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Preselection of predatory mites to improve year-round biological control of western flower thrips in greenhouse crops

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Abstract

In spring and summer, two groups of natural enemies are successfully used for biological control of western flower thrips, *Frankliniella occidentalis* (Pergande) in greenhouses: phytoseiid mites (*Amblyseius cucumeris* (Oudemans) and, to a lesser extent, *A. barkeri* (Hughes)) and anthocorid bugs (*Orius* spp.). During winter, however, these predators often fail to control the pest. One likely cause for failure is the predators' tendency to enter diapause under short day conditions. In addition, eggs of predatory mites are generally susceptible to low humidity conditions, which often arise in greenhouses when outside temperatures drop below zero, or at bright, hot days in summer. In search for a thrips predator that is not hampered by these conditions, five subtropical phytoseiid species were selected which were known to feed on thrips: *A. hibisci* (Chant), *A. degenerans* Berlese, *A. limonicus* s.s. Garman and McGregor, *A. scutalis* (Athias-Henriot) and *A. tularensis* (Congdon). These species were compared to *A. cucumeris* and *A. barkeri*, with respect to the following features: (1) predation and oviposition rate with young *F. occidentalis* larvae as prey, (2) oviposition rate on a diet of sweet pepper pollen, (3) drought tolerance spectrum of eggs, and (4) incidence of reproductive diapause under short day conditions. The results showed that *A. limonicus* exhibited the highest predation and oviposition rates on a diet of thrips larvae. Moreover, *A. limonicus* females showed total absence of diapause under the conditions tested. A major disadvantage of this species was, however, that its eggs were most sensitive to low air humidity conditions. Least sensitive to low air humidity were eggs of *A. degenerans* and *A. hibisci*. Females of *A. degenerans* and *A. hibisci* also showed total absence of diapause, and intermediate rates of predation and oviposition, on both thrips larvae and pollen. In conclusion, we argue that *A. degenerans* and *A. hibisci* are the most promising candidates for biological control of *F. occidentalis* under conditions of low humidity and short day length. The success of these candidates remains to be shown in greenhouse experiments.

Introduction

One of the major pests of greenhouse crops in Europe and North America is western flower thrips, *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) (many references in recent IOBC/WPRS-bulletins, 1993a,b). It can cause tremendous damage to plants, both by feeding and as a consequence of transmission of viruses (e.g. Ullman *et al.*, 1989). Chemical

control of *F. occidentalis* is undesirable for environmental reasons and because it interferes with biological control of other pests (van Lenteren & Woets, 1988; Shipp *et al.*, 1991). Therefore, an effective biological control agent of this thrips species is needed.

Various groups of natural enemies can be used for control of thrips: predatory mites, anthocorid bugs, hymenopterous parasitoids, and fungal pathogens. The latter two groups have not been studied enough to allow

commercial applications (Loomans & van Lenteren, 1990; Helyer, 1993). At present, the predatory mite *Amblyseius cucumeris* (Oudemans) (Acari: Phytoseiidae) and anthocorid bugs such as *Orius insidiosus* (Say), *O. majusculus* (Reuter), *O. tristicolor* (White) and *O. laevigatus* (Feiber) are used for biological control of *F. occidentalis* in different greenhouse crops (Ramakers *et al.*, 1989; Altena & Ravensberg, 1990; Tellier & Steiner, 1990; van den Meiracker & Ramakers, 1991; Jacobson, 1993). Thrips control, however, is not equally successful in every crop and under all circumstances. In some crops, such as cucumber (*Cucumis sativus* L.), *A. cucumeris* is not a very effective control agent; high numbers of predatory mites have to be introduced throughout the growing season (Ramakers *et al.*, 1989; Bennison *et al.*, 1990). Also anthocorids are not very effective in cucumber, especially at lower thrips densities (Jacobson, 1993; Y. M. van Houten, unpubl.). In sweet pepper (*Capsicum annuum* L.), *A. cucumeris* as well as the anthocorids are much more successful; predator populations can be maintained from March onwards without reintroductions. This persistence, which occurs even in absence of thrips, may be attributed to the presence of pollen as an alternative food source (Ramakers, 1990; van Rijn & van Houten, 1991; van den Meiracker & Ramakers, 1991; van Rijn & Sabelis, 1993). In the parthenocarpic greenhouse cucumber plants pollen is virtually absent.

During winter, biological control of thrips on sweet pepper is less effective. Both *A. cucumeris* and the *Orius* species enter a reproductive diapause which is induced by short-day photoperiods, at low night temperatures (Morewood & Gilkeson, 1991; van Houten, 1991; Ruberson *et al.*, 1991; Gillespie & Quiring, 1993; van den Meiracker, unpubl.). This may explain why mites and bugs failed to become established in this period despite presence of pollen. *F. occidentalis* is found year-round in Dutch greenhouses and causes problems in greenhouse crops also during winter and early spring. Another factor that may affect the success of biological control with *A. cucumeris* is air humidity. Humidity levels in Dutch greenhouses can drop to very low levels during frost periods and on bright days in summer, when ambient temperature is high. It is well known that eggs of many phytoseiid mite species are vulnerable to low air humidity (e.g. Stenseth, 1979; Sabelis, 1981; Dinh *et al.*, 1988; Bakker *et al.*, 1993; Croft *et al.*, 1993).

In this study we report on experiments that aim at selecting candidates amongst phytoseiid mites, in order

to improve year-round biological control of *F. occidentalis* in greenhouse crops. Apart from *A. cucumeris*, *A. barkeri* (Hughes) was examined. Until recently, this species was commercially applied as thrips predator in cucumber (Ramakers *et al.*, 1989; Brødsgaard & Hansen, 1992; Steeghs *et al.*, 1993). The commercially applied strain of *A. barkeri* also enters diapause under short-day conditions. In sweet pepper greenhouses in the Netherlands, however, *A. barkeri* sometimes occurred spontaneously during the winter period. Van Houten (1991) examined a strain of such mites and demonstrated a relatively low incidence of diapause. For the present study this strain of *A. barkeri* was used. In addition to *A. cucumeris* and *A. barkeri*, five species of phytoseiid mites were tested that 1) are known as predators of thrips (Tanigoshi *et al.*, 1983; Grout, 1985; Bounfour & McMurtry, 1987; J. A. McMurtry, pers. comm.), and 2) originated from subtropical regions, where reproductive diapause is less likely to occur (Wysoki & Swirski, 1971; Danks, 1987). These species are: *A. degenerans* Berlese, *A. hibisci* (Chant), *A. tularensis* (Congdon), *A. scutalis* (Athias-Henriot) and *A. limonicus* s.s. Garman and McGregor (see Appendix I for alternative nomenclature of these mites).

The seven mite species were tested for their rates of predation and oviposition, on a diet of first instar thrips larvae. The young stages are most vulnerable to phytoseiid attack (Bakker & Sabelis, 1989; van der Hoeven & van Rijn, 1990). The most voracious predator species were subjected to three additional experiments: 1) rate of oviposition on a diet of sweet pepper pollen, 2) diapause incidence under short-day conditions, and 3) egg-hatching success at different ambient humidities.

Materials and methods

Mites

Table 1 summarizes data on collection sites of the predators. Upon collection all mites were kept in a climate room, under long-day illumination (L16:D8), at 25 °C and 70% r.h. (=0.95 kPa). *A. degenerans*, *A. limonicus*, *A. cucumeris* and *A. barkeri* were reared on plastic 'arenas', as described by Overmeer (1985). Wet tissue paper was wrapped over the edges of the arenas, serving both as a water source and as a barrier. An additional Tangletrap[®] barrier on top of the tissue paper prevented the mites from escaping. *A. hibisci*,

Table 1. History of the predatory mites used in this study

<i>Amblyseius</i> species	Original collection (year, crop; location)	Collection for present study (year, location)
<i>A. barkeri</i> (Hughes)	1989; Sweet pepper, Westland, The Netherlands	1989; Berkel en Rodenrijs ¹
<i>A. cucumeris</i> (Oudemans)	1981; Sweet pepper; Naaldwijk, The Netherlands	1990; Naaldwijk ²
<i>A. degenerans</i> (Berlese)	1982; Citrus; Rabat, Morocco	1991; Riverside ³
<i>A. hibisci</i> (Chant)	1982; Avocado; Alamos, Sonora, Mexico	1991; Riverside ³
<i>A. limonicus</i> Garman & McGregor	1991; Cucumber; Auckland, New Zealand	1991; Auckland ⁴
<i>A. scutalis</i> (Athias-Henriot)	1984; Lantana; Jordan Valley, Jordan	1991; Riverside ³
<i>A. tularensis</i> Congdon	1982; Citrus; Corona, California, USA	1991; Riverside ³

¹ Non-commercial insectary culture at Koppert B. V., Berkel en Rodenrijs, The Netherlands;

² Insectary culture at the Glasshouse Crops Research Station, Naaldwijk, The Netherlands;

³ Insectary cultures at the University of California, Riverside, USA;

⁴ Cucumber crop in a commercial greenhouse near Auckland, New Zealand.

A. tularensis and *A. scutalis* were reared on detached common bean leaves (*Phaseolus vulgaris* L.) (Overmeer, 1985). The leaves were placed upside down on soaked cotton wool. The cultures of all seven species were fed with pollen of the broad bean, *Vicia faba* L.

Experiments

Predation and oviposition on a diet of thrips larvae.

Rates of predation and oviposition were determined on discs of cucumber leaves (4.5 cm²). The discs were placed upside down on pads of moist cotton wool, in a climate room at L16:D8, 25 °C and 70% r.h. (=0.95 kPa). Single gravid female mites were placed on each leaf disc. The mites originated from cohorts of eggs, collected from 0–48 h after deposition, and were reared on a diet of broad bean pollen. At the start of the experiment the mites had been ovipositing for 2–4 days. For predatory mites at this age, rates of predation and oviposition are likely to be at their maximum, and these maxima are highly correlated with phytoseiids' intrinsic rates of increase (confer Janssen & Sabelis, 1992; van Rijn & van Houten, 1991). All leaf discs were infested with 12 first instar *F. occidentalis* larvae (0.5–0.6 mm long). At this density the functional response of *A. cucumeris* females to thrips larvae was found to be at its plateau level (Shipp & Whitfield, 1991; van Rijn, unpubl.). This implies that a small decrease in number of prey does not affect predation rate. During three days the predators were transferred each day to fresh leaf discs with 12 newly emerged thrips larvae. The most voracious predators were supplied with a few extra larvae; it was ascertained that the number of live prey never dropped below 6 per disc.

Table 2. Rates of predation and oviposition of seven *Amblyseius* species on a diet of first instar *F. occidentalis* larvae (0.5–0.6 mm long), on cucumber leaf discs (4.5 cm² at 25 °C and 70% r.h. (=0.95 kPa). Predation rate: mean number of larvae killed per female, per day; oviposition rate: mean number of eggs laid per female, per day. N= number of females; s.e.= standard error

<i>Amblyseius</i> species	N	Predation rate (mean ± s.e.)	Oviposition rate (mean ± s.e.)
<i>A. limonicus</i>	23	6.9 ± 0.4	3.2 ± 0.1
<i>A. cucumeris</i>	23	6.0 ± 0.2	2.2 ± 0.1
<i>A. degenerans</i>	33	4.4 ± 0.5	1.4 ± 0.2
<i>A. hibisci</i>	20	3.5 ± 0.3	1.7 ± 0.2
<i>A. barkeri</i>	21	2.6 ± 0.2	1.5 ± 0.1
<i>A. scutalis</i>	20	1.3 ± 0.4	0.3 ± 0.1
<i>A. tularensis</i>	14	0.5 ± 0.1	0.2 ± 0.1

Numbers of killed thrips larvae and mite eggs were assessed daily. Data of the first day were omitted from calculations of predation and oviposition rates, as to 1) minimize a potential effect of the mites' food source prior to the experiment, and 2) allow for reaching a steady state distribution in gut fullness (see Sabelis, 1990). A predator's prey-capture success is determined by its gut content (Sabelis, 1990; van der Hoeven & van Rijn, 1990). By allowing for an overall equilibrium between consumption and gut-emptying to become established, the influence of pre-experimental conditions is reduced.

Oviposition on a diet of sweet pepper pollen. This experiment was performed under the same climatological

Table 3. Rate of oviposition (mean number of eggs per female, per day) of five *Amblyseius* species on a diet of sweet pepper pollen, on cucumber leaf discs (4.5 cm² at 25 °C and 70% r.h. (=0.95 kPa). N= number of females; s.e.= standard error

<i>Amblyseius</i> species	N	Oviposition rate (mean ± s.e.)
<i>A. limonicus</i>	15	1.5 ± 0.2
<i>A. cucumeris</i>	23	2.1 ± 0.1
<i>A. degenerans</i>	19	1.4 ± 0.1
<i>A. hibisci</i>	21	2.8 ± 0.1
<i>A. barkeri</i>	22	2.4 ± 0.1

Table 4. Diapause incidence in five *Amblyseius* species under short-day conditions (Light:Dark= 10(23 °C): 14(16 °C) h). N= number of females

<i>Amblyseius</i> species	N	Diapause (%)
<i>A. limonicus</i>	261	0
<i>A. cucumeris</i>	63	100
<i>A. degenerans</i>	117	0
<i>A. hibisci</i>	65	0
<i>A. barkeri</i>	126	70

conditions as the first experiment. Individual females, of the same age as the mites in the previous experiment, were transferred each day to fresh cucumber leaf discs (4.5 cm²) with ample amounts of sweet pepper pollen. Eggs were counted during three days. Like in the first experiment, the calculated rates of oviposition were based on data from day 2 and 3 only.

Diapause incidence under short-day conditions. Diapause induction experiments were done in photoperiod- and thermoperiod-controlled incubators. Cohorts of eggs, collected from 0–24 h after deposition, were carefully transferred to units identical to the rearing units. The eggs and subsequent developmental stages were exposed to short-day conditions, with light phases of 10 h, at 23 °C, and dark phases of 14 h, at 16 °C. These conditions are comparable to the conditions at which the sweet pepper crop is grown in Dutch greenhouses in February. The diet of the developing mites was supplemented with β -

carotene, since some predatory mite species fed on broad bean pollen alone do not respond to photoperiod (Overmeer *et al.*, 1989) or thermoperiod (van Houten *et al.*, 1987). Two days after the first adult females appeared, mites of all species (except *A. degenerans*) were fed with purple pollen of the iceplant, *Mesembryanthemum* spec., which has also been shown to be an adequate food source for *A. cucumeris* (Overmeer *et al.*, 1989), *A. hibisci* (McMurtry & Scriven, 1964), *A. limonicus* (McMurtry & Scriven, 1965) and *A. barkeri* (van Rijn & Jones, unpubl.). In this way egg production by individual non-diapausing females can easily be determined, as the white egg stands out clearly against the surrounding purple intestines. Since the intestines of *A. degenerans* females are much darker than those of females of the other species, there was no need to feed them with iceplant pollen. In this species an egg is clearly visible when fed on broad bean pollen. When no egg was seen in a female it was concluded that this female would not lay eggs and, hence, was in a state of reproductive diapause. It was ensured that ample males were present for insemination of the females.

Egg hatching at different air humidities. The influence of air humidity on egg viability was examined in closed plastic containers (18 × 14 × 9 cm), at 25 °C. Saturated solutions of different salts in demineralized water adjusted constant humidities, with vapour pressure deficits ranging from 0.25 to 2.16 kPa, i.e., with relative humidities from 92 to 32% (Winston & Bates, 1960). To understand effects of drought on biological features, 'water vapour pressure deficit' (or its synonyms 'saturation vapour pressure deficit' or 'saturation deficit') is a better index than 'relative humidity'. It is more directly related to the rate of evaporation, irrespective of actual temperature (Ferro & Chapman, 1979; Moraes & McMurtry, 1981). Vapour pressure deficit (VPD) is defined as the difference between saturated and actual vapour pressure. It is inversely related to relative humidity (RH): $VPD = SVP^* (1 - RH/100\%)$, where SVP is the saturated vapour pressure, which is directly related to temperature (Moraes & McMurtry, 1981). Under our experimental conditions (25 °C, at sea level) SVP equals 3.17 kPa (=23.76 mmHg).

Cohorts of eggs, from 0–16 h after deposition, were carefully transferred to small plastic plates, floating on a salt solution. In this way eggs of all different predators were exposed to a range of vapour pressure deficits. Batch sizes ranged from 48 to 143 eggs (average size: 66 eggs). After three days, when all

viable eggs should have hatched, the numbers of desiccated eggs were assessed. These numbers were then used to calculate the so-called 'critical humidity' or h_c , i.e., the vapour pressure deficit at which 50% of the maximum fraction of eggs hatch. A logistic distribution model was used: $F(h)=m/(1+e^y)$, with $y=(h-h_c)/\beta$. Here, h represents humidity level (vapour pressure deficit), m maximum survival, h_c critical humidity, and β a measure of variance (β =standard deviation * $\sqrt{3}/\pi$) (Mood *et al.*, 1974). The parameter values were obtained by a Marquardt-fitting procedure, minimizing the squared deviations between model predictions and data points.

Results

Predation and oviposition on a diet of thrips larvae. There were pronounced differences in both predation rate and oviposition rate between the seven mite species (Table 2). *A. limonicus* killed on average 6.9 thrips larvae/day, followed by *A. cucumeris*. *A. hibiscii*, *A. degenerans* and *A. barkeri*, in descending order. Females of *A. scutalis* and *A. tularensis* showed the lowest predation rates, viz., 1.3 and 0.5 larvae/day respectively. Oviposition rates were clearly associated with predation rates, and ranged from 3.2 eggs/day (*A. limonicus*) to 0.2 eggs/day (*A. tularensis*) (Table 2). Because of the relatively very low rates of predation and oviposition of both *A. scutalis* and *A. tularensis* it seems highly unlikely that these species in the end would come forward as most promising candidates for biological control of western flower thrips. Therefore, we discarded these two species from further experiments.

Oviposition on a diet of sweet pepper pollen. The five species tested were able to reproduce on a diet of sweet pepper pollen. Oviposition rates ranged from 1.4 eggs/day (*A. degenerans*) to 2.8 eggs/day (*A. hibiscii*) (Table 3).

Diapause incidence under short-day conditions. All females of *A. cucumeris* and a majority of the females of *A. barkeri* (70%) entered diapause under the short-day conditions at which they developed (Table 4). However, the females of *A. limonicus*, *A. degenerans* and *A. hibiscii* were insensitive to these conditions: they all started to lay eggs.

Egg hatching at different air humidities. Eggs of the various mite species differed considerably with respect to sensitivity to low humidity. Eggs of *A. hibiscii* were most drought resistant ($h_c=1.67$ kPa), eggs of *A. limonicus* were most sensitive ($h_c=0.88$ kPa) (Fig. 1). Fig. 1 also shows that a positive correlation existed between critical humidity and standard deviation: the more drought sensitive eggs are, the steeper the drop in survival at increasing vapour pressure deficit.

Discussion

Predation and oviposition. Only few studies regarding predation and oviposition of phytoseiid species on thrips larvae have been reported. For *A. cucumeris*, Shipp & Whitfield (1991) found a consumption rate of 6 first instar *F. occidentalis* larvae per day, at similar prey density (3 larvae per cm²) and on leaves of the same host plant, highly comparable to what we found.

According to Castagnoli & Simoni (1990), *A. cucumeris* has an initial oviposition rate of ca. 1.8 eggs per day, at 25 °C, when fed on first instar larvae of *Thrips tabaci* Lindeman. Gillespie & Ramey (1988) reported a mean oviposition rate of 1.5 eggs per day, at 20 °C, when fed on larvae of *F. occidentalis*. Both reports are in agreement with our results. Bonde (1989) found that on a diet of *T. tabaci* larvae, *A. barkeri* showed an oviposition rate that was considerably higher than what we found, viz. 2.6 eggs/day versus 1.5 eggs/day (Table 2). Since Bonde used predators from a different strain of *A. barkeri* than we did, the observed differences may partly be due to interstrain differences. For *A. hibiscii* fed on larvae of *Scirtothrips citri*, Tanigoshi *et al.*, (1983) found an initial oviposition rate of 1.3 eggs per day, at 26 °C, close to 1.7 as was found in our study. *A. scutalis*, which showed a very low oviposition rate on a diet of *F. occidentalis* larvae (0.3 egg/day; table 2), was able to produce 1.4 eggs per day when fed with larvae of *S. citri* (Bounfour & McMurtry, 1987). Possibly the greater size of the *F. occidentalis* larvae and a more active defensive behaviour (Tanigoshi, unpubl.) accounts for this difference.

Utilisation of pollen. The oviposition rates as found in our study are largely similar to those found in the literature. Van Rijn and van Houten (1991) found that both *A. barkeri* and *A. cucumeris* produced 2.5 eggs per day per female, on sweet pepper and broad bean pollen. *A. hibiscii* is reported to reproduce on various

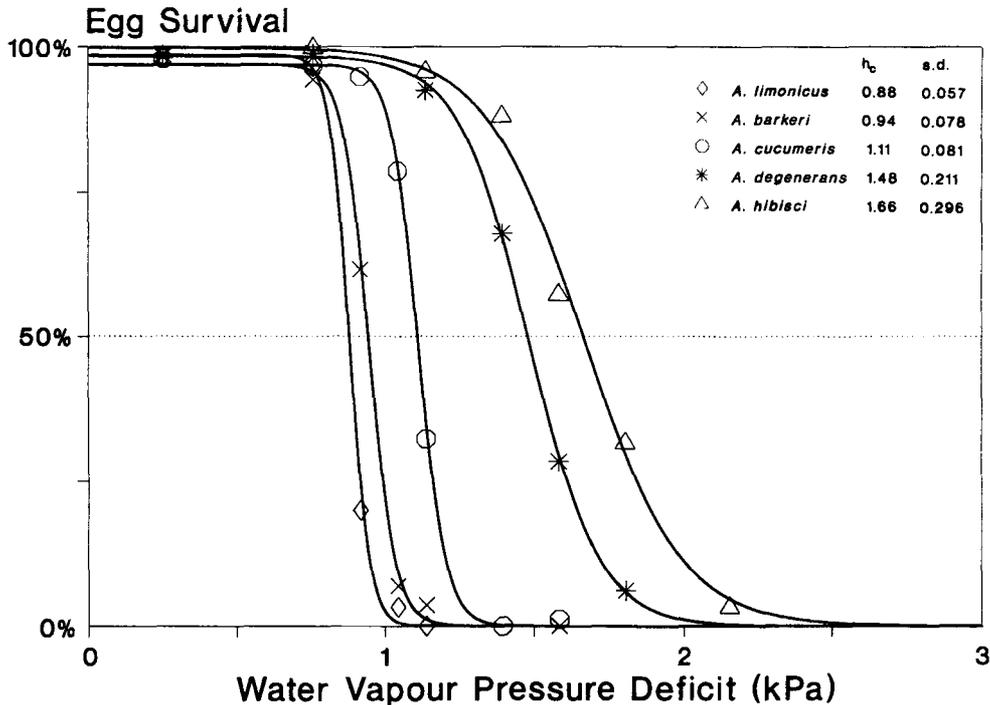


Fig. 1. Egg survival (%) of five *Amblyseius* species at different water vapour pressure deficits at 25 °C. h_c : critical humidity, i.e., humidity at which half of the maximum percentage of eggs hatch; s.d.: standard deviation (see Materials and methods-section for details)

pollen species, at rates ranging from 2.2 to 2.8 eggs per day, even higher than on some animal prey (McMurtry & Scriven, 1964; Tanigoshi *et al.*, 1983). In our study we, too, found a higher oviposition rate for *A. hibisci* on a diet of pollen (2.8 eggs/day; Table 3) than on thrips larvae (1.7 eggs/day; Table 2). Oviposition rate of *A. limonicus* on iceplant pollen was 2.0 eggs per day in a study by McMurtry & Scriven (1965), somewhat higher than what we found (1.5 eggs/day; Table 3). *A. degenerans* is reported to feed on pollen, but no quantitative data are available (Flechtmann & McMurtry, 1992).

The ability to use pollen as alternative food allows for preventive introduction and maintenance of predatory mites at low thrips densities (Ramakers, 1990; van Rijn & Sabelis, 1990). Moreover, van Rijn & Sabelis (1993) showed that pollen feeding will result in higher predator densities and consequently in lower thrips densities, compared to situations where pollen is absent.

Diapause. We found that *A. limonicus*, *A. degenerans* and *A. hibisci* did not enter diapause under short-day conditions. These results are in agreement with the sparse literature. *A. limonicus* and *A. hibis-*

ci were active during the entire winter in Californian avocado crops (McMurtry & Johnson, 1966). Wysocki and Swirski (1971), who studied overwintering of *A. degenerans* in Israel, found that during winter all postembryonic stages were active on above-ground plant parts.

The strain of *A. barkeri* used in this study exhibited a diapause incidence of 70%, which confirms the partial absence of diapause as previously found with the same strain (ca. 50%; van Houten, 1991). All *A. cucumeris* of the commercially available strain used in this study entered diapause. This result corroborates earlier results (van Houten, 1991; Morewood & Gilkeson, 1991). Presently, a strain of *A. cucumeris* is known that shows a reduced incidence of diapause (van Houten & van Stratum, 1993).

Drought tolerance. Bakker *et al.* (1993) report a critical saturation deficit of 0.82 kPa for *A. limonicus s.s.* highly comparable to the 0.88 kPa we found. McMurtry and Scriven (1965) found critical relative humidities (at 21 °C) of ca. 32% (i.e. a saturation deficit of 1.7 kPa) and 60% (=1.0 kPa), for *A. hibisci* and *A. limonicus* respectively. These values are surprisingly similar to the ones found in the present study, since Bakker *et al.*

(1993) showed that inter-strain differences in critical humidity can sometimes be larger than inter-species differences.

Pre-selection of natural enemies. The predator features studied are related to three properties that are considered important in evaluation of natural enemies: 1) maximum killing rate, 2) maximum rate of population increase (r_m), and 3) environmental tolerance space (confer McMurtry, 1981, 1992). For each property only a few related traits were studied. (1) Killing rate was examined with respect to young larvae, but not with respect to second instar larvae or adults. Because second instar larvae are well able to defend themselves against predatory mites, they were expected to be killed at a much lower rate (Bakker & Sabelis, 1989; van der Hoven & van Rijn, 1990). This was confirmed in a pilot experiment, which also suggested that among different species of *Amblyseius* the rate of killing second instar larvae was correlated with the rate of killing first instars (van Houten *et al.*, 1993). (2) Of all life history traits that determine population growth rate only initial oviposition rate was studied. However, comparison of life histories of many phytoseiid mites showed that the different life history traits are highly correlated, and that estimations of r_m can be obtained, based on peak oviposition rate only (Janssen & Sabelis, 1992). But caution should be exercised: the relations assessed by Janssen and Sabelis were based on studies where in predatory mites were fed with ample amounts of tetranychid mites. Under these circumstances (juvenile) predatory mites are likely to find unlimited numbers of easily obtainable food items, such as tetranychid eggs and/or juveniles. It remains to be shown that the relations reported by Janssen and Sabelis still hold when predatory mites feed on relatively large and active thrips larvae. (3) Environmental tolerance space was only studied with respect to two factors: air humidity and daylength. Since greenhouses form, in many respects, a favourable environment for predatory mites, not many other factors are expected to be adverse, apart from application of (non-selective) pesticides and presence of competing natural enemies.

Our study did not include a fourth important property of predators: searching efficiency. Predators can increase the rate of prey encounter by, for example, orienting on prey-associated volatiles, such as kairomones and synomones (Dicke *et al.*, 1990; Janssen *et al.*, 1990), or by various arrestment responses after encountering prey or prey-related cues (Hoy & Smilanick, 1981; Hislop & Prokopy, 1981; Sabelis

et al., 1984). Recently, it was suggested that *A. cucumeris* is able to use an alarm pheromone of *F. occidentalis* in prey-location (Teerling *et al.*, 1993). Searching efficiency will have great influence on killing rate and rate of population increase when prey density is low. When alternative food sources are available, such as pollen in a sweet pepper crop, efficiency in finding these food patches (i.e. flowers) may be important as well.

Based on the features examined, two species can be regarded as promising candidates for biological thrips control throughout the season: *A. degenerans* and *A. hibisci* showed moderate to good predation and reproduction capacities, they showed absence of diapause, and they were the most drought tolerant. Under circumstances where drought tolerance is not very important, *A. limonicus* seems to be the best candidate: these mites showed absence of diapause, and highest predation and reproduction capacities. However, whether these species are good biocontrol agents remains to be shown. Greenhouse trials have to be performed to find out if the predators are able to control thrips infestations. Initial results with *A. degenerans* show that this species seems well able of thrips control in a greenhouse-grown sweet pepper crop during winter (van Houten & van Stratum, 1993).

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Appendix 1. Alternative nomenclature of the predatory mites used in this study, according to de Moraes *et al.* (1986)

This paper	Alternative generic names	Synonyms
<i>Amblyseius barkeri</i> (Hughes)	<i>Neoseiulus</i>	<i>N. mckenziei</i> Schuster & Pritchard <i>N. mycophilus</i> (Karg) <i>N. oahuensis</i> (Prasad) <i>N. picketti</i> (Specht)
<i>A. cucumeris</i> (Oudemans)	<i>Neoseiulus</i>	<i>N. coprophilus</i> (Karg) <i>N. thripsii</i> (MacGill)
<i>A. degenerans</i> (Berlese)	<i>Iphiseius</i>	—
<i>A. hibisci</i> (Chant)	<i>Euseius</i>	—
<i>A. limonicus</i> Garman & McGregor ¹	<i>Typhlodromalus</i>	<i>T. rapax</i> (De Leon) <i>T. garmani</i> (Chant)
<i>A. scutalis</i> (Athias-Henriot)	<i>Euseius</i>	<i>E. rubini</i> (Swirski & Amitai) <i>E. gossipi</i> (Elbadry) <i>E. libanesi</i> (Dosse) <i>E. delhiensis</i> (Narayanan & Kaur)
<i>A. tularensis</i> Congdon	<i>Euseius</i>	<i>E. hibisci</i> ²

¹ We used *A. limonicus sensu stricto*, not to be confused with *A. limonicus sensu lato*, the predators found on cassava (Braun *et al.*, 1993).

² In 1985 *A. tularensis* was described as a new species (Congdon & McMurtry, 1985). Until then the species was frequently referred to as *A. hibisci*.

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