

Seasonal abundance and effect of predators (Coleoptera, Coccinellidae) and parasitoids (Hymenoptera: Braconidae, Aphidiinae) on *Myzus persicae* (Hemiptera, Aphidoidea) densities on tobacco: a two-year study from Central Greece

Nickolas G. KAVALLIERATOS¹, Christos G. ATHANASSIOU², Željko TOMANOVIĆ³, George D. PAPAPOPOULOS² & Basileios J. VAYIAS²

¹Laboratory of Agricultural Entomology, Department of Entomology and Agricultural Zoology, Benaki Phytopathological Institute, 8 Stefanou Delta str., 145 61 Kifissia, Attica, Greece; tel.: +30 2102128018, fax: +30 2108077506; e-mail: nick_kaval@hotmail.com

²Laboratory of Agricultural Zoology and Entomology, Faculty of Plant Science, Agricultural University of Athens, 75 Iera Odos, 11855 Athens, Attica, Greece

³Institute of Zoology, Faculty of Biology, University of Belgrade, Studentski trg 16, 11000 Belgrade, Serbia and Montenegro

KAVALLIERATOS, N. G., ATHANASSIOU, C. G., TOMANOVIĆ, Ž., PAPAPOPOULOS, G. D. & VAYIAS, B. J., Seasonal abundance and effect of predators (Coleoptera, Coccinellidae) and parasitoids (Hymenoptera: Braconidae, Aphidiinae) on *Myzus persicae* (Hemiptera, Aphidoidea) densities on tobacco: a two-year study from Central Greece. *Biologia, Bratislava*, **59**: 613–619, 2004; ISSN 0006-3088.

Field studies were carried out in order to evaluate the effect of predators (coccinellids) and parasitoids of *Myzus persicae* infesting tobacco in Greece. In an insecticide-free tobacco field in Tithorea (Fthiotis, C Greece) tobacco leave samples were taken from June until September, for two growing seasons (1996–1997). The aphidophagous coccinellids *Hippodamia* (*Semiadalia*) *undecimnotata*, *Adalia bipunctata*, *Adonia variegata*, *Propylaea quatuordecimpunctata* and *Coccinella septempunctata*, and the parasitoids *Aphidius colmani*, *Aphidius ervi*, *Aphidius matricariae*, *Praon staryi* and *Praon volucre* were recorded. *Hippodamia undecimnotata* was observed in higher numbers than the other coccinellids whereas *Praon volucre* was the dominant parasitoid during both years of the study. The hyperparasitoid spectrum was composed of *Asaphes* spp., *Pachyneuron* spp. and *Syrphophagus aphidivorus* with *Pachyneuron* spp. being the most abundant during both years. Generally, for both seasons, high *M. persicae* densities were recorded in July and August (mid-season) while most coccinellid individuals were found rather early in the season (June – July). On the other hand, the mummification rate showed a specific increasing trend late in the season (August – September). Furthermore, when the effect of coccinellids on mummies of *M. persicae* in the field was studied, it was observed that an increase in the number of destroyed mummies was accompanied by a decrease in the number of uneaten mummies.

Key words: *Myzus persicae*, aphid, predators, parasitoids, Greece.

Introduction

Aphids are considered to be one of the most important tobacco pests causing significant losses (DIANA & SANNINO, 1995; HARLOW & LAMPERT, 1990). In Greece, *Myzus persicae* (Sulzer, 1776) is the main aphid species infesting tobacco (BLACKMAN & SPENCE, 1992).

Tobacco is an important crop in Greece and its infestation by *M. persicae* reduces directly both yield and quality of the product (FEINSTEIN & HANNAN, 1951; GUTHRIE et al., 1956; MISTRIC & CLARK, 1978; SEMTNER, 1984). The aphid acts indirectly as a vector of viruses (KENNEDY et al., 1962) and furthermore shows resistance to insecticides (HARLOW & LAMPERT, 1990).

Little information has been available on the abundance of natural enemies of *M. persicae* on tobacco. TAKADA & TAKENAKA (1982) investigated the relative abundance of two primary and six secondary parasitoid species of *M. persicae* on tobacco in Japan. Recently, KAVALLIERATOS et al. (1997, 2001) investigated the aphidiine spectrum parasitizing *M. persicae* on tobacco indicating the presence of the species *Aphidius avenae* Haliday, 1834, *Aphidius colemani* Viereck, 1912, *Aphidius ervi* Haliday, 1834, *Aphidius matricariae* Haliday, 1834, *Diaeretiella rapae* (M'Intosh, 1855), *Lysiphlebus fabarum* (Marshall, 1896), *Praon volucre* (Haliday, 1833) and *Praon staryi* (KAVALLIERATOS & LYKOURESSIS, 1999–2000). SEMTNER (1984) studied the effects of the transplantation date on the seasonal abundance of *M. persicae* and *Hippodamia convergens* Guérin-Méneville, 1842 on flue-cured tobacco in the USA.

As reported by WHEELER et al. (1968), FRAZER & GILBERT (1976), MEYHÖFER (2001) and TAKIZAWA et al. (2000), aphidophagous coccinellids have been found to feed on mummified aphids. Generally, there is a negative influence of predators on parasitoids through their exploitation of aphid colonies (MÜLLER & GODFRAY, 1999). However, it seems that there is inadequate information about the interactions between predators and parasitoids (TAKIZAWA et al., 2000).

The aims of this study were (i) to examine the seasonal occurrence of coccinellids, aphidiines and hyperparasitoids on the populations of *M. persicae* on tobacco during the crop period and (ii) to assess the effect of coccinellids on mummies of *M. persicae* on tobacco in the field.

Material and methods

Samples were taken from an untreated field in Tithorea

(Fthiotis, C Greece), (38°35' N, 22°40' E) covering an area of 1 ha cultivated with *Nicotiana tabacum* L. (Solanaceae) plants (var. Mc Nair 944). The experimental field was a part of a larger field surrounded by other tobacco fields. This field was chosen because of the heavy infestation levels by *M. persicae*. Sampling started with the first colonization of tobacco plants by aphids and continued until the last harvest of leaves. Every ten days from 10.VI. to 12.IX. in 1996 and from 20.VI. to 19.IX. in 1997, twenty leaves were collected from ten randomly chosen plants (2 leaves per plant, 1 plant per line). Plants were topped at the flower stage and a contact sucker control agent [fatty alcohol-Royal Tac SL (*n*-decanol 66.64% + octanol 0.34% SL)] was applied immediately. Royal Tac SL is used in order to avoid the development of axillaries in tobacco plants after topping. Topping as well as the application of the sucker control agent are considered necessary in order to produce tobacco reach in carbohydrates and nicotine. In 1996, topping began on 24.VII. and it was completed on 13.VIII. Similarly in 1997, topping began on 1.VIII. and it was completed on 22.VIII.

Each leaf was placed separately in a plastic bag and it was then detached from the stem of the plant with a scissors. These bags were put inside a portable refrigerator and were next brought to the laboratory where aphids were identified to species. Living aphids were preserved in a 2:1 ratio of 90% ethyl alcohol and 75% lactic acid (EASTOP & VAN EMDEN, 1972). Mummies were placed separately in small plastic boxes. Each box was labeled with the data of the collection date and the serial number of the leaf. Next, the plastic boxes were put inside a growth cabinet until adult parasitoid emergence. On the lid of each box there was a circular opening covered with muslin for ventilation in order to maintain inside the boxes similar conditions to those existing in the growth cabinet [22.5°C, 65% RH, 16:8 (L:D)].

Furthermore, the number of the destroyed mummies (preyed upon) found at each sampling was also recorded. They are easily recognized because the edges of the irregular holes and punctures made by coccinellids and chrysopids respectively are darkly stained.

The mean number of aphids per leaf and the percentage of mummified aphids [mummified aphids to the total number of aphids] (TOMANOVIĆ et al., 1996; KAVALLIERATOS et al., 2002a, b) were calculated per sampling date. ANOVA was used to test the significance of differences in the total number of species of aphidiines which parasitized *M. persicae* (per leaf) during the whole period of the study. ANOVA was also used to test the significant differences in the total number of species of coccinellids (per sampling date) during the whole study period. Each sampling date was taken as a replicate. ANOVA was performed on transformed data $\log_{10}(x + 10)$ in the case of coccinellids recorded in 1997. Means were compared by the Tukey – Kramer (HSD) test (at $P = 0.05$), using the statistical package JMP (SALL et al., 2001). Finally, the number of coccinellid individuals on each sampling unit (leaf) was plotted against the corresponding *M. persicae* counts.

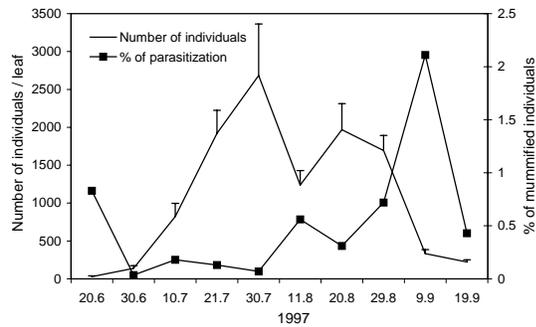
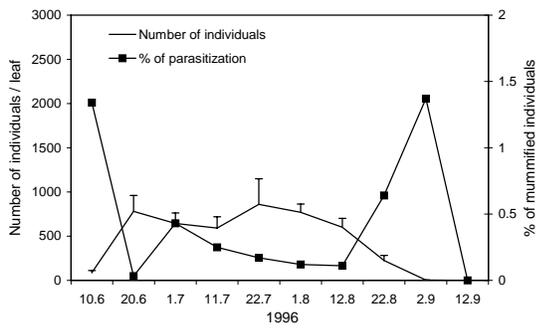


Fig. 1. Mean (+ SE) number of *Myzus persicae* per leaf and percentage of mummified individuals on tobacco plants in C Greece in 1996 and 1997.

Results

Myzus persicae was the only aphid species found in the present study. The numbers of *M. persicae* recorded in each sampling year were high mainly in the mid-season, with a peak around the end of July (Fig. 1). The highest percentages of mummified aphids were recorded at the beginning and (mainly) at the end of the crop season. However, in both growing seasons, the percentage of mummified aphids was rather low and did not exceed 2.5% (Fig. 1).

Myzus persicae was parasitized by *Aphidius colemani*, *A. ervi*, *A. matricariae*, *Praon staryi* and *P. volucre*. The hyperparasitoid spectrum was composed of *Asaphes* spp., *Pachyneuron* spp. and *Syrphophagus aphidivorus* (Mayr, 1876). The composition and numbers of the aphidiines and hyperparasitoids recorded in both years are shown in Fig. 2 and in Table 1, respectively.

ANOVA showed significant differences between the aphidiine species parasitizing *M. persicae* in both years ($F = 28.38$, $df = 3$, 396, $P < 0.0001$ in 1996; $F = 30.30$, $df = 3$, 396,

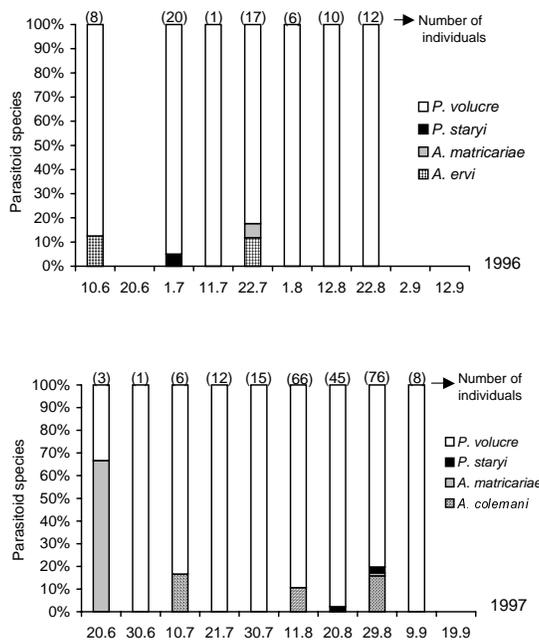


Fig. 2. Numbers of parasitoids and percentage of parasitoid species on *Myzus persicae* infesting tobacco plants in C Greece in 1996 and 1997.

$P < 0.0001$ in 1997). Means comparison showed that the mean numbers of *P. volucre* ($\bar{x} = 0.69$ in 1996, $\bar{x} = 2.07$ in 1997) was significantly higher than those of *A. colemani* ($\bar{x} = 0.20$ in 1997), *A. ervi* ($\bar{x} = 0.03$ in 1996), *A. matricariae* ($\bar{x} = 0.01$ in 1996, $\bar{x} = 0.03$ in 1997) and *P. staryi* ($\bar{x} = 0.01$ in 1996, $\bar{x} = 0.05$ in 1997). *Praon staryi* remained at very low levels during both years (Fig. 2).

Numbers of *Hippodamia (Semiadalia) undecimnotata* (Schneider, 1792) were higher than those of *Adalia bipunctata* (L., 1758) and *Adonia variegata* (Goeze, 1777) during both years (Fig. 3). Apart from the species presented in Fig. 3, low numbers of *Propylaea quatuordecimpunctata* (L., 1758) and *Coccinella septempunctata* L., 1758 individuals were also recorded in 1997: *P. quatuordecimpunctata* – 3, 5 and 7 individuals on 10.VII., 29.VIII. and 9.IX., respectively; *C. septempunctata* – 5 and 3 individuals on 21.VII. and 30.VII., respectively. Furthermore, small numbers of Chrysopidae were recorded during both years (1, 5, 2 and 1 individuals were recorded on 20.VI., 1.VII., 11.VII. and 22.VII., respectively in 1996, and 2, 1, 4 and 2 individuals were recorded on 10.VII., 21.VII., 30.VII. and 20.VIII., respectively in 1997).

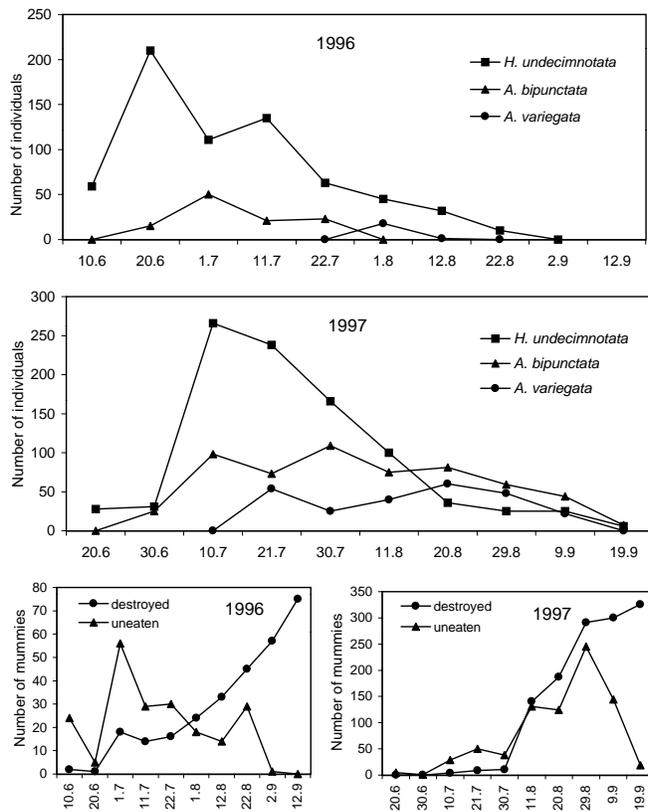


Fig. 3. Numbers of coccinellids on tobacco in C Greece and number of destroyed and uneaten *Myzus persicae* mummies.

ANOVA showed significant differences between the species of coccinellids recorded during both years ($F = 7.54$, $df = 2, 27$, $P = 0.0025$ in 1996; $F = 14.91$, $df = 4, 45$, $P < 0.0001$ in 1997). The mean numbers of *H. undecimnotata* ($\bar{x} = 66.50$ in 1996, $\bar{x} = 92.10$ in 1997) individuals were significantly higher than those of *A. bipunctata* ($\bar{x} = 10.90$ in 1996), *A. variegata* ($\bar{x} = 1.90$ in 1996, $\bar{x} = 24.90$ in 1997), *C. septempunctata* ($\bar{x} = 0.80$ in 1997) and *P. quatuordecimpunctata* ($\bar{x} = 1.50$ in 1997).

The numbers of destroyed mummies increased, whereas the numbers of uneaten mummies decreased (Fig. 3) during September of each year. No mummies destroyed by chrysopids were recorded. Moreover, coccinellid presence showed a positive trend at high aphid densities (Fig. 4). However, even at high aphid densities, coccinellid numbers were notably lower on sampling units (leaves) occupied by parasitoids.

Discussion

The reduction of aphid population observed during the two years of the study coincided with the

dates of the topping and the application of the sucker control agent (fatty alcohol). According to COLLINS & HAWKS (1993), topping stimulates the carbohydrates in the leaves and coincides with the production of nicotine, which acts as a bioicide. Furthermore, fatty alcohols are very efficacious against *M. persicae* (LAMPERT, 1989).

Praon volucre was the dominant parasitoid of *M. persicae* in both years. High incidence of parasitism of *M. persicae* by *P. volucre* has also been reported in Australia, where the parasite was transferred from Greece and Turkey for the control of *Hyperomyzus lactucae* (L., 1758) (CARVER, 1984; CARVER & WOOLCOCK, 1986). However, the superiority of *P. volucre* over other parasitoids of *M. persicae* may also be related to the host plant since it was recorded at low percentages on citrus (KAVALLIERATOS & LYKOURESSIS, 1999). *P. volucre* prefers steppe and forest habitats and represents one of the key parasitoids in the control of pest aphids in agroecosystems in Greece. It is a well-adapted parasitoid species in the Mediterranean parts of Greece with 33 aphid hosts (KAVALLIERATOS et al., 2001, 2003). These comprise about one third of the known aphid hosts

Table 1. Numbers of hyperparasitoids of *Myzus persicae* found on tobacco in C Greece in 1996 and 1997.

Dates 1996–1997	Hyperparasitoids numbers		
	A. spp.	P. spp.	S. a.
10.VI.1996	–	–	–
20.VI.1996	–	1	–
1.VII.1996	–	5	–
11.VII.1996	–	5	–
22.VII.1996	–	–	–
1.VII.1996	–	2	–
12.VII.1996	–	–	–
22.VII.1996	–	2	–
2.IX.1996	–	1	–
12.IX.1996	–	–	–
20.VI.1997	–	–	–
30.VI.1997	–	–	–
10.VII.1997	–	4	–
21.VII.1997	–	7	1
30.VII.1997	–	15	–
11.VIII.1997	2	27	–
20.VIII.1997	–	33	–
29.VIII.1997	1	59	–
9.IX.1997	–	53	–
19.IX.1997	–	1	–

Key: A. spp. – *Asaphes* spp.; P. spp. – *Pachyneuron* spp.; S. a. – *Syrphophagus aphidivorus*.

for *P. volucre* in the Palaearctic Region (TOBIAS & KIRIAC, 1986) and they mainly belong to the subfamilies Aphidinae (Macrosiphini: 22 species, Aphidini: 10 species) and Myzocallidinae: (Myzocallidini: 1 species).

The low presence of the recently described species *P. staryi* (KAVALIERATOS & LYKOURESIS, 1999–2000) during both years could be attributed to its rare presence in nature (STARÝ, 1970). The rarity of this species is reinforced by the fact that until now it has not been found on hosts other than *M. persicae* (KAVALIERATOS et al., 2001, 2003).

Hyperparasitoids were mainly represented by species of the genus *Pachyneuron* during both years. The hyperparasitoids found in the present study are obligate since they were restricted to being secondary parasitoids whose progeny can develop only in or on primary parasitoid (SULLIVAN, 1988). The hyperparasitoids did not appear in significant numbers until the aphid numbers had already started to decline in 1997. Therefore, they did not influence the impact of parasitoids on aphid density, which is more important during the aphid population built up. Furthermore, in both years, the hyperparasitoids appeared and in-

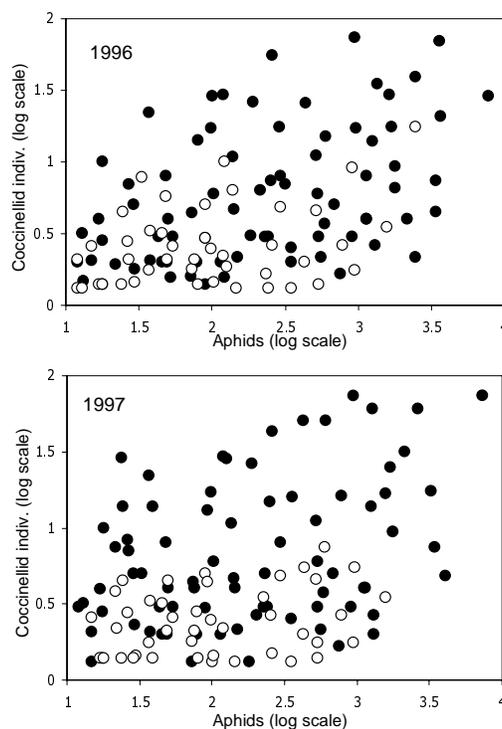


Fig. 4. Relationship between *Myzus persicae* density and coccinellid presence on each sampling unit, either free (solid circles) or occupied by parasitoids (open circles).

creased in numbers later seasonally. Similar observations on the appearance of hyperparasitoids and their effect on primary parasitoids have been made by EVENHUIS (1964), LATTEUR (1973), STARÝ (1970, 1988) and KAVALIERATOS et al. (2002a).

Adalia bipunctata and *A. variegata* remained in large numbers during August and September in 1997, when aphid populations were high. In contrast, the numbers of *H. undecimnotata* started to decrease in July (Fig. 3), although aphid populations remained high. This could be attributed to the mass migration of *H. undecimnotata* population from the valleys to the top of the mountains, which is recorded in Greece from July to September (KAVALIERATOS et al., 2002b, 2004).

Finally, the increasing number of destroyed mummies recorded (Fig. 3) indicates that Coccinellidae predators feed also on mummies. The ability of coccinellids to feed on mummies has been noted by other researchers as well (FRAZER & GILBERT, 1976; MEYHÖFER, 2001; TAKIZAWA et al., 2000; WHEELER et al., 1968). TAKIZAWA et al. (2000) showed that larvae of *C. septempunctata*, *Harmonia axyridis* (Pallas, 1773) and *Propy-*

lea japonica (Thunberg, 1781) consumed a significantly smaller amount of mummies in comparison to living and parasitized aphids. In general, this intraguild predation is defined by factors affecting the density of the extraguild prey (MEYHÖFER, 2001). Negative influence of predators on parasitoids has also been reported by MÜLLER & GODFRAY (1997, 1999) and HASSEL (1986). This stands in accordance with our findings where the presence of parasitoids on the same sampling unit resulted in a considerable reduction in coccinellid densities (Fig. 4). We assume that Coccinellidae do not prefer leaves bearing high percentage of mummified aphids, but those with a lot of living prey.

However, apart from the negative influence and several practical implications during planning of a biological control protocol, the coexistence of predators and parasitoids acts more likely as a stabilizing factor, and prevents the system from collapsing (HASSEL, 1978, 1986; HASSEL et al., 1994).

In conclusion, the small mummification percentage of *M. persicae* could be attributed to the high infestation of plants by aphids (STARÝ, 1970) as well as to the destruction of mummified aphids by coccinellids. As the present study showed, the activity of coccinellids, the topping of the plants as well as the application of the sucker control agent contributed to the reduction of *M. persicae* on tobacco. Further experimentation is required in order to assess the influence of intraguild predation on parasitoids, on *M. persicae* populations in the field.

Acknowledgements

Thanks are given to Prof. A. MAUROMOUSTAKOS, University of Arkansas for his help with the statistical analysis.

References

BLACKMAN, R. L. & SPENCE, J. M. 1992. Electrophoretic distinction between the peach-potato aphid, *Myzus persicae* (Sulzer), and *Myzus nicotianae* Blackman (Homoptera: Aphididae). *Bull. Entomol. Res.* **82**: 161–165.

CARVER, M. 1984. The potential host ranges in Australia of some imported aphid parasites (Hymenoptera: Ichneumonidae: Aphidiidae). *Entomophaga* **29**: 351–359.

CARVER, M. & WOOLCOCK, L. T. 1986. The introduction into Australia of biological control agents of *Hyperomyzus lactucae* (Linnaeus) Homoptera: Aphididae). *J. Austral. Entomol. Soc.* **25**: 65–69.

COLLINS, W. K., & HAWKS, S. N. Jr. 1993. Principles of flue-cured tobacco production. North Carolina State University, Raleigh, USA, 301 pp.

DIANA, G. & SANNINO, L. 1995. Avversità della coltura del tabacco: Insetti. *Inf. Fitopatol.* **45**: 24–31.

EASTOP, V. F. & VAN EMDEN, H. F. 1972. The insect material, pp. 1–45. In: VAN EMDEN, H. F. (ed.) *Aphid technology*, Academic Press, London, UK.

EVENHUIS, H. H. 1964. The interrelations between apple aphids and their parasites and hyperparasites. *Entomophaga* **9**: 227–231.

FEINSTEIN, L. & HANNAN, P. H. 1951. Effects of green peach aphid damage on the nicotine content of tobacco. *J. Econ. Entomol.* **42**: 267.

FRAZER, B. D. & GILBERT, N. 1976. Coccinellids and aphids: a quantitative study of the impact of adult ladybirds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). *J. Entomol. Soc. B. C.* **73**: 33–56.

GUTHRIE, F. E., RABB, R. L. & VAN MIDDELEM, C. H. 1956. Control of aphids on cigar-wrapper and flue-cured tobacco. *J. Econ. Entomol.* **49**: 602–606.

HARLOW, C. D. & LAMPERT, E. P. 1990. Resistance mechanisms in two colour forms of the tobacco aphid (Homoptera: Aphididae). *J. Econ. Entomol.* **83**: 2130–2135.

HASSEL, M. P. 1978. The dynamics of arthropod predator-prey systems, Princeton University Press, Princeton, NJ, 237 pp.

HASSEL, M. P. 1986. Parasitoids and population regulation, pp. 201–224. In: Proceedings of the 13th Symposium of the Royal Entomological Society of London “Insect Parasitoids”, Academic Press, London, UK.

HASSEL, M. P., COMINS, H. N. & MAY, R. M. 1994. Species coexistence and self-organizing spatial dynamics. *Nature* **370**: 290–292.

KAVALLIERATOS, N. G., ATHANASSIOU, C. G., STATHAS, G. J. & TOMANOVIĆ, Ž. 2002a. Aphid parasitoids (Hymenoptera: Braconidae: Aphidiinae) on citrus: seasonal abundance, association with the species of host plant and sampling indices. *Phytoparasitica* **30**: 365–377.

KAVALLIERATOS, N. G., ATHANASSIOU, C. G. & TOMANOVIĆ, Ž. 2003. A new species and a key to Greek *Praon* Haliday (Hymenoptera: Braconidae: Aphidiinae). *Dtsch. Entomol. Z.* **50**: 13–22.

KAVALLIERATOS, N. G. & LYKOURESSIS, D. P. 1999. Parasitoids (Hymenoptera: Braconidae) emerged from aphids (Homoptera: Aphidoidea) on citrus and their frequency in Greece. *Boll. Lab. Entomol. Agr. Filippo Silvestri* **55**: 93–104.

KAVALLIERATOS, N. G. & LYKOURESSIS, D. P. 1999–2000. Two new species of *Praon* Haliday (Hymenoptera: Aphidiidae) from Greece. *Entomol. Hell.* **13**: 5–12.

KAVALLIERATOS, N. G., LYKOURESSIS, D. P., PAPADOPOULOS, G. D. & VRACHA, A. D. 1997. Spatial and temporal parasitoid composition in populations of *Myzus nicotianae* Blackman in Greece. *Bol. Asoc. Esp. Entomol.* **21**: 127–128.

- KAVALLIERATOS, N. G., LYKOURESSIS, D. P., SARLIS, G. P., STATHAS, G. J., SANCHIS SEGOVIA, A. & ATHANASSIOU, C. G. 2001. The Aphidiinae (Hymenoptera: Ichneumonoidea: Braconidae) of Greece. *Phytoparasitica* **29**: 306–340.
- KAVALLIERATOS, N. G., STATHAS, G. J., ATHANASSIOU, C. G. & PAPADOULIS, G. T. 2002b. *Dittrichia viscosa* and *Rubus ulmifolius* as reservoirs of aphid parasitoids (Hymenoptera: Braconidae: Aphidiinae) and the role of certain coccinellid species. *Phytoparasitica* **30**: 231–242.
- KAVALLIERATOS, N. G., STATHAS, G. J. & TOMANOVIĆ, Ž. 2004. Seasonal abundance of parasitoids (Hymenoptera: Braconidae: Aphidiinae) and predators (Coleoptera: Coccinellidae) of aphids infesting citrus. *Biologia, Bratislava* **59**: 191–196.
- KENNEDY, J. S., DAY, M. F. & EASTOP, V. F. 1962. A conspectus of aphids as vectors of plant viruses. London, Eastern, UK, 114 pp.
- LAMPERT, E. P. 1989. Seasonal abundance and within-plant distribution of aphids (Homoptera, Aphididae) on flue-cured tobacco. *J. Econ. Entomol.* **82**: 114–118.
- LATTEUR, G. 1973. Etude de la dynamique des populations des pucerons des céréales. Premières données relatives aux organismes aphidiphages en trois localités différentes. *Parasitica* **29**: 134–151.
- MEYHÖFER, R. 2001. Intraguild predation by aphidophagous predators on parasitized aphids: the use of multiple video cameras. *Entomol. Exp. Appl.* **100**: 77–87.
- MISTRIC, W. J. J. R. & CLARK, G. B. 1978. Green peach aphid injury to flue-cured tobacco leaves. *Tob. Sci.* **23**: 23–24.
- MÜLLER, C. B. & GODFRAY, H. C. J. 1997. Apparent competition between two aphid species. *J. Anim. Ecol.* **66**: 57–64.
- MÜLLER, C. B. & GODFRAY, H. C. J. 1999. Indirect interactions in aphid-parasitoid communities. *Res. Popul. Ecol.* **41**: 93–106.
- SALL, J., LEHMAN, A. & CREIGHTON, L. 2001. *JMP Start Statistics. A guide to statistics and data analysis using JMP and JMP IN software.* Duxbury press, Belmont, Canada, USA, 491 pp.
- SEMTNER, P. J. 1984. Effect of transplantation date on the seasonal abundance of the green peach aphid (Homoptera: Aphididae) and two aphid predators on flue-cured tobacco. *J. Econ. Entomol.* **77**: 324–330.
- STARÝ, P. 1970. Biology of aphid parasites (Hymenoptera: Aphidiidae). Dr W. Junk, The Hague, The Netherlands, 643 pp.
- STARÝ, P. 1988. Aphidiidae, pp. 171–184. In: MINKS, A. K. & HARREWIJN, P. (eds) *Aphids, their biology, natural enemies and control*, Vol. 2B, Elsevier, Amsterdam, The Netherlands.
- SULLIVAN, D. J. S. L. 1988. Hyperparasites, pp. 189–203. In: MINKS, A. K. & HARREWIJN, P. (eds) *Aphids, their biology, natural enemies and control*, Vol. 2B, Elsevier, Amsterdam, The Netherlands.
- TAKADA, H. & TAKENAKA, Y. 1982. Parasite complex of *Myzus persicae* (Sulzer) (Homoptera: Aphididae) on Tobacco. *Kontyû* **4**: 556–568.
- TAKIZAWA, T., YASUDA, H. & AGARWALA, B. K. 2000. Effects of parasitized aphids (Homoptera: Aphididae) as food on larval performance of three predatory ladybirds (Coleoptera: Coccinellidae). *Appl. Entomol. Zool.* **35**: 467–472.
- TOBIAS, V. I. & KIRIAC, I. G. 1986. Family Aphidiidae, pp. 232–283. In: MEDVEDEV, G. S. (ed.) *Opredelitel' nasekomikh evropeiskoi chasti SSSR*, Vol. 3, Hymenoptera, part 5, *Opredelitel' fauny SSSR*.
- TOMANOVIĆ, Ž., BRAJKOVIĆ, M., KRUNIĆ, M. & STANISAVLJEVIĆ, L. 1996. Seasonal dynamics, parasitization and colour polymorphism of the pea aphid, *Acyrtosiphon pisum* (Harris) (Aphididae: Homoptera) on alfalfa in the South part of the Pannonian area. *Tiscia* **30**: 45–58.
- WHEELER, A. G., HAYES, J. T. & STEPHENS, J. L. 1968. Insect predators of mummified pea aphids. *Can. Entomol.* **100**: 221–222.

Received June 11, 2003
Accepted April 29, 2004