Available online at www.sciencedirect.com
ScienceDirect
Biological Control 42 (2007) 55–60
Biological Control
www.elsevier.com/locate/ybcon

The parasitoid *Copidosoma koehleri* provides limited control of the potato tuber moth, *Phthorimaea operculella*, in stored potatoes

Tamar Keasar [a,*], Adi Sadeh [b]

[a] *Department of Life Sciences, Achva College, Mobile Post Shikmim 79800, Israel*
[b] *Department of Evolution, Systematics and Ecology, The Hebrew University, Jerusalem 91904, Israel*

Received 22 December 2006
Available online 31 March 2007

Abstract

The potato tuber moth *Phthorimaea operculella* (Zeller) is a major pest of potatoes in the field, and of tubers stored under ambient temperatures post-harvest. The encyrtid parasitoid *Copidosoma koehleri* (Blanchard) effectively controls the pest in the field in some countries. We tested whether *C. koehleri* can also reduce tuber moth populations in storage. Tubers stored indoors and outdoors in Israel, under controlled initial tuber moth infestation levels, received 1–2 releases of adult parasitoids during an eight-week storage period. Tubers were repeatedly sampled for infestation, and reared out until adult insect emergence. In the indoor storage experiment, parasitoid populations increased and tuber moth populations were significantly reduced. Nevertheless, tuber infestation reached 100% in *C. koehleri*-treated tubers and in untreated controls. In potatoes stored in heaps outdoors, parasitized hosts were rarely recovered, and infestation levels of parasitoid-treated heaps did not differ from untreated controls. We discuss possible reasons for *C. koehleri*'s limited efficiency as a biological control agent.

Keywords: *Phthorimaea operculella*; *Copidosoma koehleri*; Biological control; Potato; Traditional storage

1. Introduction

The potato tuber moth (PTM) *Phthorimaea operculella* (Zeller) (Lepidoptera: Gelechiidae) is a major agricultural pest of solanaceous crops in tropical–subtropical countries around the world. In potatoes, the moth larvae feed on leaves at the beginning of the growing season, and migrate into the tubers towards harvest. Often, more than 10% of the harvested tubers are infested and unmarketable (Sileshi and Teriessa, 2001).

Harvested tubers are commonly stored for up to four months before marketing. Storage in closed, refrigerated facilities prevents the migration of moths into the store, and their subsequent reproduction and development. However, refrigerated storage space is insufficient in many potato-growing areas in developing countries. This shortage leads growers to use traditional ambient storage methods, both indoors and outdoors. Indoor stores include caves or rustic buildings constructed of wood, mud or other local material. Outdoor storage consists of heaping the tubers in a shady location in or near the field, and covering them with straw. The accidental introduction of infested tubers into these stores allows development and reproduction of tuber moths (Hanafi, 1999). The moths' life cycle is completed within three weeks at 27 °C (Badegana and Ngameni, 2000; Chi and Getz, 1988). Summer storage of potatoes in hot areas can thus enable several successive generations to develop during the storage period. Outdoor stores are also prone to migration of adult moths from adjacent fields or stores throughout the storage period, although the contribution of such migration to moth populations in the stores appears to be limited (Keasar et al., 2005). More than 50% of the harvested tubers may become infested over the period of storage (Trivedi et al., 1994). This motivates the search for control measures of the pest in non-refrigerated stores.

* Corresponding author. Fax: +972 8 8588 057.
E-mail address: tkeasar@bgu.ac.il (T. Keasar).

1049-9644/$ - see front matter © 2007 Elsevier Inc. All rights reserved.
doi:10.1016/j.biocontrol.2007.03.012

Chemical control of the tuber moth in stores has limited potential, because most insecticides cannot be safely applied to potatoes shortly before marketing for human consumption. Several botanicals (such as rice bran, *Cannabis*, and *Lantana*) reduce tuber moth infestations in stores (Islam et al., 1990; Hossain et al., 1994; Das, 1995; Das and Rahman, 1997). *Granulosis* virus and *Bacillus thuringiensis* of various strains provide varying control levels (Islam et al., 1990; Ali, 1991; Kroschel and Koch, 1996; Abdel-Megged et al., 1998; Roux and Baumgartner, 1998; Setiawati et al., 1999). The testing of natural enemies in traditional potato stores has been limited to the egg parasitoid *Chelonus blackburni* (Cameron). This wasp effectively reduced tuber moth infestation in storage trials (Pokharkar and Jogi, 2000), but has not been introduced for commercial use.

In the present study we tested the efficiency of an additional parasitoid, the encyrtid hymenopteran *Copidosoma koehleri* (Blanchard) in controlling the potato tuber moth in non-refrigerated stores. This parasitoid was successfully introduced for classical biological control of the moth in potato fields in South Africa and Australia (Horne, 1990; Kfir, 2003), but has not been systematically tested in traditional stores. Its advantages include high host specificity (Guerrieri and Noyes, 2005), and a high reproductive potential due to its polyembryonic development (Doutt, 1947). In potato stores, female tuber moths oviposit on the surface of tubers, and larvae develop inside the tubers where they often pupate. The egg stage is therefore much more susceptible to natural enemies than larval or pupal stages. Parasitoids that attack the tuber moth's egg stage are thus expected to provide better biocontrol than natural enemies that target the later, more concealed developmental stages of the host. *C. koehleri* females indeed lay their eggs in the host's egg stage, while offspring emerge from the host's last larval instar. This developmental pattern provided an additional rationale for testing *C. koehleri* for biocontrol of the potato tuber moth in storage.

2. Materials and methods

2.1. Study species

The pest *P. operculella* and its parasitoid *C. koehleri* originate from South America. In Israel, *P. operculella* infests potatoes mainly during spring and summer. Adult females feed on floral nectar and lay their eggs on plants or on nearby soil. Larvae feed on plant leaves or tubers during the four instars of development, and pupate inside the tubers, on their surface, or in the soil. *C. koehleri* females oviposit one or more eggs into hosts in their egg stage. Each egg cleaves repeatedly during early stages of host development to produce a clone of 30–40 genetically identical larvae. These larvae feed on the host's tissues, consume it at the end of its last larval instar, and pupate within the dead host's cuticle. The parasitoids' life cycle is therefore synchronized with the life cycle of their host. Adult broods emerging from a host may be all-male, all-female or mixed-sex.

2.2. Indoor storage experiment

2.2.1. Insect rearing and release

Copidosoma koehleri and *P. operculella* were mass-reared at Bio-Bee Ltd., Kibbutz Sde Eliyahu, Israel at 27 °C and a 10:14 D:L illumination cycle. We applied the optimal relative humidity for each of the species in the rearing rooms, 70% for *C. koehleri* and 30% for *P. operculella* (Kfir, 1981). Host mummies containing ca. 40 parasitoid pupae were housed individually at room temperature until emergence of the adult wasp brood. Emerging wasps were sexed, and only single-sex broods were used in the experiment.

2.2.2. Experimental design

Traditional indoors storage was simulated at a small scale in a 7×3 m room at Kibbutz Yad Mordechai, Israel during July–August, 2005. The minimal ambient temperature recorded during this period was 18.7 °C, and the maximal temperature was 38 °C. Potatoes were stored in 48 boxes of 20 l. The boxes were covered with non-woven cloth that allowed ventilation but prevented insect migration, and were arranged in an 8×6 array. We assigned 24 boxes to the *C. koehleri* treatment, and the remaining boxes to the control treatment, using a completely randomized design without blocking. Each box served as an independent sampling unit. This experimental design minimized variation in abiotic conditions among sampling units, and thus did not allow testing of the parasitoids under a wide range of abiotic parameters. On the other hand, it eliminated possible interactions between room conditions and experimental treatment, which could complicate the interpretation of the results.

We placed 36 PTM-free tubers of the *Desiree* variety in each box. We numbered the tubers, and placed them in a 3×4 arrangement, in three layers in the boxes. At the start of the experiment, we placed two PTM eggs on a tuber from the bottom layer, five eggs on a tuber from a middle layer, and ten eggs on a tuber from a top layer, totaling 17 hosts. Thus, three (about 10%) of the tubers were initially infested, reflecting typical infestation values from field samples. We released one male brood and one female brood of parasitoids in each *C. koehleri*-treated replicate, on days 1 and 15 of the experiment. This resulted in ca. 80 mated females per replicate. Laboratory experiments indicate that a parasitoid:host ratio of 1:4 suffices to parasitize all hosts (Keasar et al., 2006). In the present experiment we set up much higher ratios (ca. 80 parasitoids: 17 hosts), to ensure favorable starting conditions for the parasitoids. The control treatment received no *C. koehleri* releases.

We sampled boxes for insect populations after two, four, six and eight weeks. Six boxes from each treatment were sampled at each time interval. The assignment of boxes to the different sampling dates was random. At sam-

pling we removed tubers and insects from the boxes. We therefore excluded sampled boxes from the remainder of the experiment. Since sampling required removal of box covers, we were concerned that insects would accidentally migrate between boxes during this time. To minimize this risk, we took boxes out of the storage room before opening and sampling them. In addition, to prevent contamination of control boxes by parasitoids, we always sampled the control boxes before handling the treated ones. At sampling, we recorded the number of infested and spoiled tubers (due to rotting and fungal development) in each box. We used the frass and tunnels of PTM larvae as indicators of tuber infestation. We reared out each infested tuber in a 500-ml plastic cup for three weeks at room temperature (detailed rearing methods are provided in Berlinger & Lebiush-Mordechi, 1997). We then determined the number of PTM individuals (larvae, pupae and adults) and parasitized PTM mummies in each cup. One box of the control treatment, sampled after eight weeks, had no PTM infestation at all. We excluded this replicate from data analysis, since we suspected an error in the initial release of PTM eggs in this box.

2.3. Outdoors storage experiment

The study was conducted at the experimental farm of Eshel Hanassi Regional School in the south of Israel, during July–September, 2003. The study area is characterized by desert climate, with hot, dry summers (27 °C monthly mean high) and cool winters (12 °C monthly mean low).

To emulate field storage, we set up 18 heaps, each of 800 kg potatoes, of the *Desiree* cultivar. The heaps were 1.30 m in diameter and 0.75 m high. They were placed at 50 m distance from each other, to reduce PTM migration between heaps (Cameron et al., 2002). We divided each heap into triangular pizza-like slices using a 2 cm mesh metal net. Mesh size allowed free movement of PTM, *C. koehleri* and other insects within the heap, but separated the potatoes from different slices. This allowed us to sample potatoes from a different slice every week, without affecting the spatial arrangement of tubers in the remaining slices. The heaps were covered with a thick layer of dry straw.

Freshly harvested potatoes were used for the experiment. Initial PTM infestation in these potatoes was determined in a 6000-tuber sample, and was found to be 0.045 ± 0.041 (SD) PTM individuals/tuber. The tubers in the experimental heaps were of the 100 g size class. Each 800 kg heap therefore contained about 8000 tubers that were infested by ca. 360 PTM individuals. This infestation rate is lower than typical infestation levels in developing countries at harvest, which often exceeds 10%. To achieve realistic starting conditions for our experiment, we artificially increased initial infestation by adding seven heavily infested tubers (60 PTM larvae per tuber, on average) to the top center of each heap. This increased the number of PTM larvae by 420, to 780 individuals per 8000-tuber heap. Thus, the estimated infestation rate at the beginning of the experiment was about 1 PTM larva per 10 potato tubers.

We treated each heap as a replicate, and randomly allocated them into an untreated control treatment, a single-release *C. koehleri* treatment, and a two-release *C. koehleri* treatment. Each treatment thus comprised six replicates in a completely randomized design. We released a total of 1800 *C. koehleri* adults in each of the treatment heaps. This was done once, at the onset of the experiment, in the single-release treatment. In the two-release treatment, we released the parasitoids in two equal doses, at the onset of the experiment, and on week 6.

We sampled tubers from one slice of each heap at weekly intervals. When setting up the heaps we placed nine 30×40 cm nylon-mesh bags, each containing two PTM-free tubers, at predetermined locations within each slice. The bags' mesh size was 1 cm, allowing free movement of insects. Sampling bags were placed at the bottom of the heap (3 bags), at mid-height (3 bags) or at its top (3 bags). Two of the three bags at each height were placed at the perimeter of the slice, and one bag was placed at its center. Thus, each week we sampled 18 tubers (two tubers × three bags × three heights) from different locations in a slice. We reared out the sampled tubers, and recorded the insects that developed in them, using the same protocol as in the indoor experiment. Fig. 1 illustrates the design of the heaps, and the placing of sampled tubers.

2.4. Data analysis

When analyzing of data from the indoor and outdoors experiments, we took into account their completely randomized designs. Proportions were arcsine transformed prior to analysis. We used *SPSS 14.0 for Windows* for statistical analyses. In the indoor storage experiment, each box was sampled only once, and was therefore considered an independent replicate. For the analysis of PTM and *C. koehleri* population tends, we treated each box as a sampling unit. We therefore calculated the numbers of PTM and *C. koehleri* that emerged from all sampled tubers in each box. The number of rotten tubers varied among boxes, and increased along the experiment. This variation produces a confounding effect, since such tubers do not allow insect development. We corrected for this confound by dividing the total number of PTM and parasitoids by the number of non-rotten tubers in each box. We used ANOVA and GLM to analyze the effects of treatment and week of experiment on the corrected per-box PTM infestation levels and *C. koehleri* parasitism rates.

For the analysis of the spatial distribution of the hosts and parasitoids within boxes, we treated individual tubers as sampling units. We tested whether the location of tubers in the boxes (indicated by their number) affected the number of hosts and parasitized mummies that developed in them. We also tested whether the layer from which tubers were sampled (bottom, middle or top) affected the numbers of hosts and parasitized mummies. For these analyses, we

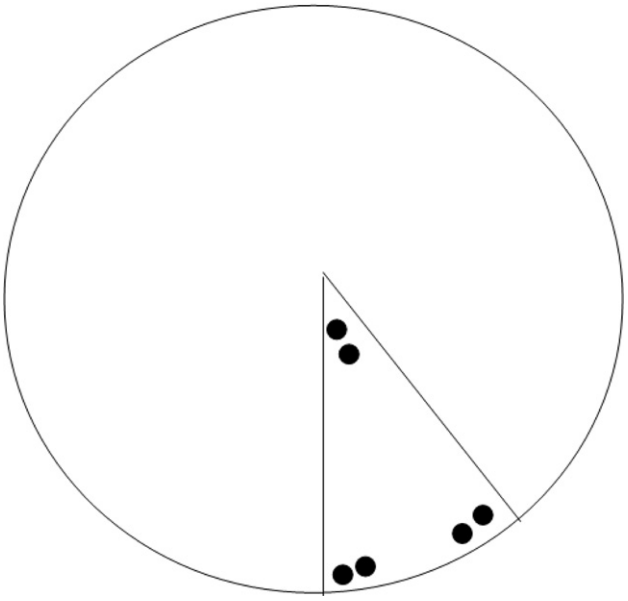

Fig. 1. Overall structure of the heaps in the outdoors experiment (top), and the arrangement of sampled tubers within each slice (bottom). One slice per heap at was sampled at weekly intervals.

treated tuber number as a random factor and layer as a fixed factor in ANOVA models. We treated box and week as covariates in these models.

Data recording in the outdoors storage experiment involved repeated sampling of the same storage heaps, i.e. each replicate was sampled on eight consecutive weeks. We therefore analyzed the data by repeated-measures ANOVA.

3. Results

3.1. Indoor storage experiment

More than 25% of the *C. koehleri*-treated and of the control tubers were damaged by PTM after two weeks of experiment, and the proportion of infested tubers reached 100% in both treatments after six weeks. The *C. koehleri* and control treatments did not differ in the proportions of infested tubers per box (Fig. 2, two-way ANOVA, treatment: $F_{(1,39)} = 1.099$, $p = 0.301$; week: $F_{(3,39)} = 78.069$, $p < 0.0001$; interaction: $F_{(3,39)} = 1.618$, $p = 0.201$). Some PTM larvae that contributed to tuber infestation in the *C. koehleri* treatment were parasitized, and were recorded as parasitized mummies after the larvae were reared out. No parasitized mummies were sampled in the control treatment. We therefore excluded data of control boxes from analyses of parasitized hosts. The number of parasitized PTM mummies in the *C. koehleri* treatment increased significantly during the course of the experiment (Fig. 3, ANOVA, $F_{(3,18)} = 4.87$, $p < 0.012$). However, the proportion of parasitized hosts, out of the total number of PTM, was not significantly affected by week of experiment (Fig. 3, ANOVA, $F_{(3,18)} = 2.386$, $p = 0.103$). The number of PTM individuals that completed normal development in the *C. koehleri* treatment was significantly lower than in the control treatment up to week 6 of the experiment (Fig. 4, ANOVA, treatment: $F_{(1,29)} = 6.998$, $p = 0.013$; week of experiment: $F_{(2,29)} = 8.193$, $p = 0.002$; interaction: $F_{(2,29)} = 4.375$, $p = 0.022$). Most of the control treatment tubers sampled on week 8 rotted during the three-week rearing period, so that PTM densities in them could not be determined.

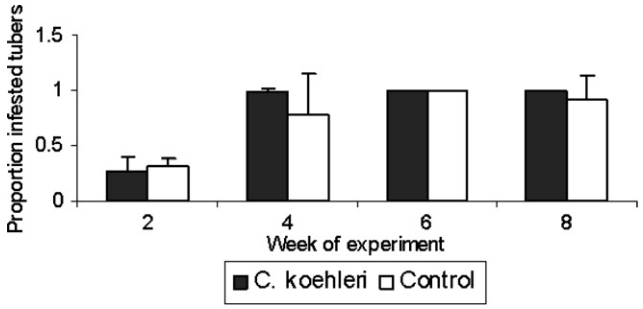

Fig. 2. Mean (+SD) proportion of infested tubers in the indoor storage experiment. Each storage box contained 36 tubers. We sampled six boxes for PTM infestation on weeks 2, 4, 6 and 8 after initial PTM release.

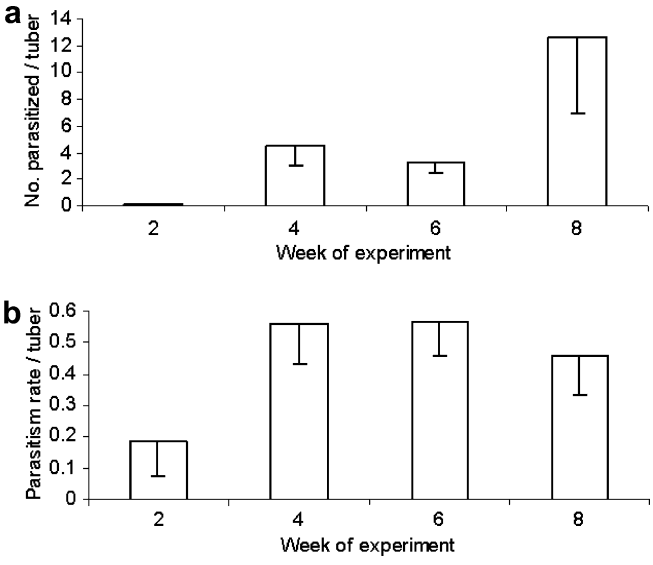

Fig. 3. Mean (+SD) numbers (bars) and proportions (line) of PTM mummies parasitized by *C. koehleri*, per infested tuber, in the *C. koehleri* treatment of the indoor experiment.

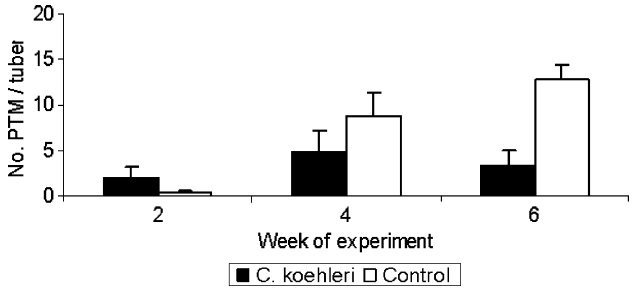

Fig. 4. Mean (+SD) numbers of normally developing PTM per infested tuber in the indoor storage experiment. Black bars – *C. koehleri*-treated boxes. White bars – untreated controls.

We estimated the number of infesting PTM larvae by adding up the number of PTM individuals with the number of parasitized mummies that developed in each tuber. The tubers' location in the box (identified by tuber numbers) did not significantly affect the number of infesting larvae ($F_{(35,220)} = 0.762$, $p = 0.831$). There were also no significant differences in infestation levels between tubers from the bottom layer (numbered 1–12), middle layer (numbered 13–24) and top layer (numbered 25–36) ($F_{(2,233)} = 0.274$, $p = 0.761$). Thus, we found no indication for heterogeneity in PTM infestation within the storage boxes. Parasitism rates by *C. koehleri* were also similar among tubers ($F_{(35,220)} = 1.118$, $p = 0.308$) and among storage layers ($F_{(2,233)} = 1.053$, $p = 0.350$).

3.2. Outdoors storage experiment

The proportion of PTM-infested tubers increased from 22–25% to 44–63% during the experiment in the different treatments (Fig. 5). Week of experiment significantly affected the proportion of infested tubers ($F_{(7,116)} = 5.902$, $p < 0.0001$), most strikingly because of the increase in infestation between weeks 2 and 3. Treatment had no significant effect on infestation rates ($F_{(2,116)} = 0.987$, $p = 0.376$). Similarly, PTM density per tuber increased significantly during the eight weeks of storage ($F_{(7,981)} = 16.104$, $p < 0.0001$), but was not significantly affected by treatment ($F_{(2,981)} = 0.434$, $p = 0.648$, Fig. 6). Only eight *C. koehleri*-parasitized mummies were recovered in five samples from the *C. koehleri*-treated heaps. Parasitoids of other species were not recorded.

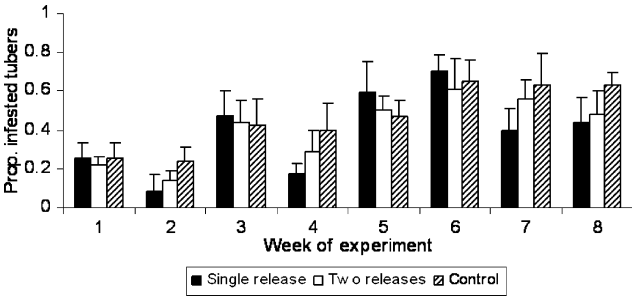

Fig. 5. Mean (+SD) proportions of infested tubers in the outdoors storage experiment. Data are based on weekly sampling of 18 tubers from each heap.

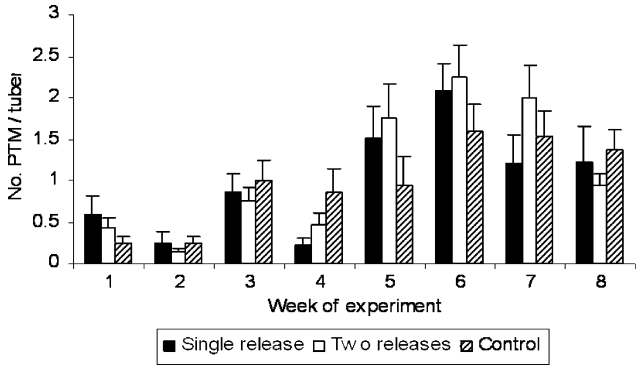

Fig. 6. Mean (+SD) numbers of normally developing PTM per infested tuber in the outdoors storage experiment. Data are based on weekly sampling of 18 tubers from each heap. PTM were reared out separately from each tuber.

4. Discussion

Our experiments demonstrate that *C. koehleri*'s potential for controlling the potato tuber moth in non-refrigerated indoor and outdoor stores is limited, in spite of its promising life-history features. These include a high reproductive rate, high host specificity, synchrony with host life cycle and targeting of an early stage of the host life cycle (Murdoch and Briggs, 1996). Recent population dynamics models applied to biological control situations highlight the importance of temporal and spatial refuges, and of host metapopulation structure, in allowing host persistence under biological control at varying spatial scales (Mills and Getz, 1996; Takagi, 1999; Hassell, 2000). The narrow time window vulnerable to parasitism within the host life cycle (the egg stage requires less than 20% of the tuber moth's life cycle) may have provided PTM with a temporal refuge from *C. koehleri* in our experiments. Owing to this narrow time window, most PTM individuals in a population may be protected from parasitism by *C. koehleri* at any given time.

In the indoor experiment we found no evidence for spatial refuges, as host populations and parasitism rates were similar in all parts of the storage boxes. The experimental design ruled out metapopulation dynamics, because we did not allow insect migration between storage boxes. Thus, a temporal refuge from parasitism for PTM seems to be the most likely explanation for its persistence in the indoor trial. Additional factors may have enabled PTM to survive and reproduce in the outdoors experiment: the clumped distribution of PTM in outdoors heaps (Keasar et al., 2005) may have promoted host–parasitoid coexistence (Hassell, 2000); the ability of adult PTM to migrate among potato heaps could provide a metapopulation structure, so that migration from untreated heaps could compensate for local reductions of host populations in treated heaps. Additionally, PTM larvae could have easily

migrated among tubers within a replicate in both experiments, possibly benefitting from reduced competition with conspecifics in doing so. Such migration could explain the high proportions of infested tubers in all treatments.

We conclude that *C. koehleri* provides partial control of PTM in indoor storage, but is not sufficiently effective in reducing economic damage. A possible direction for future research is to release *C. koehleri* in combination with other natural enemies. *C. koehleri* was successfully released together with additional PTM parasitoids (*Orgilus lepidus* Muesebeck and *Apanteles subandinus* Blanchard) in biocontrol programs in potato fields (Horne, 1990; Kfir, 2003). However, since *O. lepidus* and *A. subandinus* are larval parasitoids, they are not expected to provide good biocontrol in stored tubers. Other species of egg parasitoids, such as the egg-larval koinobiont *Chelonus blackburni* or Trichogrammatids, are attractive candidates for supplementing *C. koehleri* in traditional storage.

Acknowledgments

The study was supported by the Israeli Ministry for Industry and Trade. Data analysis and writing were supported by the Institute for Advanced Studies, the Hebrew University. We gratefully acknowledge Shimon Steinberg and Michal Segoli for helpful discussions. Ori Becher and Karen Dray provided expert technical assistance.

References

Abdel-Megged, M.I., Abbas, M.G., El-Sayes, S.M., Moharam, E.A., 1998. Efficacy of certain biocodes againt the potato tuber moth, *Phthorimaea operculella* under field and storage conditions. Ann. Agric. Sci. 1, 309–317, Special Issue.

Ali, M.I., 1991. Efficacy of a granulosis virus on the control of potato tuber moth, *Phthorimaea operculella* (Zeller) (Gelechiidae: Lepidoptera) infesting potatoes in Bangladesh. Bangladesh J. Zool. 19, 141–143.

Badegana, A.M., Ngameni, P.H., 2000. Technique d'elevage de la teigne de pomme de terr *Phthorimaea operculella* Zel. (Lepidoptera: Gelechiidae) en laboratoire, parameters biologiques et influence du taux de sucre dans l'alimentation de l'imago. Tropicultura 18, 23–25.

Chi, H., Getz, W.M., 1988. Mass rearing and harvesting based on an age-stage, two-sex life table: a potato tuberworm (Lepidoptera: Gelechiidae) case study. Environ. Entomol. 17, 18–25.

Das, G.P., 1995. Plants used in controlling the potato tuber moth, *Phthorimaea operculella* (Zeller). Crop Protect. 14, 631–636.

Das, G.P., Rahman, M.M., 1997. Effect of some inert materials and insecticides against the potato tuber moth, *Phthorimaea operculella* (Zeller) in storage. Int. J. Pest Manag. 43, 247–248.

Doutt, R.L., 1947. Polyembryony in *Copidosoma koehleri* Blanchard. Am. Nat. 81, 435–453.

Guerrieri, E., Noyes, J., 2005. Revision of the European species of *Copidosoma ratzeburg* (Hymenoptera: Encyrtidae), parasitoids of caterpillars (Lepidoptera). Syst. Entomol. 30, 97–174.

Hassell, M.P., 2000. Host–parasitoid population dynamics. J. Anim. Ecol. 69, 543–566.

Hanafi, A., 1999. Integrated pest management of potato tuber moth in field and storage. Potato Res. 42, 373–380.

Horne, P.A., 1990. The influence of introduced parasitoids of the potato moth *Phthorimaea operculella* (Lepidoptera: Gelechiidae) in Victoria, Australia. Bull. Entomol. Res. 80, 159–164.

Hossain, S.M.Z., Das, G.P., Alam, M.Z., 1994. Use of various indigenous materials and insecticides in controlling potato tuber moth in storage. Bull. Inst. Trop. Agricul. Kyushu University 17, 79–84.

Islam, M.N., Karim, M.A., Nessa, Z., 1990. Control of the potato tuber moth *Phthorimaea operculella* Zeller (Gelechiidae) in the storehouses for seed and ware potatoes in Bangladesh. Bangladesh J. Zool. 18, 41–52.

Keasar, T., Kalish, A., Becher, O., Steinberg, S., 2005. Spatial and temporal dynamics of potato tuber moth (*Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae)) infestation in field-stored potatoes. J. Econ. Entomol. 98, 222–228.

Keasar, T., Segoli, M., Barak, R., Steinberg, S., Giron, D., Strand, M., Bouskila, A., Harari, A.R., 2006. Costs and consequences of superparasitism in the polyembryonic parasitoid *Copidosoma koehleri* (Hymenoptera: Encyrtidae). Ecol. Entomol. 31, 277–283.

Kfir, R., 1981. Fertility of the polyembryonic parasite *Copidosoma koehleri*, effect of humidities on life length and relative abundance as compared with that of *Apanteles subandinus* in potato tuber moth. Ann. Appl. Biol. 99, 225–230.

Kfir, R., 2003. Biological control of the potato tuber moth *Phthorimaea operculella* in Africa. In: Neuenschwander, P., Borgemeister, C., Langewald, J. (Eds.), Biological Control in IPM Systems in Africa. CAB International, pp. 77–86.

Kroschel, J., Koch, W., 1996. Studies on the use of chemicals, botanicals and *Bacillus thuringiensis* in the management of the potato tuber moth in potato stores. Crop Protect 15, 197–203.

Mills, N.J., Getz, W.M., 1996. Modelling the biological control of insect pests: a review of host–parasitoid models. Ecol. Model. 92, 121–143.

Murdoch, W.W., Briggs, C.J., 1996. Theory for biological control: recent developments. Ecology 77, 2001–2013.

Pokharkar, D.S., Jogi, R.R., 2000. Biological suppression of potato tuber moth, *Phthorimaea operculella* (Zeller) with exotic parasitoids and microbial agents under field and storage conditions. J. Biol. Control 14, 23–28.

Roux, O., Baumgartner, J., 1998. Evaluation of mortality factors and risk analysis for the design of an integrated pest management system. Ecol. Model. 109, 61–75.

Setiawati, W., Soeriaamadja, R.E., Rubiati, T., Chujoy, E., 1999. Control of potato tuber moth (*Phthorimaea operculella*) using an indigenous granulosis virus in Indonesia. Indonesian J. Crop Sci. 14, 10–16.

Sileshi, G., Teriessa, J., 2001. Tuber damage by potato tuber moth, *Phthorimaea operculella* Zeller (Lepidoptera: Gelechiidae) in the field in eastern Ethiopia. Int. J. Pest Manag. 47, 109–113.

Takagi, M., 1999. Perspectives of pratical biological control and population theories. Res. Popul. Ecol. 41, 121–126.

Trivedi, T.P., Rajagopal, D., Tandon, P.L., 1994. Assessment of losses due to potato tuber moth. J. Ind. Potato Assoc. 21, 207–210.