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Seasonal occurrence, distribution and sampling indices for *Myzus persicae* (Hemiptera: Aphidoidea) and its parasitoids (Hymenoptera: Braconidae: Aphidiinae) on tobacco

NICKOLAS G. KAVALLIERATOS[1], CHRISTOS G. ATHANASSIOU[2], ŽELJKO TOMANOVIĆ[3], ANDREA SCIARRETTA[4], PASQUALE TREMATERRA[4] and VLADIMIR ŽIKIĆ[3]

[1]Benaki Phytopathological Institute, Department of Entomology and Agricultural Zoology, Laboratory of Agricultural Entomology, 8 Stefanou Delta str., 14561 Kifissia, Attica, Greece; e-mail: nick_kaval@hotmail.com

[2]Laboratory of Agricultural Zoology and Entomology, Agricultural University of Athens, 75 Iera Odos str., 11855 Athens, Attica, Greece

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

[4]Department of Animal, Plant and Environmental Science, University of Molise, Via De Sanctis, 86100 Campobasso, Italy

Key words. Aphidoidea, *Myzus persicae*, Aphidiinae, *Aphidius colemani*, *Diaeretiella rapae*, tobacco, seasonal occurrence, sampling indices

Abstract. Field studies were conducted, in order to assess the seasonal occurrence and the spatial distribution of *Aphidius colemani* Viereck, *Aphidius matricariae* Haliday, *Diaeretiella rapae* (M'Intosh), *Praon staryi* Kavallieratos & Lykouressis and *Praon volucre* (Haliday), all parasitoids of *Myzus persicae* (Sulzer) on tobacco. The experiments took place in western Greece (Agrinion, Aitoloakarnania), during the 1996 and 1997 growing seasons, in an area of approximately 2.5 ha, where tobacco was the main crop. The experimental field was insecticide-free and tobacco leaf samples (from the upper and lower half of plants) were taken from June until September, in both years. The distribution of the species found was also represented and discussed. Generally, high *M. persicae* densities were recorded in August (mid-season) of both seasons. The mummification rate showed a specific increasing trend late in the season (August–September). In 1996, the percentage of mummification reached almost 61% at the end of the period, whereas in 1997 it remained at very low levels (<2%). The density of *M. persicae* was higher on the leaves collected from the upper part of the plants than on those from the lower part, but without significant difference. In contrast, the numbers of mummified *M. persicae* individuals were significantly higher on leaves collected from the lower part of the plants than on those from the upper part in both years. The relative abundance of the aphidiine parasitoid species differed between the two years.

INTRODUCTION

Myzus persicae (Sulzer) is the main aphid pest infesting tobacco in several areas in Greece (Kavallieratos et al., 1997, 2004). Tobacco is an important crop in Greece and its infestation by *M. persicae* reduces directly both yield and quality of the product (Guthrie et al., 1956; Mistric & Clark, 1978). This species also acts as a vector of viruses (Kennedy et al., 1962) and furthermore shows resistance to insecticides (Wolf et al., 1994).

Based on morphological characters Blackman (1987) suggested that tobacco is infected by another aphid species, *Myzus nicotianae* Blackman, which he separated from *M. persicae*. However, Clemens et al. (2000) suggest that *M. nicotianae* and *M. persicae* are conspecific species.

Little information is available on the aphidiines parasitizing *M. persicae* on tobacco. Takada & Takenaka (1982) investigated the aphidiine spectrum of *M. persicae* on tobacco in Japan and identified *Aphidius gifuensis* Ashmead and *Diaeretiella rapae* (M'Intosh). Lykouressis & Mentzos (1995) studied the abundance and the effects of parasitoids on *M. persicae* and the ways of enhancing their action. Kavallieratos et al. (1997, 2001) investigated the aphidiine spectrum parasitizing *M. persicae* on tobacco in Greece, indicating the presence of *Aphidius avenae* Haliday, *Aphidius colemani* Viereck, *Aphidius ervi* Haliday, *Aphidius matricariae* Haliday, *D. rapae*, *Lysiphlebus fabarum* (Marshall), *Praon volucre* (Haliday) and *Praon staryi* Kavallieratos & Lykouressis. The last one was described as a new species from *M. persicae* infesting tobacco by Kavallieratos & Lykouressis (2000). In a recent study, Kavallieratos et al. (2004) examined the seasonal occurrence of coccinellids, aphidiines and hyperparasitoids on the populations of *M. persicae* on tobacco during the crop period and assessed the effect of coccinellids on mummies of *M. persicae* on tobacco in the field.

The aforementioned studies provide useful information about the seasonal activity of aphidophagous species; however, in most of the above studies the capacity of these species in suppressing aphid populations and their practical utilization was not assessed under field conditions. The high densities of beneficials that are often reported to occur in tobacco fields in Greece and elsewhere (Takada & Takenaka, 1982; Kavallieratos et al. 2004) clearly suggest that an integration of natural enemies into aphid management is feasible, and these agents may play a key role in an Integrated Pest Management-based strategy. However, there is still inadequate information about the distribution of both aphids and

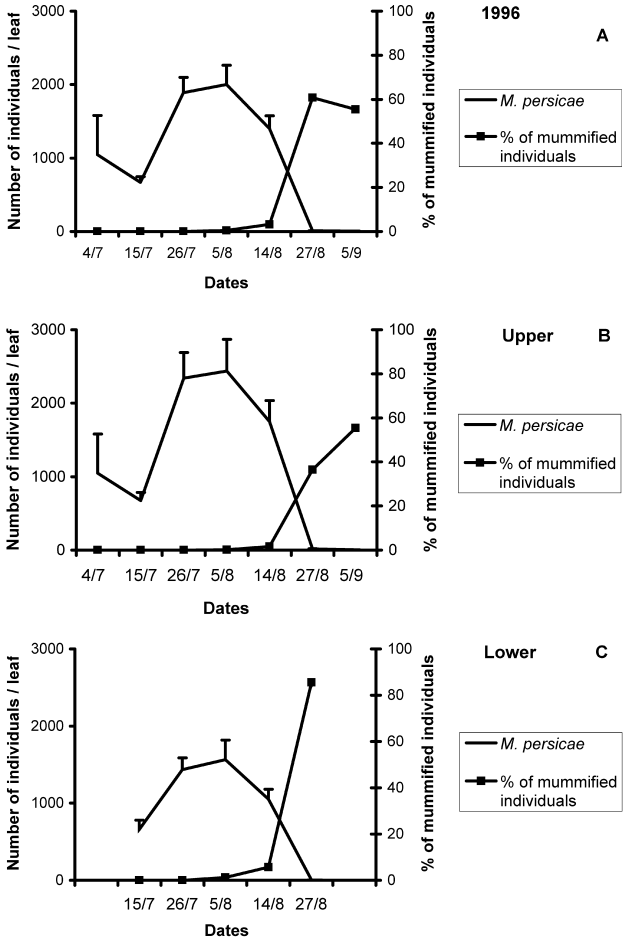

Fig. 1. Mean (± SE) number of *Myzus persicae* per leaf from upper and lower half of the plant and mummified *Myzus persicae* individuals (%) on tobacco plants in western Greece in 1996. A – upper and lower half (aver. value); B – upper half; C – lower half of the plant.

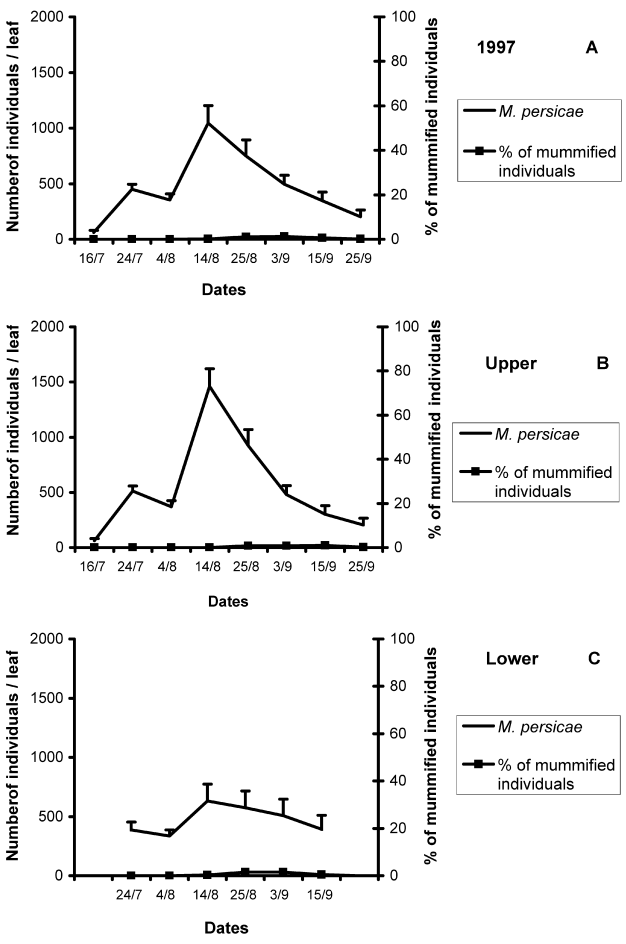

Fig. 2. Mean (± SE) number of *Myzus persicae* per leaf and mummified *Myzus persicae* individuals (%) on tobacco plants in western Greece in 1997. (For other details see Fig. 1.)

parasitoids. This is essential, in order to estimate pest and parasitoid densities, which may lead to a rational aphid management. If locally developed aphid populations are detected, the incorporation of parasitoids at those areas may be preferred before the extensive insecticidal applications. In our study, we examined the seasonal occurrence and the distribution of aphids and parasitoids on tobacco, over a two-year period.

MATERIAL AND METHODS

Samples were taken from an untreated field in Agrinion (Aitoloakarnania, western Greece), covering an area of 25,000 m^2 (100 × 250 m) cultivated with *Nicotiana tabacum* L. plants (var. Mc Nair 944). The experimental field was rectangular, with 250 rows (100 m long, 1 m apart, 2.5 plants/m in the row), and kept free from insecticidal applications. Tobacco is the main cultivation in this area. The area was chosen since samplings during the previous years indicated heavy infestation levels by *M. persicae*. There were 10 sampling points in the study field: 5 points in one row, 62.5 m and 187.5 m from the N and S edge respectively and 5 points in another row, 187.5 m and 62.5 m from the N and S edge respectively (see also Figs 3, 4, 7). Sampling started with the first colonization of tobacco plants by aphids and continued until the last harvest of leaves. Every ten days from 4 July to 5 September and from 16 July to 25 September in 1996 and 1997 respectively, twenty leaves were collected from ten plants (2 leaves per plant: one from the upper and one from the lower plant half) in the above 10 pre-selected points. Since the plants were small at the beginning of the experiment and since the lower leaves had been harvested at the end of the experiment, no leaves were cut from the lower half at the first and at the last sampling date. At those dates (4 July and 5 September in 1996, 16 July and 25 September in 1997) 20 leaves (2 leaves per plant) were collected from the upper half of the tobacco plants. 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 rich in carbohydrates and nicotine. Topping began on 7 August and it was completed on 18 August in 1996. Similarly, in 1997, topping began on 16 August and it was completed on 27 August.

Each leaf was placed separately in a plastic bag and it was then detached from the stem of the plant with a scissors. The 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

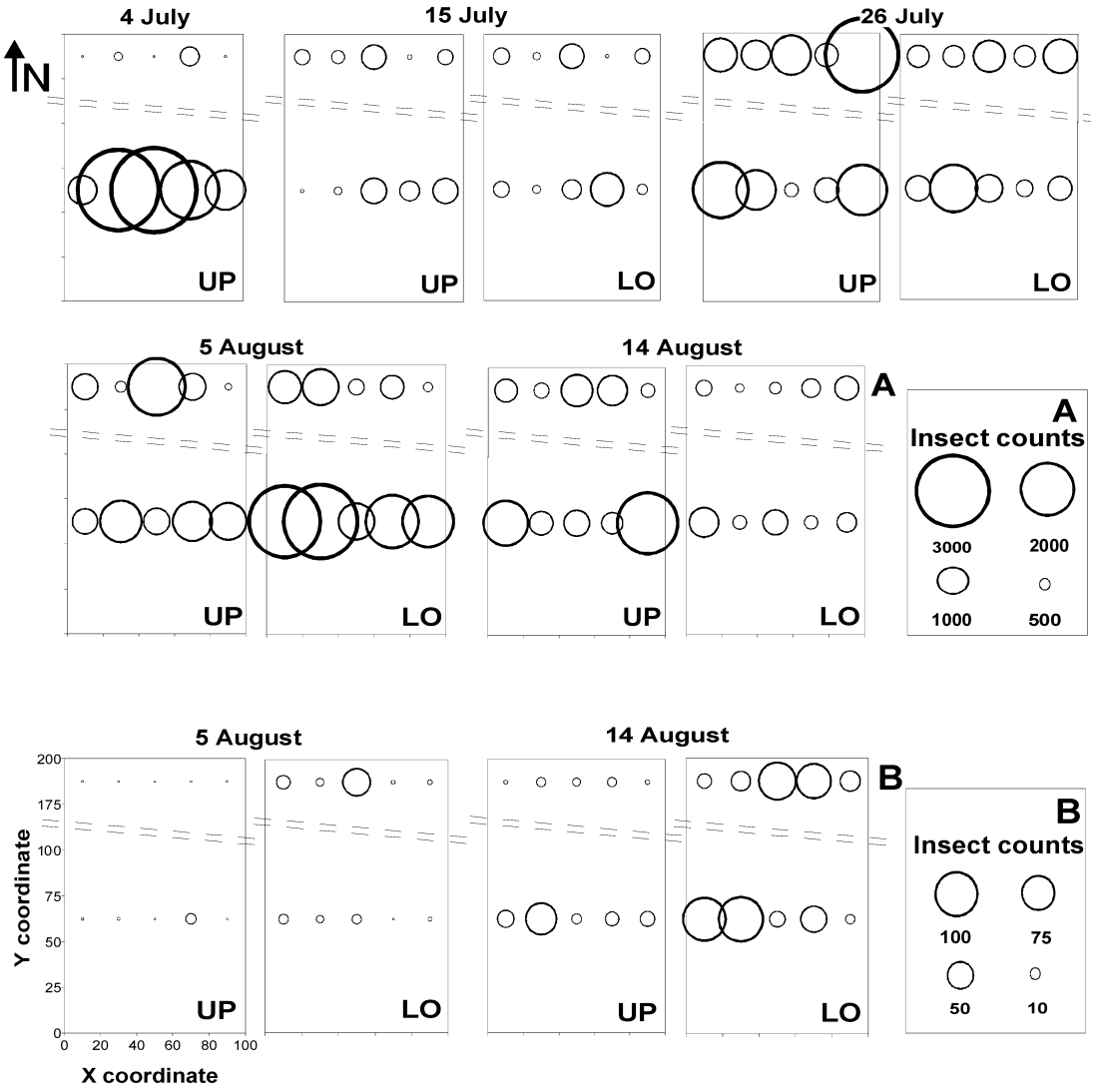

Fig. 3. Diagrams of *Myzus persicae* distribution within the sampling plot (10 points situated in two rows), during the 1996 growing season: A – living aphids; B – mummified aphids. UP and LO indicate upper and lower leaves, respectively. Coordinates *x*, *y* represent the distance in meters from the southeastern corner of the field.

box was labeled with the collection date and the serial number of the leaf. Next, the plastic boxes were put inside a growth cabinet until adult parasitoid or hyperparasitoid 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, 16L : 8D).

The mean number of aphids per leaf and the percentage of mummified aphids (to the total number of aphids) (Tomanović et al., 1996; Kavallieratos et al., 2002a, b, 2004) were calculated per sampling date.

For the sampling dates with high level of catches, the counts of insects collected within the sampling plot were visualized as scale-sized circles. In these diagrams, the counts of insects are represented according to the spatial location of sampling points in the field; the circle size being proportional to the magnitude of the individuals found. For the graphical realization, the package Golden Software (2002) was used.

Analysis of variance was made on transformed data $y_{trans} = \sqrt{y+0.5}$ in order to normalise variances and standardise means using the statistical package JMP (Sall et al., 2001). ANOVA was used to test the significance of differences in the total number of: (a) *M. persicae* individuals between the upper and lower half of the plants (per leaf) during the whole period of the study for each year; (b) species of aphidiines which emerged from *M. persicae* (per leaf) during the whole period of the study and from the upper and lower half separately during the whole period of the study for each year; (c) *A. colemani* individuals which emerged from *M. persicae* (per leaf) between the upper and lower half of the plants during the whole period of the study for each year; (d) hyperparasitoids which emerged from *M. persicae* (per leaf) between the upper and lower half of the plants during the whole period of the study for each year. Means were compared with the Tukey-Kramer (HSD) test (at $P = 0.05$).

RESULTS

The only aphid species found in the present study was *M. persicae*. Its population on the upper and lower half of the plant increased rapidly after 15 July in 1996 and after 4 August in 1997, reaching the peaks on 5 August in 1996 (2,001.3 ± 263.2 individuals per leaf) (1,046.5 ± 157.4 individuals per leaf) (Fig. 1A) and 14 August in

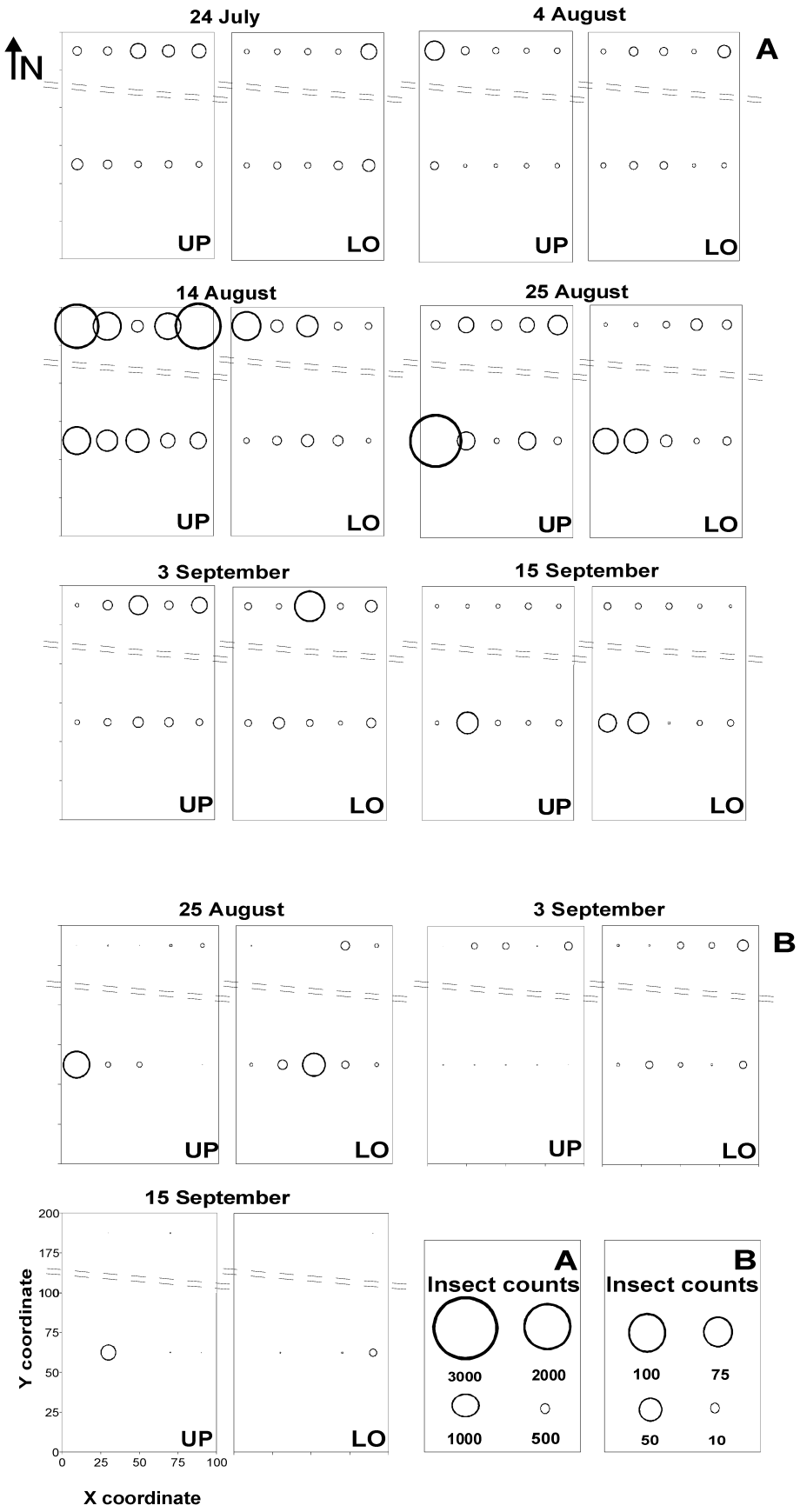

Fig. 4. Diagrams of *Myzus persicae* catches distribution within the sampling plot (10 points situated in two rows), during the 1997 growing season: A – living aphids; B – mummified aphids. UP and LO indicate upper and lower leaves, respectively. Coordinates *x*, *y* represent the distance in meters from the southeastern corner of the field.

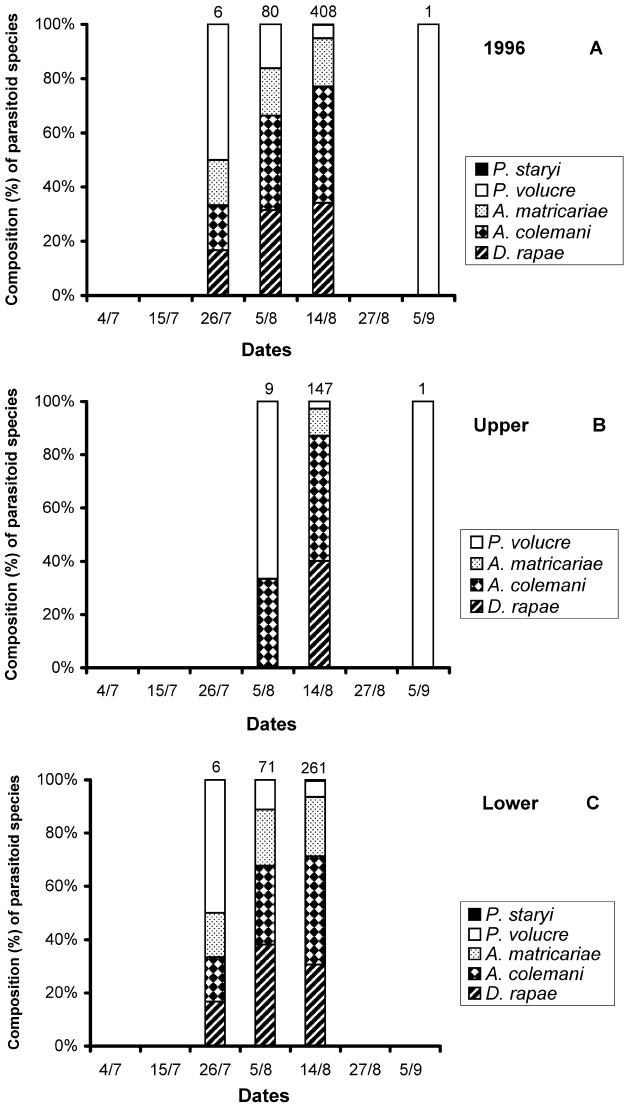

Fig. 5. Relative abundance of parasitoid species (%) on *Myzus persicae* found on tobacco in western Greece in 1996. Numbers of parasitoids (above columns) and composition. A – upper and lower half; B – upper half; C – lower half of the plant.

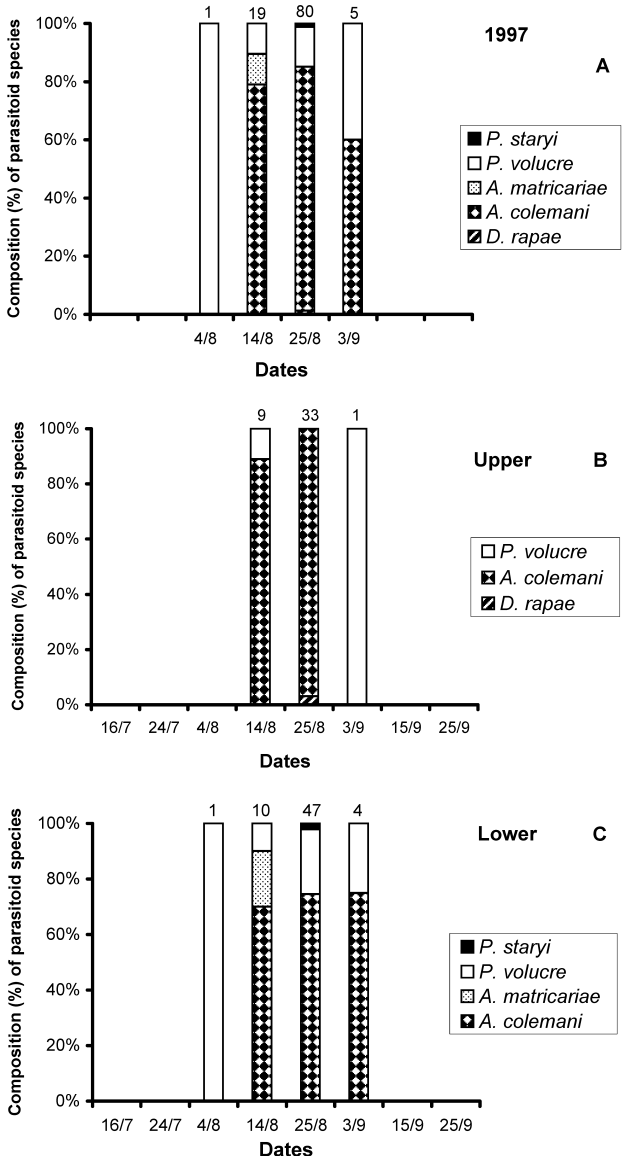

Fig. 6. Numbers of parasitoids (above columns) and composition of parasitoid species (%) on *Myzus persicae* found on tobacco in western Greece in 1997. A – upper and lower half; B – upper half; C – lower half of the plant.

1997 (Fig. 2A). High aphid densities were noted during the 1996 growing season from early July, but the population declined afterwards, and increased again from late July (Fig 3A). On the other hand, during the 1997 growing season, aphids maintained lower densities, except during August (Fig 4A). However, in both years examined, especially late in the season, density of aphids was higher in sampling locations adjacent or near the field margins.

Aphid population densities followed a similar pattern on the upper half [peak on 5 August, 2,436.1 ± 432.2 individuals per leaf in 1996 (Fig. 1B); peak on 14 August, 1,462.7 ± 213.3 individuals per leaf in 1997 (Fig. 2B)] and lower half of the plants [peak on 5 August, 1,566.5 ± 252.3 individuals per leaf in 1996 (Fig. 1C); peak on 14 August, 630.2 ± 143.6 in 1997) (Fig. 2C)]. The numbers of *M. persicae* individuals were higher on the leaves collected from the upper part of the plants compared to those collected from leaves in the lower part but without significant difference (F = 0.1; df = 1, 129; P = 0.748 in 1996; F = 1.50; df = 1, 149; P = 0.2231 in 1997).

Mummified aphids were found from the third sampling and their average number from the upper and the lower half peaked on 14 August (45.95 ± 7.26 mummies per leaf) and 25 August (8.00 ± 2.31 mummies per leaf) in 1996 and 1997, respectively. During 1996, more mummies were found in mid-August, on the lower half of the plants (Fig. 3B). In 1997, the presence of aphid mummies was low, during the entire sampling season; however, as above, most mummies were found late in the season (Fig. 4B). Mummified aphid population densities followed a similar pattern on the upper (peak on 14 August, 27.8 ± 6.56 mummies per leaf in 1996; peak on 25 August, 6.90

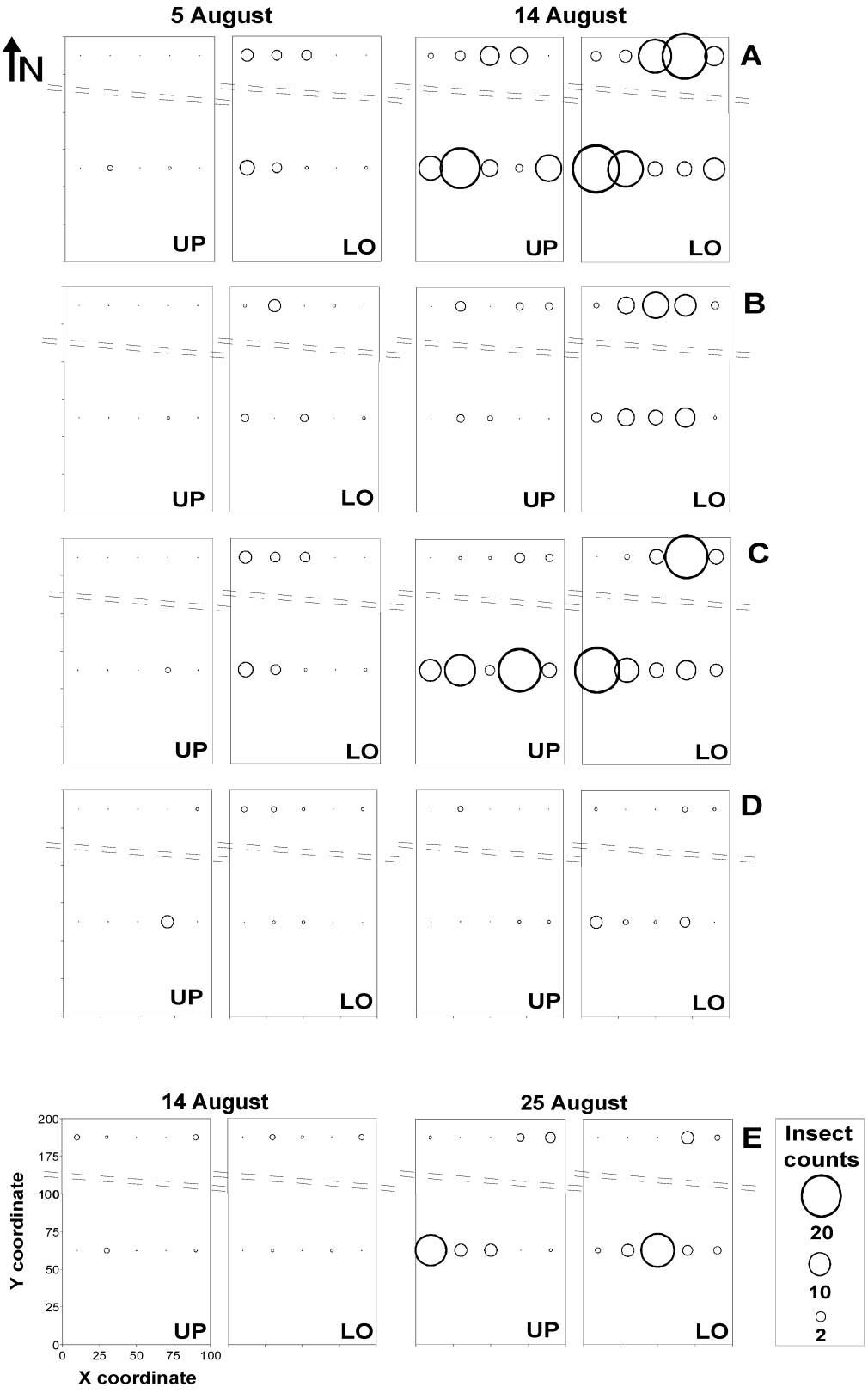

Fig. 7. Diagrams of parasitoids distribution within the sampling plot (10 points situated in two rows), collected at 5 and 14 August, during the 1996 growing season: A – *Aphidius colemani*; B – *Aphidius matricariae*; C – *Praon volucre*; D – *Diaeretiella rapae*, and 14 and 25 August during the 1997 growing season: E – *Aphidius colemani*. UP and LO indicate upper and lower leaves, respectively. Coordinates *x*, *y* represent the distance in meters from the southeastern corner of the field.

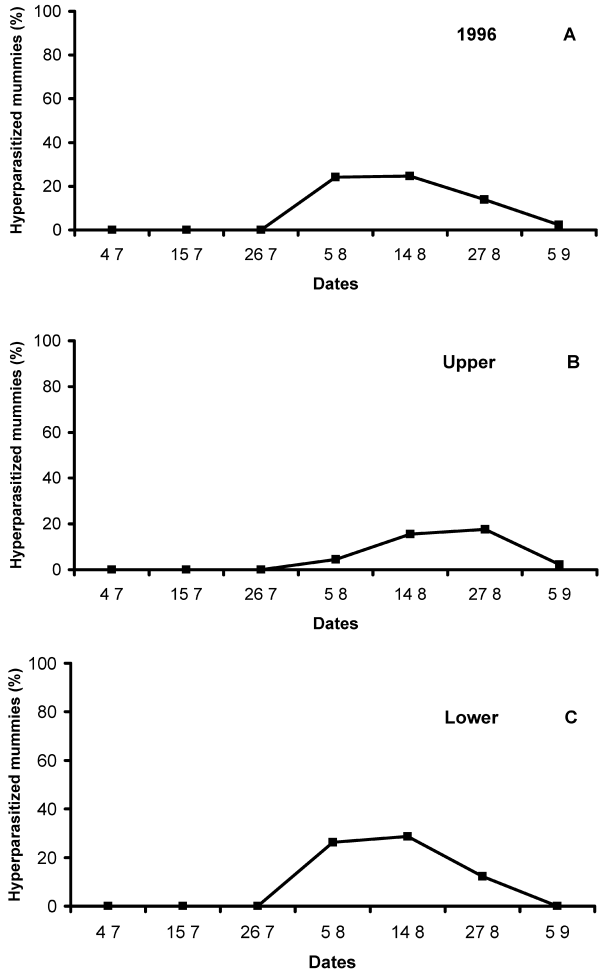

Fig. 8. Hyperparasitized *Myzus persicae* mummies (%) found on tobacco in western Greece in 1996. A – upper and lower half; B – upper half; C – lower half of the plant.

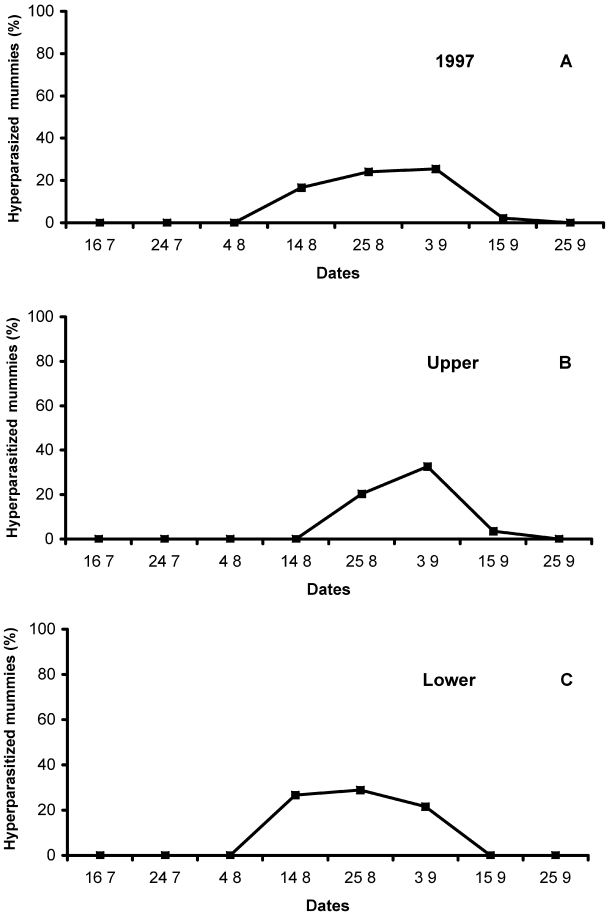

Fig. 9. Hyperparasitized *Myzus persicae* mummies (%) found on tobacco in western Greece in 1997. A – upper and lower half; B – upper half; C – lower half of the plant.

± 3.58 mummies per leaf in 1997) and on the lower half of the plants (peak on 14 August, 64.1 ± 10.3 mummies per leaf in 1996; peak on 25 August, 9.10 ± 3.07 mummies per leaf in 1997). Numbers of mummified *M. persicae* individuals were significantly higher on leaves collected from the lower part of the plants than on leaves collected from the upper part in both years ($F = 20.38$; $df = 1, 129$; $P < 0.0001$ in 1996; $F = 8.61$; $df = 1, 149$; $P < 0.0039$ in 1997). The mummification rate showed a specific increasing trend late in the season (August–September). In 1996, the percentage of mummification reached almost 61% at the end of the period (Fig. 1A) whereas in 1997 it remained at very low levels (<2%) (Fig. 2).

M. persicae was parasitized by *A. colemani*, *A. matricariae*, *D. rapae*, *P. staryi* and *P. volucre* (Figs 5A, 6A). Most of the parasitoids were found during mid-August (5 and 14 August), especially in the southern part of the field, where *A. colemani* was equally distributed between the lower and the upper plant part (Fig. 7A). For *A. matricariae*, the majority of the individuals were found during mid-August (Fig. 7B). For *D. rapae*, the majority of the individuals were found in the southern part of the field, where most individuals were located on the lower plant part (Fig. 7C). *P. volucre* was found mainly in the southern part of the field in low numbers (Fig. 7D). During the 1997 season, catches of parasitoids were low; *A. colemani* was by far the most abundant parasitoid species, with the highest level of catches on 25 August, found mainly in the southern part of the field (Fig. 7E).

ANOVA showed significant differences in numbers among the species of aphidiines that parasitized *M. persicae* on tobacco plants ($F = 5.59$; $df = 4, 345$; $P = 0.0002$ in 1996; $F = 10.48$; $df = 4, 390$; $P < 0.0001$ in 1997). In 1996 there were significantly more *A. colemani* ($\bar{x} = 1.32$) and *D. rapae* ($\bar{x} = 1.25$) than *P. staryi* ($\bar{x} = 0.71$). However, the mean number of *A. colemani* was not significantly different from that of *A. matricariae* ($\bar{x} = 1.08$), *D. rapae* ($\bar{x} = 1.25$) and *P. volucre* ($\bar{x} = 0.93$), although higher numbers were recorded ($\bar{x} = 1.32$). In 1997, there were significantly more *A. colemani* ($\bar{x} = 1.02$) than *A. matricariae* ($\bar{x} = 0.72$), *D. rapae* ($\bar{x} = 0.71$), *P. staryi* ($\bar{x} = 0.71$) and *P. volucre* ($\bar{x} = 0.79$).

M. persicae was parasitized by *A. colemani* (in 1996 and 1997), *A. matricariae* (in 1996 and 1997), *D. rapae* (in 1996 and 1997), *P. staryi* (in 1996) and *P. volucre* (in 1996 and 1997) on the upper half of the plants (Figs 5B, 6B). ANOVA showed significant differences among those species only in 1997 ($F = 2.71$; $df = 3, 276$; $P =$

0.0454 in 1996; F = 8.28; df = 2, 234; P = 0.0003 in 1997). There were significantly more *A. colemani* ($\bar{x}$ = 0.88) than *D. rapae* ($\bar{x}$ = 0.71) and *P. volucre* ($\bar{x}$ = 0.72) in 1997.

M. persicae was parasitized by *A. colemani* (in 1996 and 1997), *A. matricariae* (in 1996 and 1997), *D. rapae* (in 1996), *P. staryi* (in 1996 and 1997) and *P. volucre* (in 1996 and 1997) on the lower half of the plants (Figs 5C, 6C). ANOVA showed significant differences among those species (F = 6.17; df = 4, 245; P < 0.0001 in 1996; F = 7.98; df = 3, 236; P < 0.0001 in 1997). There were significantly more *A. colemani* ($\bar{x}$ = 1.37 in 1996, $\bar{x}$ = 0.97 in 1997) than *A. matricariae* ($\bar{x}$ = 0.97), *D. rapae* ($\bar{x}$ = 1.29 in 1997), *P. staryi* ($\bar{x}$ = 0.72 in 1996) and *P. volucre* ($\bar{x}$ = 0.94 in 1996, $\bar{x}$ = 0.72 in 1997). Furthermore, *A. colemani* numbers were significantly greater on the lower than on the upper half of the plants, but only in 1996 (F = 8.93; df = 1, 138; P < 0.0033 in 1996; F = 2.28; df = 1, 158; P = 0.1331 in 1997).

Hyperparasitization (Figs 8, 9), was significantly higher on the lower than on the upper half of tobacco plants in both years (F = 16.48; df = 1, 138; P < 0.0001 in 1996; F = 7.24; df = 1, 158; P = 0.0079 in 1997).

DISCUSSION

Seasonal abundance of aphids

The reduction in aphid populations observed during the two years of the study coincided with the dates of the topping and application of the sucker control agent (fatty alcohol). According to Hawks & Collins (1983), topping stimulates the production of carbohydrates in the leaves and coincides with the production of nicotine which acts as a biocide. Furthermore, according to Lampert (1989) fatty alcohols are very harmful to *M. persicae*. Due to those unfavorable conditions, alate adults of aphids were produced and migration followed. In 1996 the aphid population decreased rapidly after 7 August resulting in a crash in late August unrelated to parasitization (Fig. 1). In contrast, in 1997 a large number of aphids remained on the tobacco leaves (202.6 ± 61.6 individuals per leaf on 25 September) and the rate of mummification remained very low till the end of the season (Fig. 2). Hence, the results of the present study may suggest that parasitoids did not reduce aphid densities in either of the years tested, given that the aphid presence was high for most of the sampling period. This could be attributed to their delayed action since, in agreement with Starý (1988), the first mummies generally appeared after the increase of aphid population density to high levels. However, the rapid decrease of *M. persicae* population at the end of August in 1996 could be partially attributed to the parasitoids' action.

The significant higher percentage of mummies on the lower plant in both years could be attributed to the production of honeydew on the more populated upper plant which restricts parasitoids' oviposition through their immobilization (Starý, 1970). Furthermore, aphids in large colonies increase at such rate that the parasitoids can attack only a small part of them (Starý, 1970).

Species of parasitoids

Our data support that *A. colemani* and *D. rapae* are the principal parasitoid species of *M. persicae* on tobacco in western Greece. *D. rapae* appeared in lower, but not significantly, numbers than *A. colemani* in 1996. However, in 1997 its numbers were significantly lower than those of *A. colemani*. In contrast, in a recent study, Kavallieratos et al. (2004) found that *P. volucre* was the dominant parasitoid species of *M. persicae* on tobacco in 1996 and 1997 in a different tobacco growing area of Greece, whereas *D. rapae* was not recorded in that area. In both cases, the tobacco variety was the same (McNair 944) and the aphid population densities high. According to Starý (1970) interspecific relations are influenced by the geographical distribution of parasitoids which also affects their occurrence and seasonal history.

The low presence of *P. staryi* during both years could be attributed to its rare presence in nature (Kavallieratos et al., 2004). The rarity of this species is corroborated by the fact that until now it has not been found on hosts other than *M. persicae* (Kavallieratos et al., 2001, 2005).

Distribution within plants

Within plant distribution of *A. colemani* mummies on tobacco is different from the host behavior of *Aphidius nigripes* Ashmead, a parasitoid of *Macrosiphum euphorbiae* (Thomas) on *Solanum tuberosum* L., where mummies were found particularly in the apical stratum of the plant. Brodeur & McNeil (1991, 1992) offered three possible explanations: in the apical parts of the potato plants: (a) parasitoids mummifying far from the aphid colony would be in sites with less honeydew and thus could avoid the detection by some predators, such as coccinellids. Honeydew acts as a kairomone for several aphid predators (Ben Saad & Bishop, 1976); (b) the activity of the hyperparasitoids is small due to the solar radiation. Tiny insects (such as hyperparasitoids) are subject to hydrothermic stress when exposed to insolation for extended periods (Willmer & Unwin, 1981); (c) the solar radiation reduces the length of pupal development and thus shortens the period the mummies are exposed to natural enemies. According to Brodeur & McNeil (1991) the *A. nigripes* mummies were evenly distributed over the top, median and bottom leaves of *Chenopodium album* L. plants. In contrast, in the present study, the *A. colemani* mummies were mainly found on the lower half of the tobacco plants in both years. Similar observations to our results, concerning the within plant distribution of *M. persicae* mummies on tobacco, have been reported by Lykouressis & Mentzos (1995). Concerning the three above assumptions, in our case: (a) the quantity of honeydew is smaller on the leaves of the lower half than the upper half simply due to the fewer number of aphids there. However, according to our results mummies were found only inside the aphid colony and there was no evidence of movement by parasitized aphids. Many but not all aphid species leave the colony after parasitization (Müller at al., 1997); (b) hyperparasitoids' numbers were significantly higher on the lower half where they are not exposed

directly to the solar radiation. Thus, parasitoids suffered high levels of hyperparasitization on the lower part of the plants given that mummified aphids were significantly more abundant on this part than on the upper half in both years of the study; (c) solar radiation does not seem to benefit *A. colemani* mummies since these "prefer" the shaded places of the tobacco plants. Similarly, mummies of *Aphidius rosae* (Haliday) attacking *Macrosiphum rosae* (L.) on *Rosa* sp., are found on the upper side of the leaves in spring whereas in summer, when the temperature and insolation are high, the majority of mummies occur on the lower side of the leaves (Fink, 1995). Generally, the plant architecture may influence interactions over several trophic levels (Brodeur & McNeil, 1991). Another possible explanation for the differential mummification on higher and lower leaves is that parasitized aphids often drop from their feeding site and mummify on lower leaves (Chow & Mackauer, 1999).

Distribution within the field

From the spatial diagrams, it appears that, in many sampling occasions, high aphid and parasitoid densities were detected in or close to the peripheral parts of the field. Similar observations have been reported by Rabasse & Dedryver (1983), Stechmann (1988), Hradetzky & Kromp (1995) and Parker et al. (2003), who noted the presence of greater numbers of both aphids and their parasitoids and predators in the marginal parts of the field than in the inner part. However, further experimental work is needed to confirm the relationship between the complex of *M. persicae* and their parasitoids in tobacco.

One additional complication in assessing the spatial synchronization between aphids and parasitoids is the lack of spatio-temporal synchrony. In our study, although aggregated spatial patterns for both aphids and parasitoids may have been similar throughout the season, their spatial coincidence was dynamic, and this is the reason for the poor synchrony correlation. Apparently, parasitoids can reduce aphid populations on tobacco only when aphids and parasitoids are coincident spatially and temporally (Weisser, 2000; Giles et al., 2003). However, in our case, it is not clear if the decline of aphid densities at the end was mainly due to the parasitoid activity, since aphid migration is high at that season. In a recent work, Athanassiou et al. (2003) reported that the reduction of *M. persicae* densities on tobacco in central Greece was not due to the activity of biocontrol agents, but mainly to density-independent factors, such as the temperature decrease. On the other hand, the coexistence of parasitoids (as in the case of our study), acts chiefly as a stabilizing factor, that "protects" the system from collapsing (Lei & Hanski, 1997; Hanski, 1999). However, it is generally expected that competition reduces parasitization rate (Kavallieratos et al., 2002a). In a case of parasitoid coexistence, different aphidiine species seem to utilize host groups with different characteristics (size, location etc.), leading to spatial segregation and the development of local, independent populations. While this fact has been examined extensively for parasitoids of lepidopterous larvae (Lei & Hanski, 1997, 1998; Hanski, 1999) very few data are available in the case of Aphidiinae.

Further study of the coexistence of parasitoids would be focused on detailed search for the cause of their spatio-temporal trends. Practically, the study of the effect of parasitoids on the reduction of aphid numbers, and the factors that determine this effect, may help tobacco growers to incorporate natural enemy thresholds into aphid management, which will reduce the insecticidal applications.

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