in het mediterrane gebied van Europa het meest algemeen zijn. In verschillende streken van Italië zijn *Orius* soorten verzameld, afkomstig van 36 verschillende plantensoorten besmet met trips. De meest algemene soorten waren *Orius niger* Wolff, *O. laevigatus* (Fieber) en *O. majusculus* (Reuter). Er werden geen bijzondere waardplant voorkeur van deze *Orius* soorten vastgesteld (**hoofdstuk 2**).

Vervolgens zijn in het laboratorium biologische eigenschappen en predatiecapaciteit van vier *Orius* soorten onderzocht: de palaearctische soorten *O. majusculus*, *O. laevigatus* en *O. niger* en de nearctische soort *O. insidiosus*, een exoot die in eerdere jaren in Italië was losgelaten. Daarvoor zijn twee prooisoorten gebruikt: eieren van *Ephestia kuehniella* (Zell.) en volwassen exemplaren van *F. occidentalis*. Van de juveniele stadia zijn de mortaliteit en ontwikkelingstijd bepaald, van de volwassen stadia de sex-ratio, pre-ovipositie periode, overlevingstijd en eilegcapaciteit, en van beide stadia de predatiecapaciteit. Voor alle vier *Orius* soorten zijn tevens de life-history parameters bepaald: de intrinsieke groeisnelheid (r_m) en intrinsieke predatiecapaciteit ($k_m = \ln k_0/t_k$). De k_m waarden waren respectievelijk 0.23 voor *O. laevigatus*, 0.21 voor *O. majusculus*, 0.25 voor *O. insidiosus*, 0.19 voor *O. niger*. Van alle soorten bleek, dat vrouwtjes die *E. kuehniella* eieren gegeten hadden, langer leefden en een meer eieren legden dan wanneer volwassen tripsen hadden gegeten. Resultaten voor de nearctische soort *O. insidiosus* kwamen overeen met die voor *O. laevigatus* en *O. majusculus*. Massakweken van *O. insidiosus*, *O. laevigatus* en *O. majusculus* werden met succes opgezet. *O. niger* bleek daarentegen moeilijk te kweken. Op grond van onze gegevens, concluderen we dat *O. laevigatus* de beste perspectieven bied bij de bestrijding van trips (**hoofdstuk 3**).

Wanneer trips vroeg in het seizoen zich tot een plaag ontwikkeld, is het van groot belang dat een natuurlijke vijand dan niet in diapauze gaat. Gegevens over diapauze in *O. laevigatus* ontbraken bij aanvang. Daarom hebben we specifiek onderzocht of het mogelijk is om een reproductieve diapauze te induceren in deze soort. Daarvoor hebben we twee stammen bekeken: een stam 'N' uit Noord-Italië (Po vallei) en een stam 'S' uit Zuid-Italië (Sicilië). De invloed van de daglengte op eionontwikkeling in vrouwelijke *Orius* exemplaren is onderzocht. De ontwikkelingstijd, het aantal volwassen beesten, de sex-ratio, pre-ovipositie periode, eilegcapaciteit, en de aanwezigheid van rijpe oöcyten werden vastgelegd. Beide stammen van *O. laevigatus* bleken op een eigen manier te overwinteren: stam 'N' onderging een zwakke reproductieve diapauze, terwijl stam 'S' overwinterde in een vorm van quiescence (**hoofdstuk 4**).

Tenslotte hebben we voor *O. laevigatus* onderzocht of deze soort in staat was om tripsplagen (*F. occidentalis* en *Thrips tabaci* Lind.) in commerciële kassen te onderdrukken. Zodra de aanwezigheid van trips was vastgesteld, werden predatoren uitgezet in twee groentegewassen, paprika en aubergine. Reeds bij een lage prooidichtheid resulteerde dit in

een snelle vestiging van de predator in het gewas. In veel gevallen leidde dit tot een adequate bestrijding van trips (**hoofdstuk 5 en 6**).

Samenvattend bleek stam 'S' van *O. laevigatus* uit Zuid-Italië een zeer efficiënte natuurlijke vijand van trips en van *F. occidentalis* in het bijzonder. Deze stam wordt thans massaal gekweekt en op commerciële op grote schaal in Europa gebruikt ter bestrijding van trips plagen in groente- en snijbloemgewassen in kassen (**chapter 7**).

List of publications

Some chapters of this thesis, or parts of them, are or will be published as:

TOMMASINI M.G. & MAINI S., 1995. *Frankliniella occidentalis* and other thrips harmful to vegetable and ornamental crops in Europe. Agricultural University Wageningen Papers 95 (1), 1-42. – **chapter 1**

TOMMASINI M.G. Collection of *Orius spp.* in Italy – **chapter 2**

NICOLI G. & TOMMASINI M.G., 1996. *Orius laevigatus*. Informatore Fitopatologico 4: 21-26. – **chapter 2 and 3**

TOMMASINI M.G. & BENUZZI M., 1996. Influence of temperature on the development time and adults activity of *Orius laevigatus*. IOBC/WPRS Bull. 19 (1): 179-182. – **chapter 3**

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Curriculum vitae

M.Grazia Tommasini was born in December 1962, in Cesena (Italy). She obtained her MSc degree in Agriculture Science with honours at the University of Bologna (Italy) in 1989. From 1983 to 1990 she performed research on the life history and behaviour of several natural enemies (*i.e. Chrysoperla carnea* and *Edovum puttleri*) at the Institute of Entomology of Bologna University. Researches on the parasitoid *Edovum puttleri* were used for her MSc graduation thesis.

From 1991 up to August 2002 she was employed at the Centrale Ortofrutticola of Cesena (I) within the 'Research and Development Department'. She worked on biological control, and carried out biological studies for developing mass rearing techniques of natural enemies used in pest control in protected crops. From 1997 to 1999 she was the head of this research and development department, and was responsible for quality control of natural enemies of Biolab (a production unit of natural enemies) within the Centrale Ortofrutticola. From 1999 to 2002 she was head of the Centre Research on Environmental and Agriculture (CREA) in the Centrale Ortofrutticola, working mostly on biological control and IPM in fruit crops. Since August 2002 she is employed by the Research Centre on Crop Production (CRPV) in Cesena (I), where she is responsible for research and development of crop protection in fruit.

The research on predators of thrips, *i.e. Orius* spp., resulting in this doctoral thesis was started in 1991 and was partly funded by EC-project CAMAR (n. 8001-CT90-0026). Her PhD studies were done under the supervision of Prof. J.C. van Lenteren, Laboratory of Entomology, Wageningen University, and Prof. S. Maini and the late Dr. G. Nicoli of the Institute of Entomology of Bologna University.

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