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DOI

[10.1007/BF00145254](https://doi.org/10.1007/BF00145254)

Publication date

1995

Published in

Experimental and Applied Acarology

[Link to publication](#)

Citation for published version (APA):

Lesna, I. K. A., Sabelis, M. W., Bolland, H. R., & Conijn, C. G. M. (1995). Candidate natural enemies for control of *Rhizoglyphus robini* Claparede (Acari: Astigmata) in lily bulbs: Exploration in the field and preselection in the laboratory. *Experimental and Applied Acarology*, 19, 655-669. <https://doi.org/10.1007/BF00145254>

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Candidate natural enemies for control of *Rhizoglyphus robini* Claparède (Acari: Astigmata) in lily bulbs: exploration in the field and pre-selection in the laboratory

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ABSTRACT

To find suitable candidates for biological control of the bulb mite, *Rhizoglyphus robini* Claparède (Acari: Astigmata) on lilies, exploration was undertaken in areas where the bulb mite is an established pest (The Netherlands, Taiwan and Japan). Among the predators, found in association with *R. robini* in the field and under storage conditions, mesostigmatic mites predominate. The most abundant species were *Hypoaspis aculeifer* (Canestrini), *Lasioseius bispinosus* Evans and *Parasitus fimetorum* (Berlese). These predators appeared to feed and reproduce on a diet of exclusively *R. robini* and they were able to control the bulb mite in small-scale population experiments initiated with a 1 : 20 predator–prey ratio. Under laboratory conditions corresponding to lily bulb propagation (lily scales mixed with vermiculite and stored at 23°C and > 90% RH) the laelapid mite, *H. aculeifer*, was the most effective predator; the ascid predator, *L. bispinosus*, was much less effective, but being relatively small and being successful in attacking the juvenile stages of the bulb mite it may be better able to search for bulb mites hidden inside the lily bulb. The parasitoid predator, *P. fimetorum*, failed to control the bulb mite when vermiculite was used as a medium, but turned out to suppress this prey when peat was used instead. Various strains of *H. aculeifer* or closely related species were compared with respect to their impact and performance on bulb mites as prey: two Dutch strains, one obtained from Breezand and the other from 't Zand, a Taiwanese strain, a German strain that in contrast to the previously mentioned strains was not collected from lily bulbs, but from agricultural areas near Bremen and, in addition, a Canadian strain of a related species (*Hypoaspis miles* Berlese), known to control sciarid fly larvae. These comparative experiments showed that *H. miles* died out without noticeable impact on the bulb mite population whereas all strains of *H. aculeifer* were able to suppress the bulb mites to very low numbers. However, the numerical responses of the *H. aculeifer* strains differed in that those collected in association with the pest (Breezand > Taiwan > 't Zand) were superior to the strain from Bremen. These results do not provide support to the Hokkanen and Pimentel hypothesis, which states that predators forming an evolutionary new association with the pest are often more effective in biological control.

Key words: Biological control, predator–prey interaction, *Rhizoglyphus robini*, *Tyrophagus putrescentiae*, *Hypoaspis aculeifer*, *Lasioseius bispinosus*, *Parasitus fimetorum*, lily bulbs.

INTRODUCTION

Developing a method of biological pest control involves exploration for potential natural enemies and selection of suitable candidates (Luck *et al.*, 1988). Exploration usually results in a large number of species and strains of natural enemies found in association with the pest organisms. As it is not possible to test them all under practical conditions and at a practically relevant spatial scale, there is a need for pre-selection of suitable candidates, based on simple small-scale experiments in the laboratory.

In this article we report on the results of exploration for mesostigmatic predators found in association with the bulb mite, *Rhizoglyphus robini* Claparède (Acari: Astigmata), an important pest of lily bulbs in The Netherlands as in many other countries. As the co-occurrence of predator and prey does not necessarily imply a predator-prey association, at first simple feeding tests were carried out with *R. robini* as the only prey. Simultaneously with the observations to assess feeding events, oviposition was recorded since mesostigmatic predators utilize much of the food ingested for egg production. If these tests had positive results, then the species were subjected to further investigation in small-scale population experiments carried out on lily bulbs in closed vials under laboratory conditions.

Exploration for predators could be carried out under natural conditions on wild lilies and under conditions of lily bulb cultivation. However, exploring wild lilies is subject to severe constraints. Wild lilies are scattered over large areas in East Asia and they are not easy to find unless in a flowering stage and infested lily bulbs are even more difficult to find. Moreover, the sample size is limited due to regulations for protected plants. Hence, given time constraints for each foreign exploration trip (approximately 2 weeks) it seemed wise not to focus on sampling wild lilies.

Hence, exploration was concentrated on cultivated lily bulbs. Four phases of cultivation should be investigated: growth in the field for bulb production, growth in the greenhouse for flower production, bulb propagation in storage rooms (at 22–23°C) and cold storage (at 0 to –2°C). Each of these phases differs with respect to climatic conditions and in the likelihood of predators developing an association with bulb mites. To maximize the probability of finding predators associated with bulb mites we decided to direct exploration primarily to fields where lily bulbs are cultivated and to inspect plants infested by bulb mites for the presence of predators. The other cultivation phases are less likely to provide success in exploration because treatments preceding the greenhouse phase (soil steaming) and the propagation phase (hot water treatment of bulbs at 39–41°C for 2 h and pesticide applications) virtually preclude survival of the predators and cold storage conditions are simply not conducive to predatory activity.

As lily bulbs are grown world-wide, it seemed worthwhile undertaking foreign exploration in addition to exploration in The Netherlands. We selected countries and sampling areas that satisfied the following criteria: (1) evidence of the

presence of bulb mites in cultivated lilies, (2) matching climatic conditions, (3) availability of acarological expertise and (4) occurrence of wild lilies (preferably area of origin). For these reasons exploration trips were carried out in Taiwan and Japan.

The species of mesostigmatic predators collected during exploration were transferred to the laboratory at the University of Amsterdam and kept in culture on a mixture of *R. robini* and *Tyrophagus putrescentiae* (Schrank) (Acari: Astigmata). Shortly thereafter, these species were subjected to feeding and reproduction tests and small-scale population experiments on predator-prey interactions in closed vials containing lily bulbs. Comparisons were made between species and between strains of predators collected from various geographical locations in The Netherlands, Taiwan and Japan. In doing so, data are obtained that lend themselves to an evaluation of the approach of Hokkanen and Pimentel (1984, 1989) who advocated the use of evolutionary new rather than long (co-)evolved predator-prey associations.

MATERIALS AND METHODS

Exploration for predatory mites

Exploration in The Netherlands was undertaken throughout 1991 and 1992 in a number of fields near Breezand, Anna Paulowna and 't Zand in North Holland and near Lisse in South Holland. Lilies are commonly cultivated in fields of up to a few hectares with *ca* 80 bulbs per m². Fields were selected based on information from growers on damage symptoms and on subsequent identification of bulb mite damage, at the Bulb Research Centre in Lisse. In addition to field exploration, some samples from greenhouses and storage rooms were examined.

The exploration trip to Taiwan was undertaken in the last week of October 1991. Here, bulb mites are a severe pest of lilies and onions. The lily fields are mainly located in the mountains where climatic conditions match those in The Netherlands. Fields were selected based on information from Dr Ch-C. Ho, applied acarologist at the Taiwan Agricultural Research Institute. The lily fields visited in the mountains were quite small, sometimes less than 50 m² and they were scattered amidst natural vegetation. Lily bulbs were frequently subject to heavy infestation by bulb mites and nematodes. This high prey density may well have made lily fields attractive for predators from the surrounding environment. Sampling took place in Central Taiwan in the lowlands around Houli and in the mountains around Sun Moon Lake and Chin-Jin. In several cases green onion (shallot) fields located nearby the lily fields were sampled as well.

The exploration trip to Japan was undertaken in the first week of October 1992. Here, bulb mites were found to be a severe pest of lilies, leeks, shallots and also tulips in storage. The lily fields were selected close to Niigata City and Horinouchi (Niigata Province) by Dr A. Enami (Niigata Horticultural Experiment

Station) and Dr H. Nemoto (Saitama Horticultural Experiment Station). These fields were much larger than in Taiwan and were located in vast agricultural areas edging the mountains. The infestation levels of bulb mites were lower than those found in Taiwan. Together with the prolonged hot and dry period preceding our visit this low prey density may have been conducive to a lower incidence of predators. In addition, there were visits to fields with infested green onion (shallot) bulbs in Chiba, stored tulip bulbs heavily infested by bulb mites in Fukiya City and wild lily (*Lilium auratum*) on Tsukuba Mountain and near the Field Station of Kyoto University.

Species collection

Firstly, lilies infested by bulb mites were selected on site by visual inspection of the plant growth form and bulb damage symptoms. Then any predatory mites observed by the naked eye or loupe were collected and transferred by brush to a small vial (approximately 4 cm high and 2.5 cm diameter). When the aim was to identify the species, these vials contained 70% alcohol for preservation of specimens and, when the aim was to maintain live specimens for rearing, the vials were provided with a bottom layer of moistened plaster of Paris mixed with charcoal (to ensure a sufficiently humid environment and to provide the predators with a better grip on the substrate). Live specimens obviously belonging to different taxa were separated from each other as much as possible. All lily bulbs selected were taken to the laboratory for further mite collection using either a binocular microscope or Tullgren's funnel. Some of the collected predators were transferred to vials with 70% alcohol for preservation and identification. The remainder was used to start a culture in the laboratory.

Feeding tests

Live specimens of predatory mites were transferred to medium-sized vials (10 cm high and 6 cm diameter) to start rearing on a mixed diet of two species of astigmatic mites, *R. robini* (collected from lily fields in Anna Paulowna, North Holland) and *T. putrescentiae* (obtained from Koppert Ltd, Berkel en Rodenrijs, The Netherlands). The latter prey species was added because it is a prey widely accepted by many mesostigmatic mites and because it occurs as a pest in various flower bulbs (hyacinth, tulip, nerine, narcissus and occasionally also in lily). If predators were successfully reared on the prey mixture, then they were subsequently offered each of the two prey species separately to assess prey-related feeding and reproduction capacity. Predator species that did not feed and reproduce on a diet of the two prey species, in addition to those that did not feed on an exclusive diet of *R. robini*, were excluded from further experimentation.

Cultures were kept separate based on species identity and strains from different geographic locations. To start a culture the aim was to have 50–100 specimens as an inoculum, but in a few cases the inoculum size had to be smaller due to low sampling success (only 14 specimens for *Parasitus fimetorum* (Berlese) and 10

specimens of *Pergamasus primitivus* Heim & Oudemans, both collected from shallot fields in Chiba, Japan). In some cases strains and species that were not collected on bulbs were included in further studies, because it enabled inter- and intraspecific comparisons. One example is a strain of *Hypoaspis aculeifer* (Canestrini) obtained from Dr A. Ruf (University of Bremen, Germany) who had collected it in an agricultural area not related to bulb production and maintained a culture on *Caloglyphus* sp. Berlese (Acari, Astigmata) as prey since 1989. Another example is a Canadian strain of *Hypoaspis miles* Berlese obtained via Koppert Ltd (Berkel en Rodenrijs, The Netherlands) that was reared on *T. putrescentiae* and reported to be a successful predator of *Rhizoglyphus echinopus* (Fum. & Rob.), an astigmatic mite closely related to *R. robini* (Shereef *et al.*, 1981; Hoda *et al.*, 1986).

Small-scale population experiments

Predatory mites that survived the initial phase of rearing on the prey mixture and subsequently showed population growth on *R. robini* alone, were maintained under laboratory conditions (25°C, > 70% relative humidity (RH)) on a diet of *T. putrescentiae* and later tested in small-scale population experiments on lily bulbs infested by *R. robini*. In all experiments lily bulbs of *Lilium* (Asiatic hybrid) cv. Tender were used, unless explicitly stated otherwise. Bulbs were decomposed into scales (approximately ten per bulb), mixed with moist vermiculite and kept in closed jars. Each jar was filled up to 60% with a mixture of moist vermiculite and scales from ten bulbs. Jars were placed in climate rooms at a temperature of 25°C for a period of 4 weeks. The assessment of infestation by the bulb mite was made prior to the experiment by placing three bulbs on the Tullgren funnel for a period of 4 days. Mites collected in vials with alcohol were counted under a binocular microscope and the numbers of bulb mites per bulb were calculated. In the same way assessments were made of the number of prey and predators in weeks 2, 3 and 4 after the start of the experiments. All experiments were started with an initial number of approximately 120 *R. robini* (all mobile stages) per bulb and a predator to prey ratio of 1 : 20 (thus six specimens per bulb). All species and strains were simultaneously tested with three replicates per species and two replicates per strain. As a control, one experiment was carried out in three replicates.

In the case of experiments with the Taiwanese strain of *P. fimetorum*, a different scenario had to be followed. Here, it appeared to be impossible to use vermiculite as the predators died from unknown causes. Instead peat was used as a medium for the bulb scales. In addition, these experiments differed in a number of ways: (1) the lily bulb cultivar was different (*Lilium* (oriental hybrid) cv. Star Gazer, a more susceptible cultivar than Tender), (2) the initial number of bulb mites was lower (approximately 75 per bulb) and (3) the number of replicates was higher (eight replicates with predators and five replicates for control). To obtain a 1 : 20 predator-prey ratio four specimens of *P. fimetorum* were released per bulb.

RESULTS AND CONCLUSIONS

Exploration

In lily fields on sandy soil located in North Holland (Anna Paulowna, 't Zand and Breezand) and South Holland (Lisse) the laelapid mite, *H. aculeifer*, was by far the most abundant predator. In some cases 10–15 predators were found in a single bulb. Other predators were rarely found and, if so, they were either *Parasitus oudemansi* (Berlese) or *Parasitus hyalinus* (Willmann). The latter parasitid, however, was found in much larger numbers in greenhouses with soil richer in organic matter or in storages for lily propagation where peat was used as a medium for the lily scales. In the latter environment another parasitid species, *P. fimetorum*, was recorded in large numbers. Though relatively less abundant than the parasitids, *H. aculeifer* occurred frequently in peat or soils rich in organic matter.

In lily fields at Sun Moon Lake and Houli in Taiwan the laelapid mite, *H. aculeifer*, was the most abundant predator. However, when soil was rich in organic matter (Sun Moon Lake and Chin-Jin) or lily bulbs were stored in boxes filled with peat (Chin-Jin), then again the parasitid mite, *P. fimetorum*, was found in large numbers. In Houli two other species were collected: an ascid predator *Lasioseius sugawarai* Ehara and a macrochelid predator *Macrocheles glaber* (Müller). In all other bulbous crops (*Amaryllis* sp., green onion) no predators were found despite sometimes heavy bulb mite infestations (e.g. onion). This was possibly due to the use of fungicides and insecticides.

In fields with cultivated lilies in Japan only a single female of *H. aculeifer* was found in Niigata and near Horinouchi two other species of mesostigmatic predators were recorded in low numbers: the macrochelid mite, *Macrocheles nataliae* Bregetova & Koroleva and the parasitid mite, *P. primitivus* Heim & Oudemans. Sampling of wild lilies (*L. auratum*) at Tsukuba Mountain and at the field station of Kyoto University did not result in finding mite-infested bulbs nor in finding any predators. In other bulbous crops, such as green onion, several specimens of *P. fimetorum* were found. A significant collection was made on stored tulip bulbs (Fukiyama City), where large numbers of an ascid predator, *Lasioseius bispinosus* Evans, were found in association with a heavy infestation of *R. robini*. A list of the mesostigmatic mites collected is presented in Table 1, together with information on the location, crop and pest.

Feeding tests

Two species of predators were collected in insufficient numbers to start a culture (*P. oudemansi* from The Netherlands and *H. aculeifer* from Japan). Among the species collected in larger quantities, attempts to rear predators on a mixture of *R. robini* and *T. putrescentiae* failed with respect to all macrochelid predators (*M. glaber* from Taiwan and *M. nataliae* from Japan); these predators starved to death despite an ample supply of prey mites. Some parasitid predators (*P. primitivus*

TABLE 1

List of mesostigmatic mites found at various locations in association with *R. robini* (and frequently other prey such as nematodes, astigmatic mites, springtails and sciarid larvae) on lily, green onion or tulip bulbs in various phases of cultivation. The species are listed in order of relative abundance

Predator species	Host plant	Phase of cultivation	Country	Location
<i>H. aculeifer</i>	Lily	Storage	The Netherlands	Lisse
<i>H. aculeifer</i>	Lily	Field	The Netherlands	Breezand
<i>H. aculeifer</i>	Lily	Field	The Netherlands	't Zand
<i>H. aculeifer</i>	Lily	Storage, field	The Netherlands	Anna Paulowna
<i>H. aculeifer</i>	Lily	Field	Taiwan	Houli
<i>H. aculeifer</i>	Lily	Field	Japan	Niigata
<i>P. fimetorum</i>	Lily	Propagation	The Netherlands	Breezand
<i>P. fimetorum</i>	Lily	Storage, field	Taiwan	Chin-Jin
<i>P. fimetorum</i>	Onion	Field	Japan	Chiba
<i>L. bispinosus</i>	Tulip	Storage	Japan	Fukiyama
<i>L. sugawarai</i>	Lily	Field	Taiwan	Chin-Jin
<i>P. hyalinus</i>	Lily	Greenhouse	The Netherlands	Lisse
<i>P. oudemansi</i>	Lily	Propagation, field	The Netherlands	Lisse
<i>P. primitivus</i>	Lily	Field	Japan	Niigata
<i>M. glaber</i>	Lily	Field	Taiwan	Houli
<i>M. nataliae</i>	Lily	Field	Japan	Horinouchi

and *P. fimetorum* from Japan and *P. hyalinus* from The Netherlands) and an ascid predator (*L. sugawarai* from Taiwan) were observed to feed and reproduce on both prey species (and on each of the prey species alone), but for reasons unknown the laboratory cultures died out within 1–4 months.

The remaining species of mesostigmatic predators (*H. aculeifer* and *P. fimetorum* from the Netherlands and Taiwan and *L. bispinosus* from Japan) were all successfully reared on the prey mixture. All these predators showed a population increase when offered each of the two prey species alone, except *L. bispinosus* from Japan. The latter predator was observed to feed mainly on the eggs and juveniles of *R. robini*, whereas it starved to death when offered *T. putrescentiae*. Feeding on the adults of *R. robini* by *L. bispinosus* was only observed for adult females that were starved for a few days.

To enable a comparison with *Hypoaspis* species and strains that were not collected from bulbous crops, *H. aculeifer* from Bremen and *H. miles* from Canada were also subjected to feeding tests. It was found that the Bremen strain of *H. aculeifer* fed and reproduced readily on both *T. putrescentiae* and *R. robini* and that the Canadian strain of *H. miles* fed and reproduced on *T. putrescentiae*, but not on *R. robini*. In the latter case the females of *H. miles* rather starved than fed on *R. robini*. The culture of *H. miles* on *R. robini* died out within a few weeks. This result was independently confirmed by one of the authors (C.C.).

An overview of the observations on feeding and reproduction of the mesostigmatic mites on either *T. putrescentiae* or *R. robini* as prey is presented

in Table 2, together with an – admittedly subjective – indication of the relative rearing success.

Small-scale population experiments

The capacity for controlling *R. robini* in the propagation phase of lily bulbs was tested in small-scale population experiments with four strains of *H. aculeifer* from Breezand, 't Zand, Taiwan and Bremen, the Japanese strain of *L. bispinosus* and the Taiwanese strain of *P. fimetorum* (but not the Dutch strain!). The results presented in Figs 1 and 2 show that all strains of *H. aculeifer* and the Japanese strain of *L. bispinosus* are capable of suppressing *R. robini*. Whereas the control experiment showed an increase of *R. robini* from approximately 120 to approximately 615 mobile stages of bulb mites per bulb over a period of 4 weeks, the experiments with predators showed a decrease to approximately 55 bulb mites for *L. bispinosus* and to approximately 3.5, 1.5, 0.8 and 0.6 bulb mites for *H. aculeifer* from Bremen, 't Zand, Taiwan and Breezand, respectively. Simultaneously, the populations of the predators increased from 6 predators per bulb to approximately 54.8 per bulb for *L. bispinosus* and to approximately 28.6, 68.2, 86.5 and 101 per bulb for *H. aculeifer* from Bremen, 't Zand, Taiwan and Breezand, respectively.

In contrast to these successful trials the experiments with *P. fimetorum* failed; the predator population died out within 2 weeks. As this predator was found on soil richer in organic matter or on peat, it was suspected that the vermiculite used as a medium in the population experiments may have been inadequate as a substrate. Hence, it was decided to repeat the experiment using peat as a medium for the lily scales. This experiment cannot be directly compared to the others, as it differed in a number of respects, as explained in the Materials and Methods section. The results of the experiment with and without *P. fimetorum* on lily bulbs in peat are shown in Fig. 3. Whereas the control experiment showed an increase of *R. robini* from approximately 75 to approximately 1020 mobile stages of bulb mites per bulb over a period of 4 weeks, the experiments with *P. fimetorum* showed a decrease of *R. robini* to approximately 6.8 bulb mites. Simultaneously the populations of the predators increased from 4 predators per bulb to approximately 23.3.

DISCUSSION

Perspectives for biological control

The results of the pre-selection based on field exploration, feeding tests and small-scale population experiments showed that all strains of *H. aculeifer* under test are promising candidates for biological control of *R. robini* in lily bulbs under conditions of bulb propagation. The Bremen strain that was not collected from bulbous crops showed a clearly lower population increase, but not a significantly different performance as a biocontrol agent. This is probably due to

TABLE 2

Rearing success of different strains (cf. Table 1) of mesostigmatic predators on two astigmatic prey species

	<i>T. putrescentiae</i>				<i>R. robini</i>			
	Feeding	Oviposition	Development	Rearing	Feeding	Oviposition	Development	Rearing
<i>H. aculeifer</i>								
Breezand	+	+	+	+	+	+	+	+
't Zand	+	+	+	+	+	+	+	+
A. Paulowna	+	+	+	+	+	+	+	+
Bremen	+	+	+	+	+	+	+	+
Taiwan	+	+	+	+	+	+	+	+
<i>P. fimetorum</i>								
Taiwan	+	+	+	+	+	+	+	+
Japan	+	+	+	—	+	+	+	—
<i>P. hyalinus</i>								
Lisse	+	+	+	+	+	+	+	+
<i>L. sugawarai</i>								
Taiwan	+	+	+	+	+	+	+	+
<i>P. primitivus</i>								
Japan	+	+	+	—	+	+	+	—
<i>L. bispinosus</i>								
Japan	—	—	—	—	+	+	+	+
<i>M. glaber</i>								
Taiwan	—	—	—	—	—	—	—	—
<i>M. nataliae</i>								
Japan	—	—	—	—	—	—	—	—

To indicate the relative performance (based on rather subjective criteria) a scale is used ranging from unsuccessful (—) to moderately (+) and very successful (++)

the fact that juvenile predators have low prey requirements and prey suppression was already achieved by the time the second generation matured. With lower predator to prey ratios clearer differences in the control capacities between the strains would have been observed; the one with the highest capacity of population increase on *R. robini* is expected to be the most suitable candidate. Hence, we advocate the use of the strains from Taiwan and Breezand. As the latter strain is endemic, it may have traits that enable it to survive better under outdoor conditions in The Netherlands.

The ascid predator, *L. bispinosus*, from Japan showed a lower capacity of controlling *R. robini* at a 1 : 20 predator-prey ratio, than the laelapid predator, *H. aculeifer*. However, it should be kept in mind that this predator is much smaller and feeds on the eggs and juvenile prey stages only. Hence, by using higher

Fig. 1. Population dynamics of the bulb mite, *R. robini* and the laelapid predator, *H. aculeifer*, in jars with scales from lily bulbs (cv Tender) mixed with vermiculite (initial predator-prey ratio = 1 : 20). Vertical bars at either side of the mean values indicate standard deviations. Both the mean and standard deviations are calculated from $\log(x + 1)$ transformed data. (a) Mean numbers of *R. robini* per lily bulb (approximately ten scales) in the absence of predatory mites (black dots) and in presence of *H. aculeifer* from Bremen (open triangles), 't Zand (black triangles), Taiwan (open squares) or Breezand (open dots). The initial number of *R. robini* was invariably approximately 120 mobile stages per bulb. The treatments involving different strains of predators differ significantly from the control, but not between each other (multiple comparisons using paired *t*-test carried out separately for weeks 2, 3 and 4; $\alpha = 0.05$ and $\alpha' = 1 - (1 - \alpha)^{1/n}$; n denotes number of comparisons). (b) Mean numbers of *H. aculeifer* per lily bulb (approximately ten scales) for experiments with strains from Bremen (open triangles), 't Zand (black triangles), Taiwan (open squares) or Breezand (open dots). The initial number of *H. aculeifer* was invariably six mobile stages per bulb. The populations of the various strains of predators did not differ significantly except for the comparison between the strains from Breezand and Bremen (multiple comparison using paired *t*-test carried out separately for weeks 2, 3 and 4; $\alpha = 0.05$ and $\alpha' = 1 - (1 - \alpha)^{1/n}$; n denotes number of comparisons).

predator to prey ratios this predator may show a stronger impact on the prey population. Moreover, by being smaller this predator may be better able to penetrate into the bulb than all the other predators investigated.

The parasitoid predator, *P. fimetorum*, showed a capacity to control *R. robini* on lily scales mixed with peat, but not when mixed with vermiculite. The reasons for this difference are not clear and deserve more detailed biological studies. It may be either related to the structure of the substrate or to the presence of alternative food sources in peat. In any case, the application of *P. fimetorum* depends critically on the substrate used in practice. Vermiculite has the advantage that is virtually sterile, but it is more expensive than peat and it cannot be used for other purposes by the lily growers. As peat is cheaper, can be sterilized and then used in storage rooms as well as in the greenhouse, there are economic reasons for its use by the lily growers. The disadvantage is that the contamination risks with pests and diseases are higher. Currently, peat is used by a considerable number of growers, making it worthwhile to consider suitable candidates for biological control of *R. robini* in this substrate. A critical comparison between various strains of *P. fimetorum* and *H. aculeifer* is needed. Preliminary experiments on lily scales propagated in peat (C.C.) and on lily bulbs in peat soil under greenhouse conditions (I.L. and C.C.) showed that *H. aculeifer* is capable of controlling *R. robini*, but how it compares to *P. fimetorum* is yet to be investigated.

Species-wide properties or local adaptations?

One should be cautious in inferring species-wide properties from experiments based on cultures started with a small inoculum of predatory mites originating

Fig. 2. Population dynamics of the bulb mite, *R. robini* and the ascid predator, *L. bispinosus*, in jars with scales from lily bulbs (cv Tender) mixed with vermiculite. Mean numbers of *R. robini* per lily bulb (approximately ten scales) in the absence of predatory mites are indicated by black dots and those in presence of *L. bispinosus* by open dots. The mean numbers of *L. bispinosus* per lily bulb are indicated by black triangles. The initial numbers of *R. robini* and *L. bispinosus* were, respectively, approximately 120 and six mobile stages per bulb (predator-prey ratio = 1 : 20). Vertical bars at either side of the mean values indicate standard deviations. Both the mean and standard deviations are calculated on $\log(x + 1)$ transformed data.

from one particular location. It may well be that there is geographic variation or even intrapopulation variation that is of crucial importance for the impact of predatory mites. Our experiments revealed differences in the population increase between four strains of *H. aculeifer*, including two Dutch strains from locations no more than 10 km apart. To what extent these differences reflect local adaptations or are due to the small samples taken from populations with similar variations in life history traits is not clear. In addition, the method of rearing in the laboratory and the prey species used for rearing may have changed the genetic make-up of the laboratory population relative to the original population sample. Furthermore, conditioning on *T. putrescentiae*, the prey used for rearing, may have had an influence on the initial performance of the predatory mites in the small-scale population experiments, but it is not likely to explain the differences between strains as they were all subject to the same rearing procedure. For these reasons we suspect that the differences between strains probably reflect genetic differences though not necessarily differences that are representative of the populations sampled in the field.

Fig. 3. Population dynamics of the bulb mite, *R. robini* and the parasitoid predator, *P. fimetorum*, in jars with scales from lily bulbs (cv Star Gazer) mixed with peat. Mean numbers of *R. robini* per lily bulb (approximately ten scales) in the absence of predatory mites are indicated by black dots and those in presence of *P. fimetorum* by open dots. The mean numbers of *P. fimetorum* per lily bulb are indicated by black triangles. The initial numbers of *R. robini* and *P. fimetorum* were, respectively, approximately 75 and four mobile stages per bulb (predator-prey ratio = 1 : 20). Vertical bars at either side of the mean values indicate standard deviations. Both the mean and standard deviations are calculated on $\log(x + 1)$ transformed data.

A comparison of our data with those published in the literature reveals some striking differences that warrant further study. Laelapid mites of the genus *Hypoaspis*, mainly *H. aculeifer* and *H. miles*, have been reported to feed on variety of prey types, such as *Tribolium* eggs, sciarid and cecidomyid larvae, springtails, thrips, nematodes, astigmatic mites (*Tyrophagus* spp., *Rhizoglyphus* spp. and *Histiostoma* spp.) and pollen (Kevan and Sharma, 1964; Barker, 1969; Lobbes and Schotten, 1980; Inserra and Davis, 1983; Usher and Davis, 1983; Hoda *et al.*, 1986; Ragusa *et al.*, 1986; Sardar and Murphy, 1987; Ragusa and Zedan, 1988; Zedan, 1988; Gillespie and Quiring, 1990; Murphy and Sardar, 1990; Glockemann, 1992; Chambers *et al.*, 1993). It seems unlikely that these two species of *Hypoaspis*, nor the various strains investigated, have the same dietary range and the same prey preferences. Our experiments showed that a Canadian strain of *H. miles* did not feed at all on *R. robini* in contrast to four strains of *H. aculeifer*. In addition, one of us (I.L.) found that this strain of *H. miles* could not feed on a closely related bulb mite species, *R. echinopus* (Fum. & Rob.) in contrast to what has been reported by Shereef *et al.* (1981) and Hoda *et al.* (1986). Detailed studies on genetic variation within and between populations of the two *Hypoaspis* species are needed to resolve these problems.

Hokkanen and Pimentel (1984, 1989) proposed using strains of predators from locations different from that of the pest. These authors argued that when predators do not share the same evolutionary history with the pest organism, they are more likely to overcome the defence system of their victim or they are more likely to escape the attention of hyperpredators. Our studies, however, did not lend support to Hokkanen and Pimentel's (1984, 1989) 'new association' approach. The most suitable candidates were found at locations where the pest occurred and all cases of new associations (e.g. the Bremen strain of *H. aculeifer* and the Canadian strain of *H. miles*) resulted in significantly lower success or even failure. This should not be taken as an argument against Hokkanen and Pimentel's (1984, 1989) approach as there is still an impressive amount of evidence in support of it despite scrutiny of the data resources by Waage and Greathead (1988). What our experiments indicate is that this approach does not necessarily lead to more success.

ACKNOWLEDGEMENTS

The work reported in this paper greatly benefited from cooperation with Dr Ch.-C. Ho in Taiwan and Dr A. Enami, Dr H. Nemoto, Dr T. Gotoh and Dr H. Amano in Japan. They were our guides on the foreign exploration trips and were of great help in selecting suitable sites for the collection of mesostigmatic mites associated with bulb mites.

For confirming identification of *H. aculeifer* from Taiwan and Japan we thank Andrea Ruf (University of Bremen, Germany) and for identification of *L. sugawarai* from Taiwan and for confirming identification of *L. bispinosus* from Japan we thank K. Blaszk (Adam Mickiewicz University, Poznan, Poland).

For comments on the manuscript we thank Nico van Straalen. The research was funded as project ABI.003-2187 by the Technology Foundation (STW) which resides under the Netherlands Organisation of Scientific Research (NWO).

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