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Biological Control of Insect and Mite Pests in Greenhouse Solanaceous Crops

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ABSTRACT

Solanaceous greenhouse crops are susceptible to infestation by a high number of insect and mite pests that can cause serious yield losses. The most important of these pests are whiteflies, aphids, leafminers, thrips and spider mites. Biological control is an environmentally friendly method which enhances sustainability in agriculture. Biological control is based on the use of natural enemies - antagonists of the pests that may be predators, parasitoids or pathogens. Extensive research has been conducted to exploit the potential of natural enemies in biological control. Selected natural enemies have been mass reared and commercialized. The application of biological control in greenhouses has been proved effective and its use is steadily increasing, worldwide.

Keywords: aphid, leafminer, natural enemy, spider mite, thrips, whitefly

Abbreviations: IPM, integrated pest management; **CMV**, *Cucumber mosaic virus*; **RH**, relative humidity; **SIT**, sterile insect technique; **TSWV**, *Tomato spotted wilt virus*; **TYLCV**, *Tomato yellow leaf curl virus*

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INTRODUCTION

Among the methods combined in IPM strategies, biological control is the most prominent. Continuing problems with chemical insecticide resistance and environmental and food contamination support continued development of biological control. Biological control involves the use of natural enemies (predators, parasitoids and pathogens) that are antagonists of insect and mite pests. This costs two orders of magnitude less than chemical control and does not take more time to develop and implement than chemical control (Bale *et al.* 2008). The use of biological control has expanded

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considerably, as it is effective, environmentally friendly and offers permanent results (Albajes *et al.* 1999).

Greenhouse environments are suitable for the use of biological control as they are closed systems that provide barriers against the dispersal of natural enemies. Moreover, the whole system and pest densities can be supervised closely and is less vulnerable to pest invasions than crops in open fields. In addition, the conditions can be adapted so as to create an environment more favourable for the natural enemies than the pests. The protected environment of greenhouse crops also makes possible the fulfillment of a main prerequisite for the application of biological control, namely a low pest population, as appropriate sanitation measures can be timely applied to the crop. Biological control could be also effective under relatively high pest population pressure but in these cases, the cost could increase dramatically.

A reason that necessitates the use of biological control in greenhouse crops is that the pests in greenhouses are more likely to develop resistance to chemicals, when applied over long periods, since they reproduce rapidly within the closed greenhouse environment. In addition, crops are harvested frequently at close intervals, and thus intensive use of chemicals becomes questioned due to the possible contamination of products with chemical residues. Furthermore, most greenhouse vegetables are consumed fresh, which is another motivation for farmers to apply less intensive control measures and to meet the consumers' demands for produce of high quality.

In the greenhouse environment crop protection is often disrupted by the introduction of new pests due to trade (Van Driesche 2002). Such pests can find ideal conditions for multiplication, because greenhouses have similar cultivation environments worldwide. Traditionally newly introduced pests resulted in a substantial increase in the use of chemicals, with the ensuing danger of the development of resistance and the subsequent risk of market loss, mainly as a result of produce contamination with pesticide residues. This was also another reason for research into the potential natural enemies of these pests.

BIOLOGICAL CONTROL IN GREENHOUSE

The use of biological control in greenhouse crops was reported before the Second World War with the use of the whitefly parasitoid *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) (Speyer 1927). During the period after the war, the development of new synthetic insecticides, which were highly effective, reduced the expansion rate of biological control. However, the need for alternative methods in insect pest control became clear soon afterwards, mainly due to the development of resistance, the awareness of a need to protect the environment, including surface and underground water, and the high risk of contamination of produce by chemical residues. The development of resistance to organic acaricides by the mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), was observed as early as 1949 (Hussey 1985), and this gave a boost to research into the development of options based on biological control, such as the application of the phytoseiid mite *Phytoseiulus persimilis* Athis-Henriot (Acari: Phytoseiidae) which is an efficient predator of *T. urticae*.

In agro-ecosystems, several natural enemies of the pests of protected crops may be found. However, only a few of them have shown the potential to be effective in the greenhouse environment and few have been commercialized. The criteria to identify the most promising natural enemies were described by van Lenteren and Woets (1988). These are: synchronization with the host, climatic adaptation, easy mass-rearing, a high reproductive and host kill rate, high searching efficiency, negative effects on other organisms, and the existence of an effective method for introduction. The criteria can vary between the parasitoids and the predators; for example, in the former the most important factor may be related to reproduction when feeding on the pest, while for the latter the killing rate of the pest is more significant (Yano 2006).

In greenhouse crops, biological control is applied by the seasonal release of the natural enemies. In these cases, predators or parasitoids are released, aimed at creating the population required for control over a relatively long period (several months). Mass releases (inundative releases) may be used in some crops with the objective of directly reducing the number of pests, but not controlling the population over a longer period. The selection of the method to apply depends mostly on the population level of a pest at the time of initial release of the natural enemy and the characteristics of the enemy, e.g. polyphagy or phytophagy, which may permit survival during periods of prey scarcity.

A fundamental step in the successful implementation of biological control in greenhouses is the use of high quality natural enemies for release (van Lenteren 2003). For this reason, guidelines have been developed to assess the quality of the product-natural enemy that reaches the farmers. Criteria have been elaborated for certain natural enemies and these should be followed to evaluate their quality and assess their effectiveness in biological control. Results from related studies indicate the importance of regular quality evaluation of mass-reared beneficials (i.e. Blumel and Hausdorf 2002; van Lenteren 2003a).

The use of more than one natural enemy is also a recent topic in biological control, because the crop can be affected by several pests simultaneously, whereas several alternative beneficials are available on the market. The combined use of natural enemies is expected to increase the effectiveness of biological control as the specific pests can be controlled and the risk of virus infection is reduced. It is crucial, when the natural enemies are found among the native species, that these enter the greenhouse and work there to increase the effectiveness of control. Related studies have shown that between predators, the use of more than one can be positive and promote a synergistic effect (Lucas and Alomar 2002). However, when parasitoids and predators are used together, the outcome can be negative because the parasitized hosts are vulnerable to the predatory action of generalist predators, and the predator cannot discriminate between parasitized and healthy pests (Meyling *et al.* 2003; McGregor and Gillespie 2005).

In certain cases, biological control applications have led to increasing scepticism about the use of exotic natural enemies because they may become established in the new area and have adverse effects on the local fauna. The release of the predators *Coccinella septempunctata* L. and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) has been considered to be questionable since both are aggressive competitors and their release caused adverse effects on native natural enemies (Wheeler and Hoebeke 1995; Majerus *et al.* 2006; van Lenteren *et al.* 2008). Issues relevant to this topic have constituted the main objective of several publications (van Lenteren *et al.* 2006; Roy and Wajnberg 2008), and concern has increased in the light of globalization and the increased public awareness of the need for conservation of biodiversity.

Apart from 'conventional' ways to apply biological control, i.e. by the purchase and subsequent release of natural enemies, the conservation of indigenous natural enemies can also assist in the control of greenhouse pests. This method, which has recently attracted considerable attention, is a major topic for the sustainability of agro-ecosystems, because pest control is included in the functions of the ecosystem. The strategy is based on the conservation of the natural host plants of beneficial organisms within the agro-ecosystem, in order to facilitate their establishment on the crop plants. The main feature of agro-ecosystems that act as a source of natural enemies is the conservation of natural vegetation, which offers several benefits to the natural enemies, such as alternative food (Landis *et al.* 2000; Wäckers *et al.* 2005). The potential of non-crop plants to assist in biological control has been extensively investigated and applied to several agro-ecosystems, such as cereals (Thomas *et al.* 1991) but is has also been proposed in greenhouse solanaceaous crops (Sanchez *et al.* 2003).

In vegetable agro-ecosystems, there are several native parasitoids and predators that can be effective in the control of crop pests (Nicoli and Burgio 1997). In greenhouse vegetable crops, the use of natural host plants as a method to introduce natural enemies has proved positive (Albajes and Alomar 1999). Alternatively, collection of predators from naturally occurring vegetation patches, for subsequent release in greenhouses, might be a valuable practice. In addition, manipulations such as cutting of plants to trigger a predator's emigration to nearby crops could be worthwhile, as it was the case for natural enemies in conservation biological control (Altieri and Whitcomb 1979; Landis *et al.* 2000; Gurr *et al.* 2004). The conservation and utilization of the natural enemies within the agro-ecosystems are major factors in the reduction of the cost of application of natural enemies, some of which may be expensive to purchase (Yano 2008).

The current paper is focusing on presentation of recent advances in the biological control of the main insect and mite pests of the greenhouse solanaceous crops. This is a major topic in the biological control and this paper is aiming to concentrate on the most relevant and key data available in the recent literature.

WHITEFLIES

Whiteflies are major pests in greenhouse crops. The adults are white in colour, 2-3 mm in length, but immature are almost transparent and oval in shape. In general, the adults are mostly recorded in the top parts of the plants where they oviposit. The first instar is the only mobile nymphal instar. It selects a place, mostly on the undersurface of the top leaves, where it establishes itself. During the first molt it loses its legs. Adult and immature forms feed on plant phloem and excrete a high amount of honeydew, which is a substrate for the development of fungal mould, leading to lower fruit quality due to leaf (and fruit) blackening and reduced photosynthetic activity.

The most important species of whitefly in the greenhouse are the greenhouse whitefly (*Trialeurodes vaporariorum* (Westwood)) and the tobacco whitefly (*Bemisia tabaci* Gennadius) (Homoptera: Aleyrodidae). *T. vaporariorum* has an extremely wide host range, which includes plants from 249 genera and 84 families (Russel 1977). Host plant species can be ranked for suitability for development and fecundity of *T. vaporariorum* as eggplant > cucumber > tomato > sweet pepper (van Lenteren and Noldus 1990). This species completes its development on eggplant in 43, 29 and 23 days at 17, 22 and 27°C, respectively (Di Pietro 1977). On eggplant it lays 286 eggs at 22°C (Woets and van Lenteren 1976). It can transmit some viruses, but in general its potential in virus transmission is not considered to be of major importance (Schuster *et al.* 1996).

The tobacco whitefly is an effective vector of viruses and this is considered to be the most important risk linked to this pest (Gerling *et al.* 2001). It is an efficient vector of the tomato yellow leaf curl virus (TYLCV) (Mehta *et al.* 1994). The introduction of this species into new areas resulted in considerable losses in tomato crops both in the field and in greenhouses. The resulting increase in the use of insecticides quickly led to the development of resistance in the pest, and had a negative side-effect on biological control because growers hesitated to rely on natural enemies and so reduced the use of biological control in their greenhouses.

Mixed populations of both whitefly species occur and this has to be taken into account in the development of control strategies for local populations. It should be noted that the tobacco whitefly is more common in middle and late season in solanaceous crops in southern Europe (Nannini *et al.* 2006; Trottin-Caudal *et al.* 2006).

Biological control of whiteflies in greenhouse environments is mainly based on the use of parasitoids, predators or pathogens.

Parasitoids

Encarsia formosa

The most well known natural enemy of whiteflies is the parasitic wasp *Encarsia formosa*. The adult is less than 1 mm in length, with a dark head, black thorax and yellow abdomen. Its developmental period was 30-32 d at 17-18°C and the fecundity was 165 eggs (Vet and van Lenteren 1981). Its developmental threshold on *T. vaporariorum* was 12.8°C (Obsorne 1982). This species parasitizes mostly the 3rd or 4th instar nymphs of whitefly (Nell *et al.* 1976; Nechols and Tauber 1977). The female can recognize already parasitized hosts from conspecifics, so as to avoid superparasitism (van Lenteren *et al.* 1976).

E. formosa feeds on the fluids that are excreted from the wound that it causes on the host by its ovipositor. This host feeding behaviour occurs in all stages of the whitefly (van Lenteren *et al.* 1980). The host feeding increases the potential of the parasitoid in biological control considering that when 36 whitefly 4th instar nymphs were available to a single female daily during her entire life span, 442 hosts were parasitized and 101 hosts were killed by host feeding at 25°C (Arakawa 1982). Host feeding has generally been related to a higher fecundity or longevity (Heimpel and Collier 1996) but in *E. formosa* it seems that host feeding benefits are less important than in other parasitoids and comparable to honeydew feeding (Burger *et al.* 2004).

E. formosa searches for hosts at random (van Lenteren *et al.* 1980). The presence of host honeydew had a major influence on the host searching behaviour of the parasitoid (Romeis and Zebitz 1997). Light intensity (sunshine) has an important effect on the activity of the wasp (Zilahi-Balogh *et al.* 2006). The light condition can be a critical factor responsible for low effectiveness of the parasitoid in late winter or early spring when light intensity is low. This parasitoid is also a natural enemy of the tobacco whitefly, *B. tabaci*. However, it is not considered to be particularly effective against this whitefly species (Enkegaard 1993).

Methods used for the introduction of *E. formosa* into the greenhouse are the 'pest-in-first' method and periodic introductions. The 'pest- in- first' method is applied by introducing a low number of whitefly on certain plants, followed by the introduction of the wasp. This enables the best timing of wasp release, i.e. when the preferred third instar of the whitefly has formed on the plants. However, this method, which has also been applied in spider mite control, has not been widely adopted, as growers do not like to release a pest within their crop (Ekbom 1977; Stacey 1977). The alternative method of periodic releases is initiated soon after the crop has been established. There may need to be performed as many as 10 introductions of the wasp in order to achieve successful control (Parr *et al.* 1976). A modification of this method is the release of the wasp after the first adults of the whitefly have been recorded on the plants. In this case, four introductions gave satisfactory results (Woets 1978). This is the most commonly used method for the release of the wasp.

The cultural method of removing the lower leaves has to be applied with caution as it can be detrimental to the wasp population, as pupae normally develop on the lower leaves and may be discarded together with the removed leaves. It is advisable therefore to avoid removing the leaves from the greenhouse until the parasitoids emerge.

The parasitoid is effective on tomatoes but to a possibly lesser extent on non-Solanaceous crops such as cucumber, due to the higher suitability of this plant for the whitefly (Woets and van Lenteren 1976) and the long hairs that retain honeydew and increase the difficulty of the wasp in searching the environment (Ekbom 1977).

Eretmocerus spp.

Eretmocerus mundus Mercet (Hymenoptera: Aphelinidae) is a solitary ecto- endo- parasitoid of whitefly nymphs (Rose *et al.* 1996). Eggs are laid under the whitefly nymph and the first instar larva penetrates the host. This parasitoid can attack all the whitefly instars, but prefers the second instar in comparison with the fourth (Jones and Greenberg 1998). It is an effective parasitoid against *B. tabaci* (Stansly *et al.* 2005). Natural populations of *E. mundus* were effective in the control of *B. tabaci* in greenhouse tomatoes in Spain (Arno *et al.* 2005). The release of *E. mundus* together with the predator *Macrolophus melanotoma* Costa (=*M. caliginosus* Wagner) (Hemiptera: Miridae), improved the control of *B. tabaci* in comparison with the use of each natural enemy separately, particularly in spring and when high populations of whitefly occurred (Gabarra *et al.* 2006). *Encarsia* spp. could invade the greenhouses where the parasitoid *E. mundus* had been released, and in some cases became the predominant species (Weintraub *et al.* 2002).

Another species of this genus, *Eretmocerus eremicus* Rose & Zolnerowich, attack both whitefly species efficiently (Greenberg *et al.* 2002). Development of *E. eremicus* was faster using tobacco whitefly as host than *T. vaporariorum*. Mortality patterns in *E. eremicus* reflected those of the host: increasing with temperature on *T. vaporariorum*, while decreasing on tobacco whitefly (Greenberg *et al.* 2000).

Comparative studies of two strains of *E. formosa*, *E. eremicus* and *E. mundus* showed that the lower developmental threshold for development was 11.5, 8.1, 13.0 and 11.5°C, respectively. At 15°C, daily parasitism of tobacco whitefly was very low by all parasitoids. The two *Encarsia* strains had a constant, but low rate of reproduction during adult life, while the two *Eretmocerus* species had a very high rate of reproduction when one-day old, which then decreased quickly (Qiu *et al.* 2004). Research into the evaluation of new natural enemies has shown that *Eretmocerus* sp. *nr. furuhashii* Rose and Zolnerowich, an indigenous parasitoid of *B. tabaci* from southern China, was promising against whitefly at temperatures of 26-32°C (Qiu *et al.* 2007). Life table parameters of *Eretmocerus melanoscutus* Zolnerowich and Rose were higher than those reported for *B. tabaci* indicating that *E. melanoscutus* has an important potential as a biological control agent of *B. tabaci* (Liu 2007).

Hyper-parasitic species

The use of hyper-parasitic species for the control of whitefly has also been evaluated. These species are *Encarsia tricolor* Förster and *Encarsia pergandiella* Howard, which are heteronomus hyper-parasitoids, the females of which develop on the whiteflies (primary host), while the males develop either on females of the same species or on other primary parasitoids (Hunter and Kelly 1998). *E. tricolor* is a native European species which has showed promising results in biological control. Native populations can enter greenhouses and rarely cause negative effects on whitefly control (Del Bene and Landi 1991). *E. pergandiella* has been released in areas of the Mediterranean basin and can contribute to the biological control of whitefly (Giorgini and Viggiani 2000). However, it has been reported to be detrimental to the successful control of whitefly by other parasitoids (Gabarra *et al.* 1999). The combined use of *E. formosa* and *E. pergandiella* resulted in an increased effectiveness in comparison with the release of each single species (Heiz and Nelson 1996). Therefore the use of these hyper-parasitic species is worthwhile, but only under strict conditions (Loomans *et al.* 2002).

Predators

Macrolophus spp.

Among the predators of whiteflies in greenhouse solanaceous crops, *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae; **Fig. 1A**) and *M. melanotoma* (*M. caliginosus*), are considered to be the principal ones (Albajes and Alomar 1999). They are widely used on commercial scale in releases against whiteflies and other pests on vegetable greenhouse crops (Hommes and Horst 2002; van Lenteren 2003b). These species are native to the Mediterranean region. They are polyphagous, feeding on several soft-bodied pests such as the whiteflies, aphids, thrips, leafminers, mites, eggs and larvae of the Lepidoptera. They feed on their prey by inserting the stylets of their mouthparts and sucking out the body contents of the prey. *Macrolophus pygmaeus* exhibits phytophagous habits that allow it to develop successfully without prey on eggplant, tomato, cucumber, pepper and beans, whereas eggplant and tomato can support a low rate of oviposition in the absence of prey (Perdikis and Lykouressis 2000, 2004). *M. melanotoma* can also complete its nymphal development feeding on plant sap of vegetables (Tavella and Arzone 1996). Phytophagy is a main characteristic of their biology, which permits them to survive on the crop for a relatively extended period. *M. melanotoma* remained for a relatively much longer period on the plant than other predators, even when only a very low number of whiteflies were present and this could have positive impacts on its effectiveness in biological control (Montserrat *et al.* 2004). Feeding on plants could be related to damage induction. However, this potential has been reported only by Sampson and King (1996) for *M. melanotoma* on cherry tomatoes in the UK.

M. pygmaeus performed very well feeding on *T. vaporariorum* on tomato and eggplant showing an intrinsic rate of population increase of 0.104 and 0.0981 d^{-1} respectively, at 27.5°C. The incubation period of the eggs was 11 d on tomato at 25°C (Perdikis and Lykouressis 2002). This predator completed its nymphal development feeding on nymphs of the greenhouse whitefly on eggplant, tomato and beans in a period of 15.21, 17.05 and 17.01 d at 25°C (Perdikis and Lykouressis 2000). Its fecundity on tomato was 146.85 eggs and longevity of females 49.25 d (Perdikis and Lykouressis 2002). Studies on predation rates of *Macrolophus* species have proven their ability to reduce whitefly numbers. Laboratory experiments on *M. melanotoma* at 22°C on bean plants showed that predation on *T. vaporariorum* 1st instar nymphs reached about 166 per day (Enkegaard 2001). *M. melanotoma* actively consumed the eggs and nymphs of *B. tabaci* and particularly of *T. vaporariorum* (Barnadas *et al.* 1998). This predator preferred feeding on older nymphs of *B. tabaci* (Bonato *et al.* 2006). However, it preferred *T. vaporariorum* to *B. tabaci* (Barnadas *et al.* 1998; Bonato *et al.* 2006).

M. pygmaeus has shown a high potential in biological control on solanaceous crops (Perdikis and Lykouressis 1996; Hilbert *et al.* 2001; Hommes and Horst 2002). The method used for the introduction of *Macrolophus* predators is mostly periodic releases (i.e. Malausa and Trottin-Caudal 1996). An improvement of this method has been demonstrated to be their release in parallel with the addition of highly suitable food (usually eggs of Lepidoptera) on the crop plants. This aims at increasing the rate of predator establishment on the plants (Nannini *et al.* 2006) because this process may be slow under certain circumstances such as low prey availability (Castañé *et al.* 2006). Another method, focusing on more effective establishment of the predators in the crop, has been proposed by Lenfant *et al.* (2000). According to this, predators are released in the nursery together with additional food. The predators lay eggs on the young plants and after their transplantation, the predator nymphs that emerge on the plants, become distributed within the crop in relatively high numbers.

A cultural practice with negative effects on predator population establishment is leaf and lateral stem removal, which may cause a loss of 74% of young nymphs (Bonato and Ridray 2007). Therefore, it is strongly advisable, the cut stems or leaves to be retained in the greenhouse for a long enough period so that the neonate nymphs to hatch and move to the crop plants.

The natural colonization of greenhouse solanaceous crops with *Macrolophus* predators and their persistence and

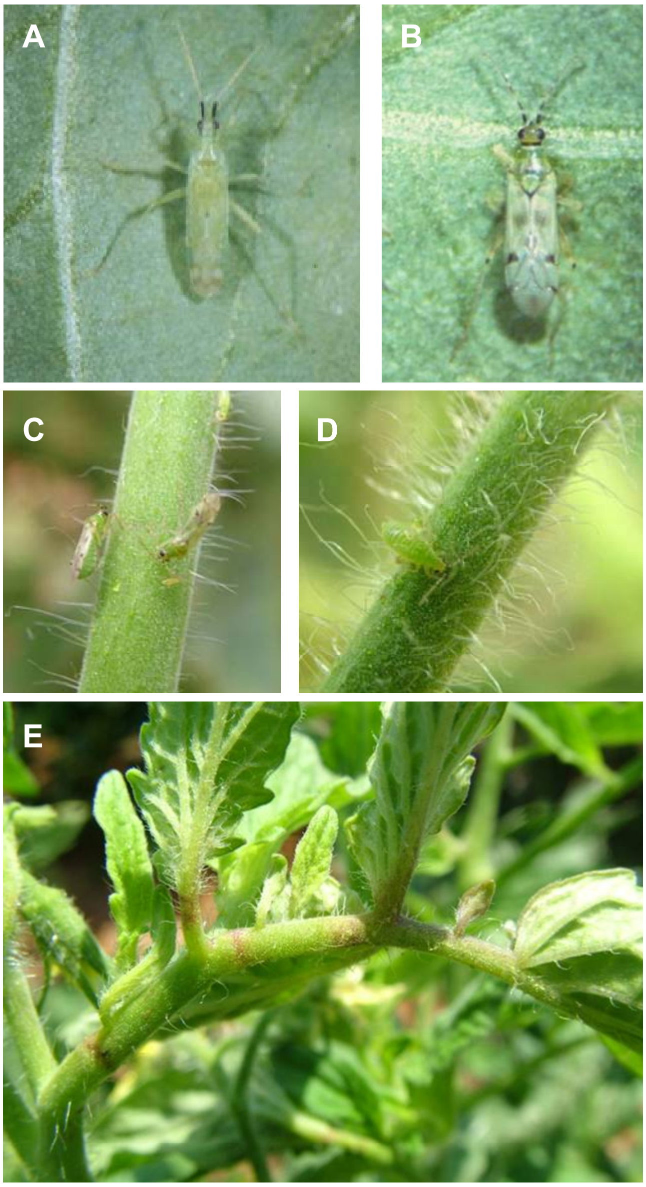

Fig. 1 Insect predators in greenhouse tomato crops. (**A**) Adult *Macrolophus pygmaeus*; (**B**) Adult *Nesidiocoris tenuis*; (**C**) Adult *Nesidiocoris tenuis* feeding on a tomato stem; (**D**) Nymph of *Nesidiocoris tenuis* feeding on a tomato stem; (**E**) Damage induced by *Nesidiocoris tenuis* on a tomato leaf.

abundance in field margins, have stimulated studies to explore the potential of native vegetation or selected non-crop plants as a means to introduce the predators into greenhouse crops or support the conservation of their populations around the solanaceous crops. The use of alternative host plants for this purpose has been evaluated with positive results for the mirid predator *Dicyphus hesperus* Knight (Hemiptera: Miridae) in greenhouse tomato crops. This predator was invariably found to be more common in greenhouses where the alternative host plants (mullein plants, (*Verbascum thapsus* L.)) had been introduced and the predator population was maintained on these plants when prey on tomato was scarce (Sanchez *et al.* 2003).

Conservation of polyphagous mirid predators has been shown to be an efficient strategy regarding the natural regulation of whiteflies, aphids and Lepidoptera pests (Albajes and Alomar 1999; Gabarra and Besri 1999; Lykouressis *et al.* 1999, 2000). The colonisation rate of the polyphagous predators *Dicyphus tamaninii* Wagner and *M. melanotoma* has been shown to increase in fields where there is a presence of winter refuges. However, it is likely that immigration from distant sources also contributed to the colonization of the tomato fields (Alomar *et al.* 2002).

The main natural reservoirs of *M. pygmaeus* and *M. melanotoma* in slanaceous crops are the non-cultivated plants *Solanum nigrum* L. (Solanaceae) and *Dittrichia viscosa* (L.) W. Greuter (Asteraceae) respectively (Alomar *et al*. 1994; Lykouressis *et al*. 2000). In the case of *M. pygmaeus* and *M. melanotoma* recent data have shown the potential of non-crop plants as suitable food sources (Perdikis *et al.* 2007; Lykouressis *et al.* 2008). In particular, *D. viscosa* was suitable for *M. melanotoma* and *S. nigrum* for *M. pygmaeus*. *M. pygmaeus* did not perform well on *D. viscosa*.

Alomar *et al*. (2002) and Castañé *et al.* (2004) reported that the colonization of tomato crops by *M. melanotoma* was higher in fields surrounded by complex environments. However, the key elements of natural vegetation that support dispersal of *Macrolophus* to tomato crops remain unclear (Alomar and Albajes 2003). These relatively limited and inconclusive data could be associated with the vague discrimination between *M. melanotoma* and *M. pygmaeus* (Goula and Alomar 1994). Recent studies using hybridization and molecular DNA analysis have proven that *M. melanotoma* and *M. pygmaeus* are different species, the first recorded on *D. viscosa* and the latter on *S. nigrum* and tomato plants (Perdikis *et al*. 2003; Martinez-Cascales *et al.* 2006), whereas in a comparative study using different scale experiments (petri dishes, caged plants, greenhouse plots) it was proved that only *M. pygmaeus* can colonize tomato (Perdikis *et al.* unpublished data). All these reports have important implications for the correct identification and nomination of the *Macrolophus* species involved in the biological control of pests on solanaceous crops and their commercial production and use.

Nesidiocoris tenuis

Nesidiocoris tenuis (Reuter) (**Fig. 1B**) is another mirid predator that is effective in the control of whitefly populations on tomato greenhouse crops. It is common in tropical and subtropical areas. It feeds mainly on whiteflies, but also on other pests such as spider mites, leafminers and early instars of Lepidoptera (Torreno 1994; Carnero *et al.* 2000; Vacante and Benuzzi 2002; Urbaneja *et al.* 2005). It can naturally colonize tomato crops and substantially contribute to the control of whiteflies (Calvo and Urbaneja 2003; Sanchez *et al.* 2003). Its population trends followed those of whiteflies, showing its potential in biological control (Sanchez 2008). This bug seems to have little potential to complete development in the absence of prey, feeding only on a plant diet, although tomato was favored more than eggplant and pepper (Urbaneja *et al.* 2005).

However, the status of this species is controversial as it may also cause damage to tomatoes (El Dessouki *et al.* 1976). This damage is related to the induction of necrotic rings on the stems (**Fig. 1C-E**) and leaves, flower drop and fruit blemishing. Damage due to feeding on the shoots does not seem to be important, although it may reduce the vigour of the plants, but flower abortion might be serious (Sanchez *et al.* 2006). In a study where a 10-20 *N. tenuis* adults or nymphs were left to feed for a period of 48 h on a single caged lateral tomato stem, caused damage that disappeared later, indicating that harm to the crop might not be significant (Arnó *et al.* 2006). Damage potential of several densities of this predator on caged tomato plants without prey, showed that this pest inflicted necrotic rings on the upper part of the stems but only in very low numbers, whereas flower abortion was not recorded (Perdikis *et al*. unpublished data). As stated by Sanchez (2008) the number of necrotic rings on tomato plants under greenhouse conditions was closely correlated with temperature but not with relative humidity. Consequently, temperature might be related to the observed flower abortion. Thus, further studies are required to qualify more closely the potential of this mirid to cause different types of damage and loss of yield, particularly with reference to the physiological state of the plants, the ambient conditions, the level of prey availability and predator's densities. This approach could be similar to that followed for *D. tamaninii*, another effective predator against whiteflies on tomato. *D. tamaninii* feeds on fruits and cause yellow spots. In this case, a tolerance population threshold has been proposed, according to which spraying is recommended when the pest population (whitefly) is less than 20 adults per tomato plant and the respective number of *D. tamaninii* individuals is higher than 4 per plant (Alomar and Albajes 1996).

Dicyphus spp.

Predatory bugs that belong to the genus *Dicyphus* (Hemiptera: Miridae) are widespread and repeatedly reported on solanaceous vegetable crops in Mediterranean and North America. The most commonly reported are *D. tamaninii*, *D. errans* (Wolff) and *D. hesperus*. *D. tamaninii* can readily colonize greenhouse tomato crops and usually becomes established and contribute substantially to the control of whiteflies and other pests (Alomar and Albajes 1996; Castañé *et al*. 2004). *D. errans* is commonly recorded towards the end of the summer and in the autumn in greenhouse tomatoes and eggplants in Greece (Lykouressis *et al.* 2000). *D. hesperus* is an effective predator and is used for the biological control of the greenhouse whitefly in greenhouses in Canada (Sanchez *et al.* 2003).

Other predators

Apart from the mirids, an effective predator of whitefly is the coccinelid *Delphastus catalinae* Horn. (formerly *D. pusillus* (LeConte)) (Coleoptera: Coccinellidae). This species is an oligophagous predator feeding on whitefly eggs and nymphs and can be very effective in reducing local high densities of whitefly. Feeding on *B. tabaci*, this predator was found to perform better at 22 and 26°C, while at 30°C it failed to complete development (Legaspi *et al.* 2008). After life-table studies, the optimum temperature for mass rearing of *D. catalinae* proved to range between 25 and 30°C (Kutut and Yigit 2007).

This predator showed a reduced potential to survive at low temperatures. In laboratory experiments eggs hatched at a percentage of 48% at 15°C. Similarly, larvae failed to survive to the pupal stage at 15°C. In comparison, at 25°C, 98% of eggs hatched and 86% of the larvae survived to the adult stage (Simmon and Legaspi 2007). The relative humidity was proved to have a serious effect on the population of the predator. It was found that approximate to 60% of the newly hatched larvae survived to the adult stage at 25% RH, whereas 50% survived to the adult stage at 10% RH, in comparison to 90% that completed development at 95% RH (Simmons *et al.* 2008). *Delphastus catalinae* larvae fed on parasitized *B. tabaci* nymphs but, interestingly, when used together with the parasitoid *Encarsia sofia* (Girault and Dodd) (Hymenoptera: Aphelinidae), the suppressing effect was increased in comparison to single natural enemy treatments (Zang and Liu 2007).

Insect predators belonging to the genus *Orius* (Hemiptera: Anthocoridae) are common on vegetable crops. The change of the predation rate of *Orius majusculus* (Reuter) and *O. laevigatus* (Fieber) in response to the increasing densities of the greenhouse whitefly showed they did not respond well in comparison to mirid predarory bugs. However, they have shown a potential to contribute to the control of *B. tabaci* when co-occurs with thrips, *Frankliniella occidentalis* Pergande (Thysanoptera: Thripidae) (Arnó *et al.* 2008),

Apart from insect predators, related studies have shown that the mite predator *Amblyseius swirskii* Athis-Henriot (Acari: Phytoseiidae) is an efficient natural enemy of both *B. tabaci* and *T. vaporariorum* (Nomikou *et al.* 2001; Hoogerbrugge *et al.* 2005). This predator feeds on pollen and therefore it can be released in pollen-producing crops, such as sweet pepper, before the emergence of the pest, (Hoogerbrugge *et al*. 2005). Experiments have proved the effectiveness of this predator on protected sweet peppers in Southern Spain (Calvo *et al.* 2006). Because it benefits from feeding on a mixed diet of thrips (*F. occidentalis*) and greenhouse whitefly, *A. swirskii* is potentially effective in the control of both species, a potential that worth further experimentation (Messelink 2008). However, it seems to have a relatively low potential for whitefly control on tomatoes due to the dense trichomes on this plant, which make foraging difficult. Another predator *Typhlodromalus limonicus* Garman & McGregor has been reported as promising for the control of whiteflies and thrips on tomatoes, but further research is needed in the greenhouse environment (van Houten *et al.* 2005). Experiments in southern Spain showed that this mite has the potential to be a key biological control agent against *B. tabaci* on sweet pepper, cucumber and eggplant (Calvo *et al.* 2008).

Entomopathogenic organisms

The use of entomopathogenic fungi is a major alternative for whitefly control. Various fungi, *Beauveria bassiana* (Balsamo) Vuillemin, *Paecilomyces fumosoroseus* (Wize) Brown and Smith, and *Lecanicillium lecanii* (Zimmermann) Gams and Zare [*Verticillium lecanii* (Zimmermann) Viégas], have been shown a high potential for whitefly control (see Fargues *et al.* 2003 and references therein). Recent developments in production process and usage of pathogenic fungi have resulted in improvements in biopesticides of *V. lecanii*, and new products of *P. fumosoroseus* and *B. bassiana*. Despite this potential, the main obstacle to the wider use of such products is their slow action, potentially negative interactions with fungicides and dependence on favourable environmental conditions. In order to enchance their efficacy major suggestions are the early application when the whitefly populations are very low, and under more favourable environmental conditions (Faria and Wraight 2001).

The pathogenic fungi are sprayed on to the plants and the spores are deposited on the body of the host, where they germinate to produce hyphae that penetrate the host's body, multiply and finally re-emerge outside the body to sporulate. The transfer to a new host is achieved by water or physical contact. These fungi are effective at high densities of the pest and under conditions of high RH. For effective establishment and control, it has been reported that 90% RH is needed, which in some cases could also encourage the development of fungal infestations of plants. It has been proposed that the sprayings should be conducted in the evening; with the windows to remain closed for two nights *V. lecanii* has been successfully used against greenhouse infestations of whitefly, aphids, and thrips. It has been proved that this fungus can be effective under conditions of high relative humidity (Ekbom 1981), but Drummond *et al.* (1987) showed evidence for variation in the requirements of different *V. lecanii* isolates. This researcher proved that *V. lecanii* could be highly effective at 70% RH providing a 96-h incubation at >95% RH. The humidity conditions prevailing at the insect–fungus level close to the leaf surface could compensate the adverse effect of dry conditions (Vidal *et al.* 2003) and should be considered in biocontrol (Fargues *et al.* 2003). In the effort to enhance its effectiveness several materials have been evaluated for their potential to favor the germination of conidia and infection of the greenhouse whitefly. Among them, sugars showed a potential for enhancing field efficacy of *V. lecanii* (Shi *et al.* 2006).

According to Mayoral *et al.* (2006), the fungus *B. bassiana* can be 72.3-82.8% effective against whiteflies on tomato and eggplant. Results of Fargues *et al.* (2003) agree with those of Wraight *et al.* (2000) that a high control potential of *B. bassiana* and *P. fumosoroseus* can occur under ambient dry conditions, in laboratory assays (56–75% mortality at 49–54% RH) and in small-scale field trials (76% control at 39–85% RH).

Applications of entomopathogenic nematodes have also shown a considerable potential for the biological control of whiteflies. Experiments have proved that they are effective against *B. tabaci* (Head *et al.* 2004; Cuthbertson and Walters 2005). In laboratory and greenhouse experiments the entomopathogenic nematode *Steinernema feltiae* (Filipjev) caused high mortality of second instar of *B. tabaci* (> 90% and > 80%, respectively) and thus, it has been considered as showing a significant potential for use in management of this pest (Cuthbertson *et al.* 2007). These nematodes move through a thin film of water on the leaf surface. Therefore, conditions that affect the maintainnance of this film are crucial for the effectiveness of the nematodes. In order to optimize efficacy, favorable conditions should be kept for a period of 6-8 h after their application (Cuthbertson and Walters 2005).

Supplementary measures

In the control of pests by biological control agents, the application of sanitary and precautionary measures can be of significant supporting value. These target low initial levels of crop infestation, which are considered to be fundamental for the subsequent success of biological control. Releases of the parasitoid *E. formosa* should be initiated before the *T. vaporariorum* population exceeds the density level of 10 adults per 100 tomato plants (Ekbom 1977). The aim of low initial pest population levels in the crop is supported by the use of exclusion nets that cover the greenhouse openings and the construction of double doors, both focusing on the prevention of entry of pests into the crop. The use of nets has been experimentally evaluated and proved to be effective in reducing the pest inocula (Hanafi *et al.* 2002). The nets should be installed before planting (Trottin-Caudal *et al.* 2006) and possible adverse effects on RH, with the risk of increased fungal disease, must be taken into consideration (Chyzik *et al.* 2005). Yellow sticky traps are the most widespread method for the detection and monitoring of whiteflies in greenhouses, as their catches show a strong relationship with the whitefly population in the greenhouse. Further research has focused on the development of an appropriate sequential monitoring plan so as to improve the efficacy of yellow sticky traps for the timely application of the control measures. In the study of Kim *et al.* (2001), it was shown that cylindrically shaped yellow sticky traps should be placed at least 12.5 m apart to obtain a spatially independent, unbiased estimation of mean of *T. vaporariorum* densities in greenhouse cherry tomato crops.

Plastic cup traps equipped with light-emitting diodes have shown a high potential in the monitoring of adult *B. tabaci* with little negative effect on the released parasitoids (Chu *et al*. 2003).

An alternative method that has recently been evaluated against several pests in greenhouse crops is the use of plastic covers that exclude UV radiation. The lack of UV caused difficulties in whitefly flight orientation and reduced dispersal activity (Antignus *et al.* 2001; Doukas and Payne 2007). However, it has been shown to influence the flight behaviour of parasitoids as well (Chiel *et al*. 2006). Thus, although the use of this method has positive results against pests, on the other hand, it may negatively affect the natural enemies. Further studies are required as it could also affect pollinators making its use questionable for crops such as tomatoes (Hemming *et al*. 2006).

APHIDS

Aphids are serious pests of the Solanaceae and other vegetables crops. The most common species are the melon or cotton aphid *Aphis gossypii* Glover, the green peach aphid *Myzus persicae* (Sulzer) and the potato aphid *Macrosiphum euphorbiae* (Thomas) (Homoptera: Aphididae). They are major pests because they can reproduce asexually, complete several generations within a growing season and they actively feed on the plant sap by inserting their stylets into the phloem, which leads to a loss of plant vigor and productivity. Aphids excrete large amounts of honeydew, which promotes the growth of sooty molds, causing a reduction in photosynthesis and the market value of the fruit. They are extremely polyphagous and this makes the infestation of the new crops easier. They are also effective vectors of plant viruses. In particular, *M. persicae* is able to transmit more than 100 plant viruses, for example cucumber mosaic virus (CMV) which is one of the most important and damaging viruses of vegetable crops. Moreover, aphids are a difficult group to control because they relatively easily develop resistance to insecticides (Foster *et al.* 2000; Critini *et al.* 2008). This attribute was a main motivation for the change from chemical to biological control (Devonshire 1988). Aphids are attacked by several natural enemies, including parasitoids, predators and entomopathogens.

Parasitoids

Aphid parasitoids belong to the families Aphidiidae and Aphelinidae of the Hymenoptera. The adults of the Aphidiidae are usually 2-3 mm long. Their colour can be partially black, brown, yellow or orange. The adults feed on honeydew. Females of the aphidiids insert a single egg (solitary parasitoids) in the abdomen of the aphid victim (host). The larva of the parasitoid develops inside the host body consuming its fluids and later the tissues. The host can continue to feed and develop (koinobiont parasitoids). The larva completes its development inside the host and pupates inside the host. At the pupation time the host is killed, having been entirely emptied as the larva consumes all the internal tissues of the host. At this stage, the host skin hardens and swollen and becomes a ‘mummy’ (Rabasse and Wyatt 1985). The fully developed larva cuts a hole in the underside of the host and attaches it to the plant by silk. The adult emerges through a round hole that is created in the dorsal side of the abdomen of the host, in the region close to the siphunculi. Parasitized aphids are not easily distinguished from healthy ones during the early stages of the parasitoid’s development. Later, they become less mobile and more rounded (swollen) in shape.

Usually young aphids are preferred for oviposition, although all instars can be accepted (Rabasse and Wyatt 1985). The preference for smaller hosts can be related to their less developed defence behaviour (Chau and Mackauer 2000; Walker and Hoy 2003). However, in koinobiont parasitoids the suitability of a given host is not based only on its size, since the host continues feeding during parasitization, and this may result in a variable availability of nutrients, irrespective of the host’s size at parasitization (Harvey *et al*. 2000, 2004; Colinet *et al.* 2005). The aphidiids can enter diapause at the larval or pre-pupal stages in the host. *Aphidius ervi* (Haliday) entered diapause under a photoperiod of 12 h light:12 h dark, at a higher proportion at 12°C than at 15°C, whereas the second larval stage of the parasitoid was more sensitive (Christiansen-Weniger and Har-die 1999).

Although there are many parasitoid species that attack aphid species in the open field, only a few of them have shown potential to control aphids in greenhouse environments. Among four aphid parasitoids (*Aphidius colemani* Viereck, *Ephedrus cerasicola* Stary, *Lysiphlebus testaceipes* Cresson and *Aphidius matricariae* Haliday), *A. colemani* was the most effective against *A. gossypii* in laboratory experiments (van Steenis 1995). The fecundity of *A. colemani* was 302 eggs at 20°C and 388 eggs at 25°C, and the developmental period lasted 12.7 and 10.0 days, respectively. The intrinsic rate of population increase was comparable to that of *A. gossypii* (van Steenis 1993). This parasitoid can parasitize all instars of *M. persicae* and *A. gossypii*, and prefers the younger ones. Hosts parasitized at the 1st and 2nd instars become mummified before reaching the adult stage (Perdikis *et al.* 2004). This preference may have considerable implications for biological control, considering that aphids parasitized early in their life do not reach adulthood and thus do not produce offspring (van Steenis and El-Khawass 1995), while young aphids are more abundant at the early stages of an aphid population increase (Lykouressis 1982; Lykouressis and van Emden 1983) and in effective biological control, it is crucial to suppress the pest population at its early stage of establishment on the crop. In the search for effective natural enemies of aphids in protected crops in Brazil, the native parasitoids *A. colemani* and *L. testaceipes* proven to prefer *A. gossypii* to *M. persicae* (Bueno *et al.* 2006). The optimum temperature for the development of *A. colemani* on *A. gossypii* was 22°C and the lowest developmental temperature threshold was 5.94°C, whereas mummies were not produced at 31°C (Sampaio *et al.* 2007).

Aphidius colemani is widely used in biological control programmes against *A. gossypii* on eggplant and cucumber. Apart from its introduction by periodic release, open-rearing units (banker plants) based on maize, wheat and ryegrass plants infested with aphid species that do not infest the vegetable crops showed a high potential as a strategy for the introduction of the parasitoid in glasshouse cucumbers (Jacobson 1998; Yano 2006).

The use of banker plants for the control of insect pests in vegetable greenhouses offers several benefits, such as lower cost, increased efficiency, early release of biological control agents and constant release of natural enemies in the greenhouse. Continuous release has a stabilizing effect on the aphid-parasitoid system, but problems may arise due to parasitization of secondary parasitoids, that is detrimental to the population of the primary parasitoids i.e. the parasitoids that control aphids, and aimed to be established in the greenhouse (such as *A. colemani*). Thus, another system based on an aphid predator is being developed on banker plants (Yano 2008).

The apheliniid parasitoids (Hymenoptera: Aphelinidae) of aphids belong to the genera *Aphelinus* Dalman and *Mesidia* Forster. They are smaller that the aphidiids (usually less than 1 mm in length) and are koinobiont solitary endoparasitoids. The host is transformed into a mummy, but in this case the mummies are black and elongated (Hagen and van den Bosch 1968). Adults feed on honeydew, but they also feed on the host's fluids (Stary 1988). The female inserts her ovipositor in the host's body and feeds on the fluid that emerges from the wound. The host afterwards fails to survive. *Aphelinus abdominalis* (Dalman) shows a longer life span than the aphidiids as it completes its development within a period of 23.5 days at 20°C (Haart and Holler 1992). Its fecundity was 158 eggs on *M. euphorbiae* on eggplants at 26°C (Jarosik *et al.* 1996). However, host mortality due to the consumption of body fluids (host-feeding) might not be important, as in another species each female killed only one host per day (Bai and Mackauer 1990). *Aphelinus abdominalis* is used against the aphid *M. euphorbiae* in greenhouses with positive results (Holler and Haardt 1993). This parasitoid could establish in unheated tomato greenhouses and contributed to the control of *M. euphorbiae* (Alomar *et al.* 1997). The evaluation of the parasitoid *Aphelinus asychis* (Walker) againt *A. gossypii*, *M. persicae* and *M. euphorbiae* showed that this species could be an effective biological control agent against these pest aphids and therefore further evaluations should be undertaken (Tatsumi and Takada 2005).

Predators

Aphid populations are suppressed by a high number of predators. In greenhouse vegetable crops the predators that are used in aphid biological control are the predatory midges (Diptera: Cecidomyiidae), chrysopids (Neuroptera: Chrysopidae), coccinellids (Coleoptera: Coccinellidae) and mirids (Hemiptera: Miridae).

Predatory midges belong to the insect order Diptera. The adults are brown-red with a length of about 2.5 mm (Nijveldt 1988). Predators of aphids occur within the family Cecidomyiidae. Although this family includes mainly phytophagous species, there are a few exceptions. *Aphidoletes aphidimyza* Rondani feeds only on aphids and is highly polyphagous as it feeds on more than 80 aphid species (Yukawa *et al.* 1998). Its life cycle includes the egg, the larval stage (3 instars), the pre-pupa, pupa and the adult. The eggs and larvae are orange in colour. The fully developed larvae reach 2.5 mm in length, and pupate in the ground by creating a cocoon from soil particles.

The larvae are predaceous on aphids and feed by piercing the aphid body with their mouthparts. This paralyzes the aphid and the body fluids are sucked out. The adults feed on honeydew to support the maturation of the eggs (Uygun 1971). Adults are nocturnal (Uygun 1971).

The females actively search and efficiently locate the aphid colonies (El Titi 1974). The honeydew presence aids them to locate the aphid prey. Females of this predator showed an olfactory response to honeydew excreted by *M. persicae* under laboratory conditions. Female midges laid more eggs on pepper plants infested with higher densities of *M. persicae* (Choi *et al.* 2004). Generally, the females prefer to lay eggs in dense aphid colonies or nearby as the larvae move for only short distances. Oviposition rates were proven to increase with density of the aphid *M. euphorbiae* (Lucas and Brodeur 1999). *Aphidoletes aphidimyza* has been proven effective against *M. persicae* on tomato, eggplant and sweet pepper (Markkula *et al.* 1979; Meadow *et al.* 1985).

Aphidoletes aphidimyza enters diapause in response to short day conditions in autumn. Diapause is induced in the last larval instar and in the pupual stage. At photoperiods below 15 h, 100% of the larvae entered diapause. However, the use of low intensity radiation during the night prevented diapause (Gilkeson and Hill 1986a). Extensive research was successful to find and commercialize non-diapausing biotypes (Gilkeson and Hill 1986b). Diapausing larvae have been used as a suitable storage stage of the predator with promising results (Košťál *et al.* 2001). The predator showed a reduced potential for establishment when the glasshouse floor was covered with plastic, as this is a barrier to the pupation of larvae. For this reason some kind of protection by the addition of peat or other material could be considered (Gilkeson 1990a). The pupation of the predator in the soil also has important consequences in the development of its rearing techniques. In mass rearing, normally the larvae develop within dense colonies of aphids and when they mature they fall from the plants to the soil or a suitable substrate to pupate. The substrate is such that enables the easy removal of the pupae. Pupae are durable to the transport conditions and this is the stage which is suitable for commercialization and release of the predator. The potential for long-term low-temperature storage of this natural enemy is crucial for its wider use. Larvae in diapause (in their cocoons) could be stored for 3 months at 4°C with a RH of 100%, with a mortality of 25% (Havelka 1980). Diapausing or non diapausing larvae stored at 5°C for a period of 8 months survived showing less than 9% mortality (Gilkeson 1990b). Variation in diapause intensity of different populations can be associated with the variability of the results of the low-temperature storage and cold hardiness in populations of *A. aphidimyza* (Košťál *et al.* 2001).

The green lacewing, *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae), is the most important lacewing used in aphid control (New 1988). It passes through the egg, larva (3 instars), the pre-pupa, pupa and the adult stage (Canard and Principi 1984). The longevity of the adults can be several months (Canard and Principi 1984). One female can produce up to several hundred eggs (Chang *et al.* 2000). The presence of aphids is not a perquisite for the selection of an egg-laying site. The larvae feed on aphids, and the adults on pollen and honeydew. A single larva can kill about 400 aphids, of which 80% are consumed in the third instar (Scopes 1969). *Chrysoperla carnea* consumed 292.4 or 272.6 late instar nymphs of *A. gossypii* or *M. persicae* respectively, during developmet. The proportions of aphids consumed by each larval instar was 3.9-7.1% by the first, 12.0-16.8% by the second, and 78.1-83.9% by the third instar (Liu and Chen 2001). Prey preference of the predatory lacewing *Dichochrysa prasina* Burmeister (Neuroptera: Chrysopidae) was investigated among various prey and it was demonstrated that nymphs of *M. persicae* were among the most favorable for enhancing development and adult longevity and fecundity (Pappas *et al*. 2007).

The prey is recognized by direct contact and prey search is random (Canard and Duelli 1984). The larvae cannot distinguish between the parasitized and non-parasitized aphids, and therefore they consume both (Bay 1993). In periods of prey absence, cannibalism occurs (Canard and Dueli 1984). In short photoperiods, the adults enter diapause and the larval is the most sensitive stage (Canard and Principi 1984). Larvae of *C. carnea* have been successfully used to control aphids on peppers and eggplants (Hassan 1977; Castaldi 1999). On cucumber the results were not satisfactory as the leaf trichomes interfere with the searching activity of the larvae (Scopes 1969). In general, the results of the application of this predator were better on plants with dense foliage and evenly spread prey (Tulisalo 1984).

Ladybirds (Coleoptera: Coccinellidae) are major predators of aphids. The adults and the larvae are predacious, but adults can also feed on pollen, nectar or fungi. However, feeding on aphid prey is required for egg production (Sundby 1968). In general, four larval instars are present. Fecundity depends on the aphid species, while voracity depends largely on the age of the predator and the age and species of the aphid prey. During development a single larva can consume several hundreds of aphids and particularly in the last larval instar. The use of coccinellids against aphid infestations in greenhouse environments has been evaluated in certain cases. Final-instar larvae of *Semiadalia undecimnotata* (Schneider) were released against *Aulacorthum solani* (Kaltenbach) (Homoptera: Aphididae), *M. euphorbiae* and *M. persicae*, on eggplants. Although there was a considerable reduction on the aphid numbers the application of the method in large scale was questioned due to several constraints such as the the need for large numbers of predators' larvae but also the adult mobility. It was proposed that the problem of adult mobility could be overcome if better adapted exotic strains or less mobile predators were used (Ferran and Larroque 1984). As it was proposed by Hodek and Honěk (1996) coccinellids may be more suitable for releases when large numbers of aphids have been developed on the plants that might occur in cases of failure of control measures. The use of the convergent lady beetle *Hippodamia convergens* Guerin-Meneville and the Asian lady beetle *H. axyridis* for aphid biological control in greenhouse crops has given variable results, mainly due to their tendency to emigrate. This tendency is stronger when the prey in the greenhouse cannot cover the nutritional needs of the predators (Obrycki and King 1998). To reduce this potential, larvae of the predators were released in the greenhouses instead of adults, but in this case there was a failure in population build up or delayed dispersion within the greenhouse (Lommen *et al.* 2008). Efforts to avoid these discrepancies include the rearing of flightless *H. axyridis* adults (Tourniaire *et al.* 2000). Lommen *et al.* (2008) used naturally occurring *Adalia bipunctata* L. flightless morphs against aphids on pepper plants, and the results showed that the effectiveness of these predators was higher than that of the winged conspecifics, as they remained for a longer time on the plants. However, the aphid population was not eradicated and thus further research is required to investigate the effectiveness of flightless morphs under more realistic conditions.

Predatory bugs of the family Miridae are considered to be effective in aphid control (Albajes and Alomar 1999; Lykouressis *et al.* 1999-2000). Predation rates have been studied against the main aphid pests in solanaceous greenhouse crops. *Macrolophus pygmaeus* showed high predation rates on *M. persicae* and relatively lower on *M. euphorbiae*, a result that was mostly attributed to the larger size of the latter species (Lykouressis *et al.* 2007). This predator feeds on all instars of both aphid species showing a preference to the smaller ones (Lykouressis *et al.* 2007). The rate of population increase of *M. pygmaeus* when feeding on *M. persicae* on tomato was $0.0981d^{-1}$ at 27.5°C (Perdikis and Lykouressis 2002). The potential of this predator to develop a population when feeding on *A. gossypii*, on cucumber proven to be low in laboratory experiments (Perdikis and Lykouressis 2003). However, on eggplant with *A. gossypii* it completed development at a period similar to that when feeding on *M. persicae* (Perdikis and Lykouressis 2000). Temperature also had a significant effect on the predation rate of the mirid predator *M. pygmaeus*, being highest at 30°C, whereas the 5th instar nymphs and the females showed a higher predation rate than the younger nymphs and the males (Perdikis *et al.* 1999). *Macrolophus melanotoma* (previously named *M. caliginosus*) also feeds actively on *M. persicae*, *M. euphorbiae* and *A. gossypii* (Alvarado *et al.* 1997). *Dicyphus tamaninii* has been also proven to cause a significant impact on the population densities of *A. gossypii* as it can consume a high number of *A. gossypii* individuals and particularly those of the young nymphal instars (Sengonca and Saleh 2002).

In addition, the predatory bugs *Anthocoris nemorum* (L.) and *Anthocoris nemoralis* (Fabricius) (Hemiptera: Anthocoridae) showed potential as biological control agents of aphids, particularly *M. persicae*, on which they showed a higher predation rate than on other aphid species (Meyling *et al.* 2003). The predatory bug *Orius similis* Zheng (Heteroptera, Anthocoridae), originated in China, showed a high potential to utilize aphids such as *A. gossypii* (Sengonca *et al*. 2008).

Entomopathogenic fungi

The entomopathogenic fungi that can be used against aphids are *B. bassiana*, *Metarhizium anisopliae* Metchnikoff and *V. lecanii* (Lipa and Smits 1999). The effectiveness of pathogens is greatly affected by the humidity levels. *V. lecanii* requires 90% RH for at least twelve hours in the microenvironment of the spores and maximum infection occurs at 100% RH (Milner and Lutton 1986). The optimum temperature range for spore germination is 20-25°C (Hall 1981) and natural infestations occur at high aphid densities. Six applications of *V. lecanii* at 14 day intervals successfully controlled *A. gossypii* in greenhouses where the RH was kept at sufficiently high levels (Heyler 1993). In formulations, a substrate is added to support sporulation on the insect surface. This fungus has been shown to be more effective against *M. persicae* than *A. gossypii* (Hall 1985).

RH has a great influence on the germination /sporulation of *B. bassiana* (Wraight *et al.* 1998). Shipp *et al.* (2002) showed by cage trials that this fungus can be effective in greenhouses not only against *A. gossypii*, but also against *F. occidentalis* and *T. vaporariorum* on tomato and cucumber. The percentage of pest infection was 81-96% at 85-91% RH. However, to achieve sufficient control, repeated applications of the fungus should be conducted. The use of a fungus can interfere with the use of parasitoids. For example, females of the parasitoid *A. ervi* were unable to discriminate between infected and healthy hosts of the fungus *Pandora neoaphidis* (Remaudière and Hennebert) Humber, until the host was dead and sporulation had started (Baverstock *et al.* 2005).

LEAFMINERS

Leafminers of the genus *Liriomyza* Mik (Diptera: Agromyzidae) are important pests of vegetable crops. These species are polyphagous, have developed resistance and are widely distributed in regions outside their area of origin. The main species are *Liriomyza trifolii* Burgess, *Liriomyza bryoniae* Kaltenbach and *Liriomyza huidobrensis* Blanchard.

L. trifolii was reported from the eastern United States (Spencer and Steyskal 1986), but later dispersed to several, distant areas of the world (Minkenberg 1988). *L. huidobrensis* is an American species (Spencer and Steyskal 1986) which in the late 1980s was recorded in Europe, mainly due to the import of infested plant material. *L. bryoniae* is a species native to the arctic region. This species has been mainly related to tomato, but is in fact a polyphagous species (Spencer 1990).

The females feed on the drops of plant sap that emerge from the wounds they create on the leaves using their ovipositors. The males also feed on these fluids. The wounds are easily recognized on the leaves, and particularly the younger ones. They are considered to be the first sign of the presence of the pest in the greenhouse. These punctures could reduce photosynthesis and also provide enter points to pathogens (Matteoni and Broadbent 1988). The larvae feed inside the leaf tissue and create mines that are elongate and narrow but widening as the larva grows. The larva passes through 3 instars and then pupates on the leaf or in the ground. In beans, the pupae can remain on the leaves as they are stacked by the trichomes. The colour of the pupae can vary between the winter and summer periods.

The optimum temperature for the development of *L. huidobrensis* is 25°C and the lowest developmental threshold is 8°C (Minkenberg and Helderman 1990). *L. trifolii* is less adapted to low temperatures as population increase occurs at temperatures higher than 16°C (Minkenberg 1988). The rates of natural population increase of *L. trifolii* at 25°C on tomato and melon were 0.1607 and 0.1429, respectively and its population growth rate was highest at 25°C (Ozawa *et al.* 1999). *L. bryoniae* and *L. huidobrensis* were able to overwinter outside the greenhouses (van den Linden 1993). The ability of leafminers to survive winter in conjunction with their polyphagy indicates that phytosanitary measures within and in the close proximity of the greenhouses are essential to reduce the damage potential of these insect pests.

The damage that leafminers cause is primarily a lowering of the photosynthetic potential of the plants, but the seriousness of this damage is difficult to assess because the plants may have the ability to compensate for the loss of photosynthesis by increasing that of the remaining leaves. Ledieu and Heyler (1982) showed that the yield of plants heavily damaged by leafminers was only 17% lower than the controls. It appears that the effect of the infestation is related to the location of the damaged leaves on the plants. Damage to the lower leaves is of minor importance, but damage to the leaves close to the tomato truss, when the fruits are less than half developed, can be significant (Wyatt *et al.* 1984). For example, in this case, damage levels of 30 mines per leaf resulted in a yield reduction of 10%.

Natural enemies

Leafminers have several natural enemies, which are mostly parasitoids. The natural enemies that are commercialized for leafminer control are the parasitoid species *Diglyphus isaea* Walker (Hymenoptera: Eulophidae), *Dacnusa sibirica* Telenga (Hymenoptera: Braconidae) and *Opius palipes* Wesmael (Hymenoptera: Braconidae).

Diglyphus isaea is an ectoparasitoid that lays its eggs in the mine, beside the leafminer larva. The female lays 1-5 eggs in each mine but finally only one larva completes its development. The females paralyze their hosts with venom and prefer to oviposit on or near hosts of the 2nd or 3rd instar (Ode and Heinz 2002). The parasitoid larva is clearly seen in the mine by the aid of backlighting. An important characteristic of this parasitoid, with significant value for its effectiveness as a biological control agent, is the host feeding. The female pierces the leafminer larva body with her ovipositor and feeds on the fluids that are excreted. As a food source, it uses larvae of the 1st or 2nd instar of the leafminer (Ode and Heinz 2002). Host feeding can contribute 15-40% of the total mortality of the pest population (Minkenberg 1989). At 15°C, larvae of *D. isaea* needed about 28 days to complete development on *L. huidobrensis* and about 27 days on *L. trifolii*. At 25°C, parasitoid development was completed within about 10 days. The theoretical threshold was 9.2°C and optimum temperatures for female and male development on *L. trifolii* were 33.3 and 32.3°C, and on *L. huidobrensis* 32.6 and 31.0°C, respectively (Bazzocchi *et al.* 2003).

The mass production of *D. isaea* has attracted interest for the collection of data on its ecological aspects. This is because, despite its effectiveness, it was relatively expensive to produce due to the high proportion of males in the progeny. Host stage- dependent sex ratio studies revealed that the larval stage of the host (small and large larvae given together) should be used for the production of a higher ratio of females in the progeny (Chow and Heinz 2005).

Natural parasitism can be important in the regulation of leafminers, as there are several natural enemies indigenous to the areas of origin of these pests (Benuzzi and Radoni 1992). Parasitism of *L. sativae* Blanchard on cucumber was found to reach 39% in unsprayed greenhouses, with *D. isaea* the most common species in Iran (Fathipour *et al.* 2006). Their natural parasitism is low early in the season, but increases considerably later (Parella 1987).

Dacnusa sibirica is a Palearctic, solitary endoparasitoid that lays its egg in the body of the leafminer larva and the adult emerges from the host pupa. It prefers to oviposit on larger hosts although all instars are accepted (Hendriske *et al.* 1980). This species is less adapted at higher temperatures as its fecundity and longevity were found to be similar between 20 and 25°C (Minkeberg 1990).

A comparative study on the suitability of *L. sativae*, *L. trifolii* and *L. bryoniae* as hosts for the parasitoid *O. pallipes* showed that it can be a useful biological control agent of *L. trifolii* and *L. bryoniae*, but is not able to control *L. sativae* (Abe *et al.* 2005). Results on the developmental time and offspring size of a solitary koinobiont parasitoid, *Gronotoma micromorpha* Perkins (Hymenoptera: Eucoilidae), indicated that *L. trifolii* and *L. bryoniae* are both acceptable and suitable hosts, and this parasitoid may be a useful biological control agent of both leafminer species (Abe 2006).

Kaspi and Parella (2006) evaluated the potential of using *D. isaea* in parallel with the application of the sterile insect technique (SIT). In SIT a large number of sterilized mass reared insects (usually with radiation) is released under the aim the sterilized males to succefully compete with the wild ones for the copulation with the wild females. If succeded, then the number of the offspring in the next generation are highly reduced (Kaspi and Parella 2003). In the case of leafminers, a synergistic effect was found and control was more efficient than the use of either method alone. This was attributable to the fact that the numbers of adults are suppressed by the SIT and that of larvae with the parasitoids (Kaspi and Parella 2006). This technique has been tested in greenhouse experiements also against whiteflies but although the pest population was reduced it was not proven adequately effective (Calvitii *et al.* 1998).

Foliar applications of entomopathogenic nematodes against leafminers have been tested and have been shown to be potentially effective (Williams and Walters 2000). They belong mostly to the genus *Steinenerma*, and can contribute to the control of the leafminers, but their co-use with the parasitoids is questioned as they may also infect the parasitoid larva. The combined use of the eulophid parasitoid wasp *Diglyphus begini* Ashmead and the entomopathogenic nematode *Steinernema carpocapsae* Weiser for control of the leafminer *L. trifolii* on chrysanthemums showed that it could be effective, but interspecific interference and intraguild was recorded and thus further research is required to investigate the proper time of application of the beneficials (Sher *et al.* 2000).

THRIPS

Thrips (Thysanoptera: Thripidae) are elongate insects of small size, with an adult length <2.5 mm and life stages comprising the egg, larval stage with 2 instars, the prepupal and pupal stage and the adult. The kidney-shaped eggs are laid under the leaf surface. The larva feeds on the plant tissue which can be the leaf, flowers or fruits. The pupal stages are found on the plants but usually in the upper layer of the soil. The damage is caused by the adult and the larval stage. When feeding on the plants they destroy the plant cells and as a result the leaves can curl, and the photosynthetic capacity of the plant is reduced. They prefer to feed on the young developing tissues. They are commonly recorded on the flowers, where they feed on pollen and nectar and on the young developing tissues of the reproductive organs, resulting in fruit deformations. Some of these species can be very destructive as they are also vectors of plant viruses of the family Tospoviridae.

Only a very small number of species cause damage to protected crops. However, they are considered to be serious pests as they are polyphagous, damage the fruits, show a relatively high reproductive potential, have a short generation time, easily develop resistance to insecticides, vector plant pathogens, can be active during winter, are protected in the crevices or other concealed places on the plants, and certain life stages (e.g. eggs and nymphs) are protected in the plant tissue and soil, respectively.

The major pest species of concern to vegetable crops in protected cultivation are the species *Frankliniella occidentalis*, *Thrips tabaci* Lindeman and *Thrips palmi* Karny (Thysanoptera: Thripidae). *F. occidentalis* is considered to be the most important of these species. It originates from the western USA, but in the 1970s and 1980s it was distributed to protected crops worldwide. It is considered to be a cosmopolitan species. It can cause economic damage to greenhouse crops by feeding or ovipositing on developing fruits and leaves. It is highly polyphagous, with a host list that includes more than 244 plant species from 62 families. It is a serious pest of more than 200 species of vegetables and ornamentals (Lewis 1997). It can relatively easily develop resistance to insecticides (Brødsgaard 1994; Broadbent and Pree 1997) and is a very effective vector of tospoviruses, such as the tomato spotted wilt virus (TSWV) (German *et al.* 1992). This virus causes bronzing of the young leaves that roll inward and turn chlorotic. On fruits, spots 10 mm in diameter develop with concentric, circular markings. The spread of this virus might not be avoided by chemical treatments as the adults can successfully transmit the virus before they die (Momol *et al.* 2004). However, biological control combined with other methods (trapping, exclusion nets, sanitary measures) can substantially aid in the control of the pest in the greenhouse environments (Jacobson 1997).

Thrips tabaci is a species that originated in the Middle East but subsequently has become widespread worldwide. *Thrips palmi* originates from south eastern Asia, but has relatively recently become distributed to other areas, such as North America and the Caribbean (Cannon *et al.* 2007).

Natural enemies

For the control of thrips, careful application of phytosanitary measures is essential. These include the transplantation of plants that are free of the pest, prevention of an invasion by adults in the greenhouse and the avoidance of emergence of thrips from the soil where it may have survived from the previous growing season.

The main biological control agents of thrips in protected vegetable crops are predatory mites, heteropteran bugs and entomopathogenic fungi, but also nematodes and parasitic wasps. In many cases more than a single agent is used. Predatory mites are the most commonly used means of biological control of thrips. They belong mostly to the family Phytoseiidae. The phytoseiid predators were primarily considered to be mostly related to spider mites, but proved to be effective against thrips. The reasons for their effectiveness relate to their potential to utilize alternative food sources and their numerical response to the prey population (Sabelis 2008).

A major biological attribute that make phytoseiids useful in biological control is their utilization of pollen. Their phytophagous habits enable these predators to maintain populations on the plants in the absence of thrips and therefore existing populations can control thrips at the initial phase of crop colonization. Peppers are particularly compatible with the use of phytoseiid mites because they continually produce a high amount of pollen.

To aid establishment, the predators are released in the greenhouse within sachets, which are rearing units where stored product mites are available as food for the predators. This technique enabled the use of the predators on plants, such as eggplant or cucumber, which are less efficient pollen producers. The addition of pollen on cucumber as an alternative food source can facilitate the establishment and reproduction of predatory mites (van Rijn *et al.* 1999).

The range of hygrothermal conditions that might occur in the greenhouse can influence the rate of predation of *Neoseiulus cucumeris* Oudemans on *F. occidentalis* (Shipp *et al.* 1996). *Iphiseius degenerans* Berlese proved to be more effective than *N. cucumeris* when released at the same rates in sweet pepper, and was more efficient than *N. cucumeris* in reducing the numbers of thrips on the flowers (van Houten and van Stratum 1995). *Neoseiulus cucumeris* feeds mainly on first instar larvae and thus, thrips' population could continue to increase (Bakker and Sabelis 1989). Therefore, late release of the predator may resut in insufficient control of the pest due to lack of sychronization (Shipp and Wang 2003).

A new thrips predator that is being evaluated and mass reared is the phytoseiid *Typhlodromips montdorensis* Schicha, which showed promise against *T. tabaci* on cucumber and has recently become commercially available (Steiner and Goodwin 2002).

The predatory mite, *Amblyseius swirski* has shown effectiveness against *F. occidentalis* (van Houten *et al.* 2005). It was introduced to the market in 2005 for the control of thrips (Bolckmans 2005). This predator can reach places where the thrips are sheltered, but mostly kills 1st-instar larvae (Chow *et al.* 2008). Immatures of this predatory mite fed upon first larval instars of both *F. occidentalis* and *T. tabaci* whereas females readily accepted first instar larvae. However, less than one-third of immature reached adulthood and females oviposited less than one egg per day at 25°C. Therefore, its effectiveness against thrips should not be closely associated with the suitability of thrips as food source for the predator but possibly to other factors such as the simultaneous availability of other prey (such as whiteflies) on the plants (Wimmer *et al.* 2008). However, the potential of this mite in thrips control requires further exploitation.

Predatory bugs are also major biological control agents of thrips in greenhouse environments. The most important of these predators are the species of the genus *Orius* (Hemiptera: Anthocoridae). They are commonly recorded in flowers and thus they share the same niche as their prey, which indicates their potential in the control of thrips. They can also feed on pollen and then can be effectively established in periods when their prey is not present. Nymphs of *Orius insidiosus* (Say) failed to complete development on bean leaves without prey or pollen; but when pollen was added they managed to complete developmet at a high rate (Kiman and Yeargan 1985; Richards and Schmidt 1996). This has been also proved for other species such as *Orius tristicolor* (White) (Salas-Aguilar and Ehler 1977). Control of thrips with the use of *Orius* was more effective on plants that produce a lot of pollen, such as sweet peppers. On plants that produce less pollen (e.g. cucumber) they face difficulties in establishing, with adverse consequences for the establishment of the second generation. However, *Orius* are less effective on tomatoes. *Orius insidiosus* failed to establish on tomato crops (Shipp and Wang 2003). This species showed a poor functional and numerical response to thrips on tomato (Coll and Ridgway 1995). These researchers suggested that *Orius* searching activity was serioudly imposed due to the presence of glandular trichomes on the tomato leaves and stems. Adverse effects of tomato on *Orius* species such as difficulties in foraging activity and walking speed to even the death of the nymphs or failure to reproduce, have been also reported in other studies (Coll *et al.* 1997; Lykouressis *et al.* 2002).

Orius species feed not only on the larvae, but also on the adults of thrips. Experiments on predation rates of the predator *Orius sauteri* Poppius showed that nymphs killed more *T. palmi* larvae than adults, but this difference was not recorded in adult predators (Nagai and Yano 2000). The predation rates of *O. insidiosus* were proven higher on second instar larvae than adults of *F. occidentalis* in arenas with pepper flowers. Predation of both larvae and adults was most likely to occur inside flowers (Baez *et al.* 2004).

The biological characteristic of *Orius* that has to be taken into serious consideration when selecting the species to be used in biological control is their tendency to enter diapause under low temperatures and short day lengths. Exposure of fifth instar of *O. insidiosus* to short photoperiods (10:14 L:D) resulted in the production of more than 50% of females with preoviposition period exceeded 14 days. The adults less than 14-d old also were sensitive to photoperiod (Ruberson *et al.* 2000). For this reason, a major research effort continues to be the search for new species or biotypes which are less vulnerable to photoperiodic induction. In this respect, *Orius albidipennis* Reuter is an interesting species because it does not enter diapause (Cocuzza *et al.* 1997). Another characteristic of *O. albidipennis* is that this is better adapated to high temperature conditions than *O. laevigatus*. The fecundity of the two predators was similar at 20, 25 and 30°C, but at 35°C it was significantly higher for *O. albidipennis* (Sanchez and Lacasa 2002).

The phytoseiids are more efficient in searching for thrips in concealed places of the flower whereas the bugs readily feed on the adults. In general, *Orius* can be more effective in reducing the pest population quickly as they feed on both the larvae and the adults and they show a higher predation rate than the phytoseiids. In small arenas the predation rates of *O. laevigatus* were proven higher than *N. cucumeris* and *I. degenerans* on *F. occidentalis* (Scott Brown *et al.* 1999).

The combined use of *Orius* predators with phytoseiid mites provides more effective control of thrips because of their differences in feeding rates on the different stages, and also their searching efficiency in the different plant parts (Brodsgaard and Enkegaard 2005). The predatory bugs are released with the aim of becoming established and developing populations, whereas the phytoseiids are used with the aim of quick control. It has been reported that *Orius* should be released on pepper crops nearly one month after transplanting, when the plants start flowering (Tavella *et al.* 1996).

Orius species have been recorded on several non-cultivated host plants that offer refuges and places with alternative prey and pollen resources. Research recently focuses on the evaluation of native, non-crop host plants for the conservation of *Orius* species. The aim is that populations already present can enter the greenhouse and establish on the crops. *Orius niger* and *O. laevigatus* can naturally colonize greenhouses and highly contribute to the control of thrips if not disturbed by chemical applications (van de Veire and Degheele 1992; Tavella *et al.* 1996, 2003).

Recent studies have proved the potential of native *Orius* species, such as *O. sauteri* to provide effective control against *T. palmi. Orius strigicollis* Poppius has been a main natural enemy used in the control of thrips due to its lower incidence of diapause and ease of mass production (Shimizu and Kawasaki 2001; Yano 2004). Yano (2008) reported that the conservation of *O. strigicollis* on natural host plants rich in pollen had a positive impact on the biological control of thrips on eggplant and pepper. The main criteria for selection of the species most suitable for commercialization were their reproductive diapause and ease of mass production. Among these species *O. sauteri* has been most studied (Nagai and Yano 2000). Knowledge of the minimum number of eggs required for mass rearing of the predator is considered to be an essential prerequisite for developing more suitable techniques for its mass rearing (Yano *et al.* 2002).

In addition to the *Orius* species, predatory bugs of the genera *Macrolophus* and *Dicyphus* (Hemiptera: Miridae) have shown an important potential for the control of thrips on vegetable crops (Riudavets and Castañé 1998).

Among fungal pathogens, *V. lecanii* can be an effective biological control agent of thrips (van der Shaaf *et al.* 1991). The major climatic condition that influences the effectiveness of this fungus is the RH, and particularly the humidity on the plant surface (Shipp *et al.* 2003). The stage of the host is also a significant parameter in its effectiveness. The eggs are well protected under the leaf tissue. The larvae are little affected as they molt and by doing this most of the spores are removed before the hyphae enter the body (Vestegaard *et al.* 1995). In addition the larvae exist mostly in the flowers and this dramatically reduces exposure to the pathogen. On the other hand, pupae are also protected under the substrate. For these reasons, this fungus should be used in combination with other means of control. In this concept, it becomes important to study their compatibility with other biological control agents. Related studies have shown that *B. bassiana* can be readily combined with the predatory mites and immature parasitoids (Jacobson *et al.* 2001).

In thrips control there are also several biological control agents that in certain cases have shown a potential for effectiveness. Parasitoids of thrips have been evaluated in depth, but are proved to have a relatively low potential (Loomans 2003). The predatory mirid bug *D. hersperus* can reduce the population of *F. occidentalis* on greenhouse tomatoes. However, this predator may cause damage to the tomato fruit when the thrips population is low. The ratio for effective control and low risk of damage was 0.5-1:10 *D. hesperus*: *F. occidentalis* when the thrips population density ranged from 60-150 thrips per plant (Shipp and Wang 2006).

Finally, entomopathogenic nematodes have shown a potential to reduce the population of thrips at the pupal stage (75-97% mortality) (Helyer *et al.* 1995).

SPIDER MITES

Spider mites belong to the family Tetranychidae. Some of these are serious pests of greenhouse and open field crops. The most important is the two-spotted spider mite (*Tetranychus urticae*). The adult female two-spotted spider mite has a straw-yellow to green colour with two dark spots on both sides of the body. Young individuals are similar in appearance to the adults. The lowest threshold for development is 12°C (Jeppson *et al.* 1975). The female lays more than 100 eggs (Shih *et al.* 1976). Most damage occurs on the under surface of the leaves but can be seen from above as pale areas. Severely damaged plants turn pale yellow and may be covered by webbing produced by the mites. Damage can result in defoliation, and even in the death of the plant.

Natural enemies

Biological control of the spider mite is mostly based on the use of predatory phytoseiid mites, the most important of which are the specialist predator *Phytoseiulus persimilis* and the generalist *Neoseiulus californicus* McGregor. *Phytoseiulus persimilis* is commonly used against *T. urticae* worldwide on cucumber, tomato and sweet pepper (van Lenteren and Woets 1988). The adult is red in colour and larger than the female of *T. urticae*. Its developmental rates on beans were optimum at 27°C (at 60-85% RH) and under these conditions the control of the spider mite was most effective in comparison to temperatures ranging from 15-27°C. A considerable reduction in egg viability was recorded at 27°C and 40%RH, conditions under which the predator proved to have a low potential for spider mite control (Stenseth 1979). Under high temperatures and low humidity conditions, spatial segregation has been observed between the spider mite and the predator as the former accumulate on the top of the plants and the latter in the lower parts. This results in a failure of mite control (Nihoul 1992). The effectiveness of *P. persimilis* has frequently been considered to be lower in plants that are covered with trichomes, such as tomato. Mortality of the predators increased under spring and summer conditions and this was related to the phenology of the trichomes (Nihoul 1994). The predator faced serious difficulties moving on the tomato plants and for this reason it was proposed that it should be released only on plants that were already infested by the mite (Vanharen *et al.* 1987). The rearing of the predators for 4 generations on tomato instead of bean has been shown to considerably increase the performance and effectiveness of the predator on tomato (Drukker *et al.* 1997).

Other phytoseiid mites that have been used in the control of spider mites are *Neoseiulus barkeri* Hughes, *N. fallacis* Garman and *N. californicus*. *Neoseiulus barkeri* showed a high capacity to reduce the number of spider mites in laboratory experiments (Fan and Pettit 1994). It was also effective in the control of the spider mite in laboratory experiments (Karg *et al.* 1987). *Neoseiulus californicus* performance and particularly its egg viability were affected by the RH and this is a critical factor for its effectiveness in the control of the spider mites. The evaluation of different strains of the predator showed sufficient variability in their resistance to low RH and thus more efficient strains could be selected for use in biological control programmes (Walzer *et al.* 2007). The intrinsic rate of increase of these predators was highest at 30°C (Gotoh *et al.* 2004). This species showed a high population increase when feeding on several mite species including *T. urticae.* However, the performance of this predator and *P. persimilis* was considerably reduced when feeding on *Tetranychus evansi* Baker and Pritchard, a recently introduced pest in Europe and Africa (Escudero and Ferragut 2005). This potential requires further investigation as the plant can play a significant role in the effectiveness of the predator (Koller *et al.* 2007).

Iphiseius degenerans is another effective predator of spider mite. Its threshold for development was found to be about 11°C and its intrinsic rate of increase was highest at 25-30°C. This species seems to be well adapted to the high temperatures that occur in the Mediterranean region (Tsoukanas *et al.* 2006).

Feltiella acarisuga Vallot (Diptera: Cecidomyiidae) is a gall midge that feeds on many species of spider mite. This species was considered to be effective in the control of spider mite on cucumber (Wardlow and Tobin 1990). The larvae have predatory habits and pupate near the veins of the leaves. Third-instar larvae consumed 87.2 *T. urticae* eggs daily, at 26.7°C. Development was completed in a period of 17.4 days. Adult longevity was 13.0 d and fecundity was 33.3 eggs (Mo and Liu 2007). This species responded to changes in prey density and showed a type II functional response (Opit *et al.* 1997). However, extended periods of RH <60% can reduce the potential of the predator in suppressing the population of the spider mite (Gillespie *et al*. 2000). It diapauses as pre-pupae but only a low incidence of diapause was induced under a 8h photoperiod at 25°C and a 16 h skotoperiod at 15°C (Gillespie and Quirring 2002).

Stethorus punctillum Weise is a coccinellid predator of spider mites. This species was able to establish on cucumber and pepper, but not on tomato (Raworth 2001). The activity of the predator increased as temperatures rose from 20 to 25 and 30°C, whereas RH had no significant effect (33, 65 and 90%). It was most active on pepper (Rott and Ponsonby 2000).

The predatory bug *M. melanotoma* has also been shown to be a voracious predator of spider mite eggs, which indicates its potential for the control of this pest (Enkegaard *et al.* 2001). The life table characteristics of this predator were studied when fed on spider mites, and it was revealed that this prey was less suitable than other pests (e.g. whiteflies) for the population increase of the predator (Hansen *et al.* 1999). A related study showed that *M. pygmaeus* can complete its development feeding on *T. urticae* in a period similar to that when whitefly was used as prey on eggplant (Perdikis and Lykouressis 2000). Therefore, *Macrolophus* species can contribute to the control of the spider mite.

TOMATO RUSSET MITE

The tomato russet mite *Aculops lycopersici* (Massee) is a cosmopolitan mite infesting many Solanaceae. It is a worm-like mite of the family Eriophyidae, very small in size. The adults are about 0.2 mm long, not visible without magnification. The data on their development varies. Rice and Strong (1962) stated that optimum conditions were 26.7°C and 30% RH. Threshold development is 10.5°C (Kawai and Haque 2004). It destroys the epidermal cells of the leaflet, resulting in a curling of the leaflet edges, a rusting of damaged tissue, desiccation and plant death (Keifer *et al.* 1982; Royalty and Perring 1988).

Natural enemies

There are a few of predators that feed on the tomato russet mite, but most of them do not seem feasible for a biological control program yet. Bailey and Keifer (1943) observed that a predatory mite, *Seiulus* sp. was effective in home gardens but was not effective as a commercial biological control agent. Predatory mites reported in association with *A. lycopersici* are *Typhlodromus occidentalis* (Nesbitt), *Pronematus ubiquitus* (McGregor) and *Lasioseius* sp. (Rice 1961).

Since then, some predatory mites of the family Phytoseiidae have been tested for their predatory capability on *A. lycopersici*. De Moraes and Lima (1983) observed that *Euseius concordis* (Chant) fed on tomato russet mite but its effectiveness was limited by the presence of *Tetranychus evansi* (problem encountered due to webbing of tetranychid mite). Studies of phytoseiid species by Brodeur *et al*. (1997) showed that *Phytoseiulus persimilis* had actually no predation on tomato russet mite, *Amblyseius cucumeris* developed successfully but failed to reproduce and only *Amblyseius fallacis* showed efficient predation, in laboratory conditions. *A. fallacis* appears to posses several of the biological attributes required to control the mite. It attacks all stages and displays excellent survival (92%), adequate rate of development (6.3 days at 22°C) and good reproductive capacity.

Perring and Farrar (1986) reported a potential use of *Homeopronematus anconai* (Baker) as biological control agent, as this predator is effective in controlling the mite in the laboratory. Haque and Kawai (2002) also reported significantly lower population of *A. lycopersici* in glasshouse tomato plants when *H. anconai* was present and later after studied its predatory effects suggested that it could be used as a bio-control agent against *A. lycopersici* (Haque and Kawai 2003). An adult *H. anconai* consumed an average of 69 *A. lycopersici* deutonymphs per day in laboratory (Kawai and Haque 2004).

Osman and Zaki (1986) reported that *Agistemus exsertus* Gonzalez (Prostigmata: Stigmaeidae) at 30°C and 75% RH devoured 60.3 eggs and 45.3 individuals per day.

BROAD MITE

The broad mite, *Polyphagotarsonemus latus* (Banks) belongs to the family Tarsonemidae. The adult female is 0.2 mm long, light yellow to amber in colour with an indistinct light median stripe. The hind pair of legs is reduced to whip-like appendages. It causes terminal leaves and flower buds to become malformed. The mite's toxic saliva causes twisted, hardened and distorted growth in the terminal of the plant. Leaves turn downward and turn coppery or purplish. Internodes shorten and the lateral buds break more than normal. The blooms abort and plant growth is stunted when large populations are present (Denmark 1980).

Natural enemies

Sixteen species of predators have been reported associated with *P. latus* (Pena *et al.* 1996), most of them belonging to the mite family Phytoseiidae. Moutia (1958) reported that *Amblyseius ovalis* Evans controlled *P. latus* populations very effectively on chilli in Mauritius, by feeding on the eggs end larvae. In the laboratory *A. ovalis* eliminated the broad mite on chilli to 1:100 rate but could not overcome the pest at the ratio 1:150 (Hariyappa and Kulkarni 1989). Smith and Papacek (1985) reported that *Euseius victoriensis* (Womersley) afforded effective biological control of the pest on citrus in Queensland, and Wu (1984) stated that good results were obtained with *Amblyseius nicholski* Ehara and Lee in citrus in China. Efforts to identify predators of *P. latus* were undertaken by Badii and McMurtry (1984) who studied the feeding behavior of several phytoseiids. *Typhlodromus annectens* De Leon, *T. porresi* McMurtry and *T. rickeri* Chant preferred prey larvae, while *E. stipulatus* fed on all but the nymphal stages. Kolodochka and Prutenskaya (1987) reported that *Amblyseius agrestis* prefers spider mites over the broad mite.

CONCLUSIONS AND FUTURE PERSPECTIVES

The use of biological control against insect and mite pests in Solanaceous crops has proven to be both effective and reliable. It shows advantages in comparison with conventional chemical control, such as practically zero resistance development, zero risk of pesticide residues in the produce and environmental protection. For these reasons it is expected that pest control in greenhouse solanaceous crops will increasingly rely on biological control. This trend is clearly shown by the considerable increase in adoption of biological control in southern Europe and other countries worldwide.

The emerging challenges that biological control will continue to face in the future, as in the past, is the introduction of pests in new areas through expanding trade and invasiveness due to climate change. Biological control has proved mostly effective against new pests. However, in the future, biological control agents should be mostly searched for among indigenous natural enemies, due to the potentially negative effects to the native fauna if exotic natural enemies are released in a new area.

Conservation biological control is another perspective as several natural enemies occur within the Solanaceous agro-ecosystems. The exploitation of these beneficial organisms would be worthwhile due to the low cost of application and the enhancement of sustainability, which is a major topic in modern agriculture strategies.

Research focusing on new natural enemies may become a major topic, particularly due to the use of biological control in new areas with variable climatic conditions. Investigations of new biotypes of already commercialized natural enemies will continue further so as to provide improvements in the efficacy of biological control programmes.

The effort to reduce the cost of application of biological control through the development of more efficient mass rearing methods of natural enemies will be also a main objective.

Studies on the relationships among natural enemies are also expected to expand as higher effectiveness could be achieved through the use of combined natural enemies, as opposed to a single natural enemy.

Biological control will continue to provide solutions to pest problems in greenhouse crops in order to serve public awareness of enhanced sustainability in food production.

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