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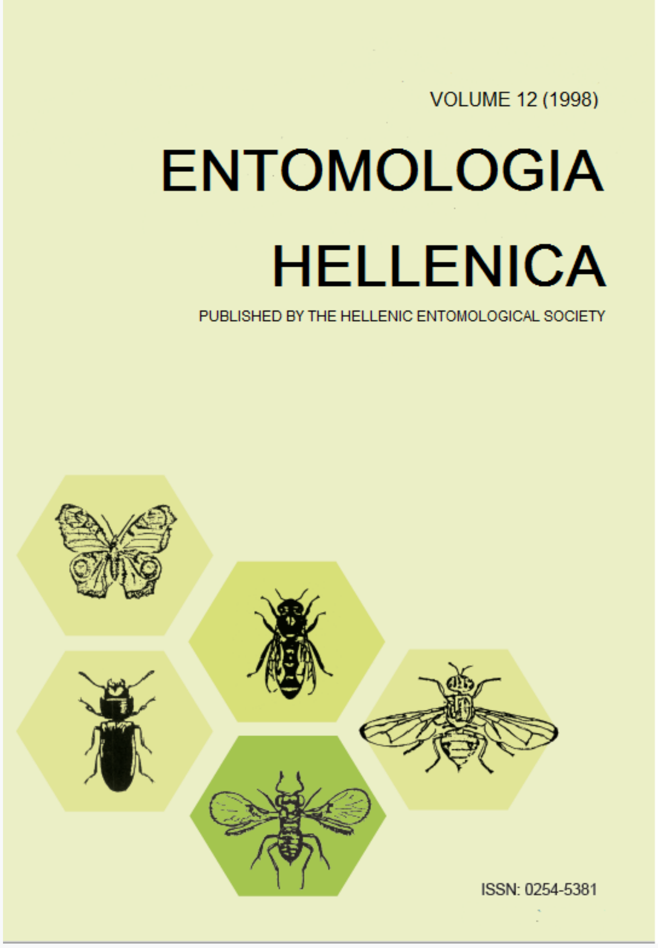

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The Spatial Pattern of *Aphis gossypii* on Cotton[1]

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ABSTRACT

The spatial distribution of *Aphis gossypii* (Glover) on cotton was studied by using Taylor's power law, the negative binomial parameter k and the i_δ-index of aggregation. Both k and i_δ were related to density with curvilinear relationships and indicated that aggregation decreases as density increases up to densities of, approximately, two individuals per leaf. At the very high densities (more than three individuals per leaf) the calculated values of the two indices recognized a tendency for an increased aggregation again. A strong linear relationship between the log mean and the log variance of the population density was obtained confirming the wide applicability of Taylor's power law. However, the established relationship (b=1.433) assumes, for the range of the observed densities, a continuous decrease in the degree of aggregation as density increases. It is suggested that the changes in the degree of aggregation throughout the season and in relation to density are related to natural mortality.

Introduction

Aphis gossypii (Glover) (Homoptera: Aphididae) has occasionally become a serious pest of cotton in Greece. The problem seems to have been created by non rational chemical treatments that have caused detrimental effects upon its natural enemies (mainly predators) and, certainly, it has been amplified by the development of resistance of *A. gossypii* to common aphicides.

Population studies of *A. gossypii* have been recently initiated in Greece (region of Magnesia) to provide the bases for the development of Integrated Pest Management on cotton. As a first step, it was considered useful to determine in the field, under no chemical treatment conditions, the pattern of its distribution in space and the possible changes in this pattern throughout the growing season and in relation to population density. This information was considered essential because the spatial pattern of a population is determined by the interaction between the species behaviour and the environmental factors. Therefore, the knowledge of the changes in the spatial pattern allows suggestions to be made about the action of the various environmental factors including natural enemies and moreover contributes in the interpretation of the dynamics of the populations. Furthermore, an efficient sampling programme for intensive population studies should be based, among others, on the spatial distribution of the species involved (Elliot 1977, Southwood 1978, Taylor 1984).

The spatial pattern has been studied for several species of aphids (e.g. Taylor 1970, Dean 1973,

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Pennacchio and Tremblay 1986, Asante et al. 1993), but not for *A. gossypii.* It is, usually, described by the negative binomial model for the greater part of the range of population densities (Robert et al. 1988).

This paper presents information on the spatial pattern of *A. gossypii* on a cotton plantation by means of three indices of dispersion (the exponent k of negative binomial distribution, Morisita's index of dispersion and the coefficient b of Taylor's power law) and discusses the possible relationship of the changes in the spatial pattern throughout the growing season and in relation to density with the action of natural mortality.

Materials and Methods

The study was carried out in a 0.2 ha cotton field in the area of Magnesia (Central Greece), which was kept free from insecticidal treatments, and lasted for two growing seasons, 1992 and 1993. The experimental field was rectangular with 40 rows, one meter apart, and ten plants per meter on the row. On the east and south of the field were cotton fields, on the west an abandoned wheat field and on the north a rural road across which there was a peach orchard. In 1992, samples were taken, usually at weekly intervars, from the beginning of August to the end of October while in 1993 sampling started at the beginning of the season, in May, and condinued as in 1992.

In 1992, 112 plants in total were sampled systematically (eight rows, one every fifth row with 14 plants per row, one plant every four meters). Each plant was divided in two sections, upper and lower, according to previous information about the distribution of aphids within the plant (Kapatos et al., 1996). From each section 5 leaves were taken randomly (112 x 5 x 2 = 1,120 leaves). The leaf was considered to be the natural sampling unit because it is the unit of habitat where an aphid colony develops. In 1993, other aspects of the population dynamics of *A. gossypii,* such as assessment of birth and death rates, were considered. The number of plants sampled was therefore reduced and ranged from 30 to 60 according to the aphid population density and the available personnel. In 1993, in the first six sampling dates (until 30 June), when the number of leaves per plant was low (usually less than 20), all leaves of the selected plants were examined. In both years, the samples were examined in the field *in situ* and population density was expressed as number of individuals (of all stages) per leaf.

The data for each sampling date were classified into frequence distributions and were fitted to two mathematical distributions (i.e. the Poisson distribution representing a random pattern and the negative binomial representing a contagious pattern) by using the chi-square test for goodness of fit. The values of the exponent k of the negative binomial were calculated with the maximum likelihood equation by iteration after obtaining a preliminary estimate of k with the approximate method ($\bar{x}^2/s^2 - \bar{x}$) (Elliot 1977).

To describe the changes in the spatial pattern of population of *A. gossypii* during the season, two indices of dispersion were calculated for each sampling date, i.e. the exponent k of the negative binomial, and the I_δ Morisita's index of aggregation (Morisita 1962, Elliot 1977). The smaller the value of k the greater the degree of aggregation while the reverse holds for I_δ. The number of sampling units in each sample influences the calculation of both (Elliot 1977, Southwood 1978) but it was assumed that the variable sample size used in 1993, different from that used in 1992, would not affect the results because in all cases it consisted of several hundreds sampling units.

The relationship betweem the mean and the variance of the population density was investigated by applying the Taylor's power law (Taylor 1961). The variances were plotted against the corresponding means on a log/log scale and the parameters a and b in the expression of the power law ($s^2 = a\bar{x}^b$) were estimated.

Results

Tables 1 and 2 give the mean and the variance of the population density (number of individuals per leaf), the two calculated indices of dispersion (k and I_δ) and the statistical significance of the χ^2-test for agreement with the negative binomial distribution (NBD) for 1992 and 1993 respectively (agreement with the Poisson distribution was not observed in any case).

In 1992, population densities were generally very low ranging from 0.023 (7 August) to 0.753 (22 October). The calculated values of k were also very low ranging from 0.011 (for a population density of 0.023) to 0.362 (for a density of 0.753) while the calculated values of I_δ ranged from 68.923 (for a mean density of 0.023) to 5.819 (for a mean density of 0.753).

In 1993, the mean densities of the population were, on certain sampling dates, much higher than in 1992. Excluding the three sampling dates with zero counts (22 June, 30 June, 20 September) they ranged from 0.013 (1 October) to 3.527 (19 August). The mean population density was high at the beginning of the season (late May-beginning June) but it soon dropped to very low levels. From late July it started increasing again and reached high levels in the middle of August. Immediately after, the population declined again and was maintained at low levels up to the end of the season. The calculated values of k ranged from 0.005 (for a density of 0.013) to 0.388 (for a density of

TABLE 1. The mean and the variance of the population density, the calculated values of two indices of dispersion (k and I_δ) and the statistical significance of the χ^2-test, for agreement with the negative binomial distribition for each sampling date in 1992.

Date	Sample size	Mean	Variance	k	I_δ	Statistical significance
7/8/92	1120	0.023	0.058	0.011	68.923	n.s.
14/8/92	1120	0.158	0.542	0.070	11.905	n.s.
21/8/92	1120	0.381	1.455	0.155	8.398	n.s.
28/8/92	1120	0.605	2.993	0.158	7.520	n.s.
3/9/92	1120	0.442	3.301	0.088	15.655	n.s.
10/9/92	1120	0.186	0.696	0.064	15.868	*
17/9/92	1120	0.126	0.679	0.032	36.085	**
23/9/92	1120	0.171	1.239	0.041	37.899	**
1/10/92	1120	0.170	1.374	0.046	43.041	*
8/10/92	1120	0.676	3.041	0.186	6.180	n.s.
15/10/92	1120	0.680	3.347	0.246	6.764	n.s.
22/10/92	1120	0.753	3.482	0.362	5.819	n.s.
29/10/92	1120	0.405	2.120	0.117	11.447	n.s.

n.s. = not significant
* = significant at the 0.05 level
** = significant at the 0.01 level

TABLE 2. The mean and the variance of the population density, the calculated values of two indices of dispersion (k and I_δ) and the statistical significance of the χ^2-test, for agreement with the negative binomial distribition for each sampling date in 1993.

Date	Sample size	Mean	Variance	k	I_δ	Statistical significance
24/5/93	225	3.427	138.487	0.136	12.466	**
1/6/93	215	3.163	167.305	0.133	17.360	n.s.
8/6/93	464	0.280	1.291	0.074	13.950	n.s.
15/6/93	666	0.030	0.056	0.032	31.540	n.s.
22/6/93	400	0.000	—	—	—	—
30/6/93	480	0.000	—	—	—	—
6/7/93	480	0.044	0.100	0.040	32.000	n.s.
13/7/93	560	0.054	0.126	0.042	27.030	n.s.
20/7/93	580	0.107	0.310	0.084	19.020	n.s.
30/7/93	400	0.540	2.911	0.166	9.147	*
6/8/93	360	1.900	15.695	0.388	4.816	**
16/8/93	360	2.094	14.621	0.382	3.850	**
19/8/93	330	3.527	84.961	0.253	7.530	n.s.
30/8/93	400	0.585	2.940	0.175	7.890	n.s.
7/9/93	400	0.450	2.003	0.127	8.690	n.s.
13/9/93	360	0.167	0.479	0.080	12.410	n.s.
20/9/93	400	0.000	—	—	—	—
27/9/93	400	0.050	0.133	0.033	35.790	n.s.
1/10/93	300	0.013	0.027	0.005	100.000	n.s.
8/10/93	400	0.125	0.516	0.029	26.450	n.s.
18/10/93	320	0.025	0.043	0.018	32.490	*

n.s. = not significant
* = significant at the 0.05 level
** = significant at the 0.01 level

1.900) and the values of I_δ ranged from 100.00 (for a density of 0.013) to 3.85 (for a density of 2.094).

The results of tables 1 and 2 indicated also that in most cases (22 out of 31) the frequency distribution of counts of *A. gossypii* fit the negative binomial distribution. In 4 other cases the statistical significance was only at the 0.05 level ($0.05 > P > 0.01$). However, in the 5 sampling dates of 1993 (24 May, 1 June, 6 August, 16 August and 19 August) where the mean density was relatively high, agreement with the negative binomial was observed only in two cases (1 June, 19 August).

Figure 1 shows the relationship of k with the mean density of the population. The value of k increased as population density increased up to a mean density of approximately one individual per leaf. At higher mean densities (i.e. more than two individuals per leaf) the value of k decreased considerably. The relationship between mean aphid density and k was curvilinear with a high coefficient of determination (r^2=0.838). Figure 2 shows the relationship of I_δ, an index of aggregation of entirely different origin from that of k of NBD, with the mean population density. I_δ decreased as mean density increased but at the highest values of the observed ranges of population densities it showed a tendency to increase.

To better understand and explain the changes in the values of k and I_δ in relation to density, the proportion (%) of infested leaves in each sampling date was plotted against the corresponding mean density and their relationship is shown in Figure 3. The proportion of the infested leaves increased as mean density increased but at the high densities (2-3.5 individuals per leaf) the proportion of the infested leaves remained rather constant at an infestation level of about 40-50%.

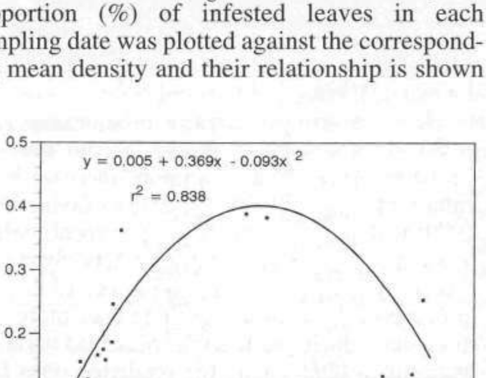

FIG. 1. The relationship of the negative binomial parameter k with the mean population density (number of individuals per leaf).

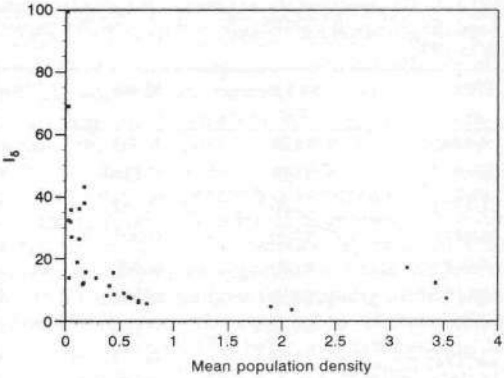

FIG. 2. The relationship between the I_δ-index of aggregation with the mean population density

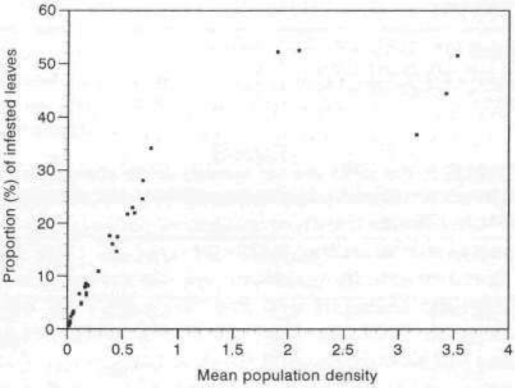

FIG. 3. The proportion (%) of infested leaves in relation to mean population density.

Figure 4 shows the relationship of the mean and the variance of the population density (on a log/log scale) in applying Taylor's power law. A very high coefficient of determination was obtained ($r^2 = 0.958$) and the value of b, which is also used as an index of dispersion, was calculated to be 1.433. Despite the high coefficient of determination, however, great differences were observed between the observed and the predicted variances (not easily seen in logarithm scale) for the densities higher than 1 individual per leaf.

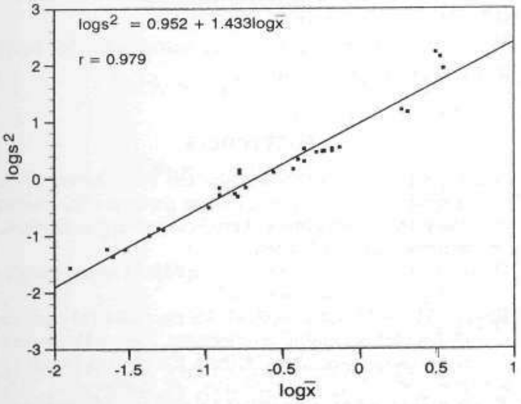

FIG. 4. The relationship between the mean and the variance of the population density.

Discussion

The results obtained in the present study indicated that the distribution of counts of *A. gossypii* on cotton follows, in most of the cases, the negative binomial distribution with fractional values of k varying according to the mean population density. This justidies the use of k to describe the changes in the spatial pattern of *A. gossypii.* The relationship between the k values and the mean density was curvilinear with a very high coefficient of determination. However, the part of the curve up to a density of one individual per leaf, which comprised most of the sampling occasions, appeared to be linear and only five sampling occasions with higher population densities determined curvilinearity. The final shape of the curve was determined by three sampling occasions with mean densities higher than 3 individuals per leaf, in one of which agreement with NBD was not observed. Therefore, reservations may be expressed for the precise shape of the curve but, nevertheless, this relationship indicated a decrease in the degree of aggregation as population density increases from the very low densities up to densities of approximately two individuals per leaf. At higher densities the degree of aggregation increased considerably. Thus, the intensity of aggregation was smaller in the intermediate densities than in the lower and higher ones. Because of the strong interrelationship between k and mean density, the calculation of a "common" k (k_c) cannot be justified, as in many other cases (Taylor 1984).

The usefulness of k (or 1/k) as an index of aggregation has been strongly questioned (Taylor et al. 1979), mainly for the following reasons: a) a common value for all densities cannot be obtained or it is not related to mean density by a simple function and b) its use is limited to the cases where the negative binomial is a suitable model. However, the changes in the calculated values of I_δ, an index of aggregation of entirely different origin from k, rather confirmed the changes in the degree of aggregation as they are assumed by k. Additional evidence for the above suggestions is obtained from the relationship between the proportion of the infested leaves and mean density. The results indicated that the increase in the mean density up to two individuals per leaf was mainly due to the increase in the proportion of the infested leaves and this, apprarently, leads to a decrease in the degree of aggregation. At the higher densities, on the contrary, it was the development of the population on the already infested leaves (the proportion of the infested leaves remained constant) that is reflected in the increase of the mean density and consequently the degree of aggregation increased.

The close relationship between the mean and the variance of the population density observed in this study confirms the general applicability of Taylor's power law. The established relationship indicated a rather "moderate" degree of aggregation in the distribution of the population of *A. gossypii.* Respective values of b for some other aphid species vary from values similar to the one calculated for *A. gossypii* (e.g. *Therioaphis trifolii* (Monell) 1.40, *Acyrthosiphon pisum* (Harris) 1.38) to higher ones such as for *Aphis fabae* (Scopoli) (1.72) and *Eriosoma lanigerum* (Hausmann) (1.87) (Taylor 1970, Pennacchio and Tremblay 1986, Asante et al. 1993).

The established Taylor's relationship ($b = 1.433$, $1 < b < 2$) assumes, for the range of densities observed, a continuous increase in the values of k as density increases (Taylor et al. 1979) which is not entirely in agreement with the relationship of these two parameters oberved in this study. At the three sampling occasions with high mean population densities (i.e. more than three individuals per leaf) the observed variances were much higher than the predicted ones from Taylor's relationship and were reflected in the corresponding values of k and I_δ, indicating an increase in the degree of aggregation. These high variances could have been due to sampling errors (and consequently the corresponding values of k). However, it is more probable that they express a change in the environmental pressure upon the population of *A. gossypii* which affected both the population size and the spatial pattern, as it is for instance a change in the action of density dependent mortality factors. Southwood (1978) suggested that the scatter of points around the regression line of Taylor's relationship is a measure of the effect of habitat variation on the extent of aggregation. Conclusively, it is suggested that Taylor's power law, as well as k of NBD and I_δ, described satisfactorily the changes in the spatial pattern of *A. gossypii* at the low and medium population densities. At the high densities observed, however, k and I_δ, recognised a change in the spatial pattern (an increase in the degree of aggregation) which in Taylor's relationship appeared as deviations from the predicted variances.

The biological interpretation of the spatial pattern of a species in field conditions is always difficult because the factors, both behavioural and environmental, that determine it are not measured but only the condition of the population is described. The differences in density up to a certain level (two individuals per leaf) are mainly due to different proportions of colonized leaves by winged aphids from other fields but, probably, high mortality rates kept the size of aphid colonies in the infested leaves at generally low levels. This explains the reduction in the degree of aggregation at increasing densities. At some periods (e.g. at the beginning of the season and in the middle of August), however, the conditions for the development of the population were favourable (e.g. low mortality rate). This allowed the build up of aphid colonies in the aldready infested leaves, and because "diffusion" of the infestation does not occur unless the size of the colonies becomes very large, both the population size and the degree of aggregation increased. The above suggestions are supported by the preliminary results of an ongoing study on the demography of *A. gossypii,* at the same experimental site, which have indicated clearly that mortality rates at the periods with high densities (at the beginning of the season and in August) were much lower than at other periods of the years (Kapatos et al., unpublished data).

The results obtained in this study provided a first indication that under conditions with no insecticidal treatments environmental pressure upon the population of *A. gossypii* is very strong for most of the season not allowing the build up of the aphid colonies. They were also used together with other data (optimum size of the sampling unit, number of samples, type of sampling, etc.) to develop an efficient sampling program for the population of *A. gossypii* (Kapatos et al., 1996).

Acknowledgment

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KEY WORDS. *Aphis gossypii,* Spatial distribution, Cotton.

Χωροταξική κατανομή του *Aphis gossypii* στο βαμβάκι

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ΠΕΡΙΛΗΨΗ

Η χωροταξική κατανομή του πληθυσμού του *Aphis gossypii* (Glover), στο βαμβάκι, μελετήθηκε χρησιμοποιώντας το νόμο του Taylor, την παράμετρο k της αρνητικής διωνυμικής κατανομής και τον δείκτη διασποράς του Morisita (I_δ). Παρατηρήθηκε μια ισχυρή γραμμική συσχέτιση ανάμεσα στη μέση πυκνότητα και τη διακύμανση του πληθυσμού (σε λογαριθμική κλίμακα) επιβεβαιώνοντας την ευρεία εφαρμογή του νόμου του Taylor. Η παρατηρηθείσα σχέση ($b = 1.433$) υποθέτει για το εύρος των πληθυσμιακών πυκνοτήτων που παρατηρήθηκε, μια συνεχή μείωση του βαθμού ομαδοποίησης όσο αυξάνει η πυκνότητα του πληθυσμού. Και οι δύο δείκτες διασποράς (k και I_δ) σχετίστηκαν με την πυκνότητα του πληθυσμού με καμπυλόγραμμες συναρτήσεις που έδειξαν ότι ο βαθμός ομαδοποίησης μειώνεται όσο αυξάνει ο πληθυσμός. Όμως οι δείκτες αυτοί στις υψηλές πυκνότητες πληθυσμού (περισσότερα από 3 άτομα ανά φύλλο) κατέγραψαν μια τάση αύξησης του βαθμού ομαδοποίησης. Γίνεται η υπόθεση ότι οι μεταβολές του βαθμού της ομαδοποίησης στη διάρκεια της καλλιεργητικής περιόδου και σε σχέση με τις μεταβολές της πυκνότητας του πληθυσμού σχετίζονται με τις μεταβολές της φυσικής θνησιμότητας.