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Factors which determine the composition of field communities of adult aphidophagous Coccinellidae (Coleoptera)

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Abstract

In 1979–1981, factors influencing population density of adult *Coccinella septempunctata*, *C. quinquepunctata*, and *Propylaea quatuordecimpunctata* were investigated in central Bohemia. Coccinellids were sampled by sweeping in stands of alfalfa and clover, or by hand sampling from 6–15 m^2 area in cereals. We calculated partial linear regressions and correlations of coccinellid density (CD) upon (1) 9–11 parameters characterizing aphid population density, plant density, position of sample within a field, and the type of landscape and (2) upon principal components processed from these primary variables.

Statistically significant relations to primary parameters of aphid and plant density explained 9.9–32.6 % of variance in CD. Correlations with principal components which may be interpreted as aphid or plant density explained 10.2–59.9 % of variance in CD. Effects of sample position within a field, and of the type of landscape were demonstrated only as significant relations to principal components that explained 8.5–46.5 % of variance in CD. The importance of all determinants of CD differed according to coccinellid species and varied also with year and crop. This was caused mainly by different degree of between-stand differentiation of crop and aphid density, and low coccinellid abundance in some years. Plant density had an important effect in genus *Coccinella*, especially at the time of settling of adult populations. *C. quinquepunctata* particularly preferred sparse stands. Aphid density was important in *C. septempunctata* and P. *quatuordecimpunctata*. The type of landscape caused area specific differences in population density of both these species in late May, but these differences were smoothed later on. The vicinity of forest caused only a transitory imbalance in composition of field coccinellid communities.

1 Introduction

The stands of field crops contain specific coccinellid communities. In Bohemia these communities consist mainly of *Coccinella septempunctata* L. and *Propylaea quatuordecimpunctata* (L); *C. quinquepunctata* L. and other species represent only a small fraction of total coccinellid population (HONĚK and REJMÁNEK 1982). These communities differ from coccinellid communities of trees and weeds which are richer and dominated by other species. The composition of coccinellid communities is largely determined by environmental and demographic factors (IPERTI 1965). Microclimatic conditions influenced through plant density (HONĚK 1979), prey density (GALECKA 1962; NEUENSCHWANDER et al. 1975; RADCLIFFE et al. 1976), annual changes in abundance of coccinellid species (HONĚK 1981), differences in rate and timing of migration (BANKS 1955; HODEK 1960; GALECKA 1962; BOURNOVILLE 1978), and geographic position of the locality may influence the composition of coccinellid communities.

The first two factors appeared most important in communities of field

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crops. We attempted at (1) quantitative evaluation of the effect of aphid density, crop density, position of sampling site within a field, and type of landscape on abundance of three above mentioned coccinellid species and (2) the evaluation of effect of nearby forests and coccinellid migration on composition of their communities.

2 Material and methods

In 1979–1981 the population density of adult *C. septempunctata* and *P. quatuordecimpunctata* was determined in stands of alfalfa and clover (forage leguminosae, FL), and of these species and *C. quinquepunctata* in cereals (wheat, barley, rye). The samples of coccinellid communities were collected in central Bohemia and, on FL in 1981, also in south Slovakia. The investigated localities represented three types of landscape: 1. Flat, largely deforested lowland with intensive agriculture, in 110–250 m altitude above the sea level (Elbe basin, the lowland of south Slovakia 50–100 km east of Bratislava); 2. The hilly landscape with a mosaic of forests and arable fields, in 250–400 m altitude (surroundings of Praha-Ruzyně, Krupá, 50 km W, and Dubá, 50 km N of Praha; 3. Submontane regions with larger forest complexes, meadows and smaller proportion of arable fields than at above localities, in 500–700 m altitude (Miličín, 70 km S, and Žlutice, 90 km W of Praha).

The coccinellid density (CD) in FL was determined by sweeping. At each collecting site (a square of about 50 × 50 m) we made 4 or 5 × 50 sweeps. In cereals CD was determined by hand sampling from an area of 6–15 m^2. In different years 46–52 samples were taken in FL and 30–44 in cereals. The samples were collected in a short period (of about 1 week) first in lowlands and later in highlands to minimize the biases caused by temporal changes in development of vegetation and insect communities. The samples of FL were collected in last decade of May, these of cereals in last decade of June.

The environmental determinants of CD were measured as 9–11 parameters of natural environment further called (primary) variables. They are enumerated in tables 1 and 2. The density of aphid populations was determined in FL by sweeping (VORONINA 1972), in cereals by counting the aphids at 3 × 50 tillers directly at the site of coccinellid sampling. The species composition of aphid population in cereals was expressed as the percentage of *Metopolophium dirhodum* in total aphid population. The density of plants was estimated in FL from dry weight of above ground parts from 5 randomly placed areas of 0.03 m^2. In cereals it was expressed as leaf area index (LAI, leaf area per unit area of field surface). The height of plant stands and, in FL, the crop species were also introduced as variables. The position of sampling site within a field was characterized by a distance (square root) from field margin. The type of landscape was characterized by variables which had to express its orological and ecological diversity: altitude, distance from nearest forest (square root), number of 10 m isohypses crossed by 6 km long N–S and E–W transects with centres at the site of collection, the number of forest edges crossed by the same transects, and proportion of these transects under forests. Geographic data were read from 1 : 50,000 maps.

The sets of data for every crop end year were subjected to multiple regression and correlation analysis. The primary environmental parameters served as independent, population density of coccinellid species as dependent variables. We could apply only least square linear regressions. However, in some cases the amount of variance explained would be greater if non-linear relationships were assumed (see 3.4). To specify the patterns of co-variation of independent variables principal components (PC) were processed from original primary variables. The WHRSM procedure of IBM Corporation was used. The PC with eigenvalue > 1 were interpreted as biological determinants of coccinellid density. Multiple regressions and correlations of coccinellid populatin density on these PC (their factorial scores) as independent variables were also calculated (HARMAN 1967).

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3 Results

The effects of aphid density, plant density, position of sample within a field, and type of landscape were different according to coccinellid species, crop and year of investigation. We will first discuss the importance of these determinants of CD in general, then in particular species.

3.1 General evaluation of importance of environmental factors which determined the coccinellid density

Aphid density was generally the most important determinant of CD in FL, where partial correlations were statistically significant in 5 of 6 cases investigated (table 1). In 2 of 6 cases it had significant effect also in cereals (table 2). No effect of species composition of aphid communities could be demonstrated.

Plant density was an important factor influencing CD in cereals. In 4 of 6 cases significant linear correlations with LAI were found, and in at least still one case the correlation was significant but not linear (see 3.4). By contrast, in FL plant density had virtually no effect on CD. However, the stands of alfalfa and clover had, in some cases, significantly different CD even when their density (gravimetrically determined) was similar. The height of plant stand per se had no influence on CD either in FL, or in cereals.

Primary variables which characterized the position of sample within a field and the type of landscape (variables 5–10 and 6–11 in tables 1 and 2 resp.) revealed significant correlations with CD in 13 of 72 cases. After logical evaluation we supposed that these correlations to particular variables had little biological meaning.

Partial linear correlations with particular primary variables explained up to 40.3 % of variance in CD. The multiple correlation coefficients explained 41.4–71.0 % of variance in FL, and 31.9–68.4 % of variance in cereals. They were, with two exceptions, statistically significant.

PC analysis specified, in all sets of data from particular year × crop combinations, 3 or 4 PC which were interpreted as five types of determinants of CD (table 3): type of landscape (This PC absorbed, after varimax rotation, 14.8–50.0 % of variance of primary variables), aphid density (17.0–25.6 %), plant density (15.1–16.2 %), crop species in FL (16.2 %), and distance from field margin (10.0–14.0 %). In particular cases all interpretable PC absorbed 71.0–78.9 % of variance of primary variables. PC "type of landscape" was composed by deliberately selected original variables and thus absorbed greatest proportion of their variance and appeared in all sets of data. Other PC represented annually changing variables and therefore appeared irregularly.

The type of landscape, evaluated synthetically as PC, revealed apparent effect on CD. Statistically significant correlations to factorial scores of this PC explained 8.5–46.5 % of variance in CD. This area-specific effect was more apparent in populations of FL collected in late May, than in populations of cereals collected in late June. This effect was perhaps caused by retardation of phenological development in submontane regions which was more apparent in the earlier part of season but largely smoothed later on. PC "aphid density" was highly important in FL, where it explained 59.1–59.9 % of variance of CD in 1979. In cereals it explained only 21.3–26.4 % of variance of CD in 1980. In 1979 this PC had no significant effect. PC "crop density" revealed no significant effect in FL, but in cereals explained 10.2–35.6 % of variance of CD, in 1980. PC "crop species" (alfalfa or clover) appeared important only in 1980 (18.5 % variance of CD explained). PC "distance from field margin" appeared in 3 cases. Significant correlations explained 12.7–32.0 % of variance of CD in FL, but no apparent effect in cereals was observed.

Table 1. Forage leguminosae: partial correlation (r), regression (k), multiple correlation (R) coefficients and total percentage of variance explained (R^2) by linear regressions of CD on 10 environmental variables

		Environmental variables^c											
		1	2	3	4	5	6	7	8	9	10	R	R^2
C. septempunctata													
1979 (n = 52)	r	.635^b	.229	–.334^a	–	–.318^a	.048	.180	–.312^a	.083	.025	.8322^b	69.26
	k	7.7777^b	.0669	–3.5065^b	–	–.3421^a	.0207	.0116	–.1734^a	.2834	.0514		
1980 (n = 49)	r	.432^b	–.047	–.199	.117	–.057	–.042	.089	–.050	–.125	.153	.6677^b	44.58
	k	2.3414^b	–.0119	–1.6051	.0634	–.0486	–.0110	.0058	–.0265	–.2423	.3225		
1981 (n = 46)	r	.439^b	.105	.101	–	–.161	.048	.258	–.323^a	.218	.266	.8131^b	66.11
	k	2.5538^b	.0099	.5926	–	–.0994	.0060	.0088^a	–.1341^b	2988^a	.1649^a		
P. quatuordecimpunctata													
1979 (n = 52)	r	.599^b	–.015	–.328^a	–	–.314^a	–.211	.028	–.272^a	.038	–.037	.8425^b	70.97
	k	5.0636^b	–.0030	–2.4628^b	–	–.2411^a	–.0665	.0013	–.1064	.0920	–.0557		
1980 (n = 49)	r	.147	.037	–.243	–.077	–.323^a	–.191	–.305^a	–.059	.287^a	.191	.6437^b	41.43
	k	.1946	.0025	–.5331^a	–.0111	–.0779^a	–.0136	–.0055^b	–.0085	.1546^a	.1087		
1981 (n = 46)	r	.342^a	.213	–.036	–	–.235	–.082	.302^a	–.387^b	.341^a	.138	.8005^b	64.08
	k	2.3911^b	.0258	–.2648	–	–.1855	–.0130	.0131^b	–.2077^b	.6087^b	.1043		

[a] $p < 0.05$. – [b] $p < 0.01$. – [c] 1 = no. of aphids *(Acyrthosiphon pisum)* per 100 sweeps, 2 = crop density, 3 = crop species, alfalfa or clover, 4 = plant height, 5 = distance from field margin, 6 = distance from nearest forest, 7 = altitude above the sea level, 8 ≐ no. of isohypses per two 6 km, N–S and E–W transects, 9 = no. of forest edges per the same transects, 10 = proportion of forest under the same transects (for further explanation see text, section 2).

Table 2. Cereals: partial correlation (r), regression (k), multiple correlation (R) coefficients and total percentage of variance explained (R^2) by regressions of CD on 11 environmental variables

		Environmental variable^{c}												
		1	2	3	4	5	6	7	8	9	10	11	R	R^2
C. septempunctata														
1979 (n = 30)	r	.181	–.160	.137	–.374^{a}	–.001	.231	–.169	–.338	.297	–.351	.128	.6229	38.30
	k	.2661^{a}	–.3070	.0700	–.2674^{a}	–.0001	.0278	–.0040	–.0009	.0077	–.0493	.0306		
1980 (n = 44)	r	–.247	.571^{b}	–.117	–.331^{a}	–.130	–.034	–.003	–.257	.157	.154	–.178	.8328^{b}	69.36
	k	–.0805	.7923^{b}	–.0005	–.0886^{a}	–.0021	–.0025	–.0001	–.0006^{b}	.0024	.0110	–.0261		
P. quatuordecimpunctata														
1979 (n = 30)	r	.278	–.334^{a}	.139	–.135	.232	.005	.096	–.107	–.022	.181	–.156	5.650	31.92
	k	.2007^{b}	–.3214^{a}	.0343	–.0435	.0050^{b}	.0003	.0011	–.0001	–.0003	.0116	–.0180		
1980 (n = 44)	r	–.116	.293^{a}	–.018	.356^{a}	–.209	.047	–.255	–.286	.185	–.315^{a}	–.069	.6607^{a}	43.65
	k	–.0204	.1941	–.0001	.0536^{a}	–.0019	.0019	–.0037^{a}	–.0003^{b}	.0016	–.0131^{a}	–.0055		
C. quinquepunctata														
1979 (n = 30)	r	–.025	.163	.106	–.426^{a}	–.114	–.210	.108	–.249	.168	–.314	.425^{a}	.7163	51.31
	k	–.0147	.1265	.0220	–.1265^{b}	–.0020	–.0102	.0010	–.0003	.0017	–.0177	.0453^{a}		
1980 (n = 44)	r	–.017	–.108	–.225	–.116	–.210	–.090	.159	.198	.162	.137	–.122	.6822^{b}	46.54
	k	–.0032	–.0754	–.0006	–.0180	–.0021	–.0041	.0025	.0003^{a}	.0015	.0060	–.0108		

[a] $p < 0.05$. – [b] $p < 0.01$. – [c] 1 = no. of aphids (mostly *Sitobion avenae* and *Metopolophium dirhodum*) per m^2 of field surface (ln), 2 = % of tillers occupied by aphids, 3 = % of *M. dirhodum* in total aphid population, 4 = leaf area index, LAI, 5 = plant height, 6 = distance from field margin, 7 = distance from nearest forest, 8 = altitude above the sea level, 9 = no. of isophypses per two 6 km, N–S and E–W transects, 10 = no. of forest edges per the same transects, 11 = proportion of forests under the same transects (for further explanation see text, section 2)

3.2 Factors influencing population density of *C. septempunctata*

Aphid density had an important effect on population density of *C. septempunctata* in FL and, in 1980, also in cereals. Significant correlations with primary variables characterizing aphid abundance explained 18.7–40.3 % of variance of *C. septempunctata* density (tables 1 and 2). Significant correlations with PC "aphid density" explained 26.4 % (cereals, 1980) and 59.1 % (FL, 1979) of variance. The importance of aphid density as a factor determining CD decreased if its between-site differences were small (e.g. in cereals, 1979). By contrast, the effect of aphid density could be particularly well demonstrated in FL, 1977, when large populations of overwintered *C. septempunctata* adults from 1976 were available, and aphid population density varied dramatically between different FL stands, being extremely high at some places (fig. 1). It appeared that the relation between *C. septempunctata* and aphid population density may be described by power function.

Plant density had an important effect in cereals, where LAI was main determinant of *C. septempunctata* population density in both years of investigation (14.0 and 11.0 % of variance explained, table 2). Correlation with PC "plant density" explained 35.6 % of variance (1980). By contrast, in alfalfa we failed to demonstrate any effect of plant density (see 4). In 1979 (table 1) and 1980 (table 3) we observed also significant preference to alfalfa stands while clover stands were avoided.

Distance from field margin (PC) influenced *C. septempunctata* density in FL (12.7–26.9 % variance explained). Some preference of the species to field margins could be demonstrated.

Type of landscape (PC) revealed significant correlations with species'

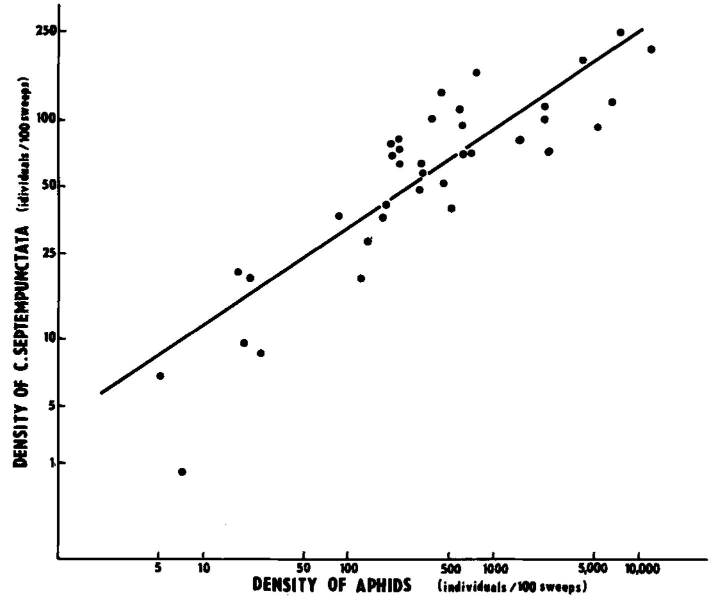

Fig. 1. Relation between aphid (*Acyrthosiphon pisum*) and *C. septempunctata* adult population density in forage leguminosae. May 6–24, 1977

population density in FL (27.4 % and 46.5 % of variance explained in 1979 and 1981), and also in cereals (18.2 % in 1980).

The multiple linear correlation coefficients with primary variables explained in total 38.3–69.4 % of variance of population density (tables 1 and 2). Both plant density and aphid population density appeared important determinants of population density of overwintered adults of *C. septempunctata.*

3.3 Factors influencing population density of *P. quatuordecimpunctata*

Aphid density was by far the most important factor that regulated species' population density, both in FL and in cereals. Significant partial correlations with variables characterizing aphid density explained 8.6–35.7 % of variance in CD (tables 1 and 2). Correlations with PC "aphid density" explained 13.9 % and 21.3 % of variance in cereals, and 10.2 % and 59.9 % of variance in FL in 1981 and 1979, resp. (table 3).

Plant density, contrary to *C. septempunctata,* evidently did not negatively influence species' population density. Even significant positive partial correlation with LAI was observed in cereals, 1980 (table 2). The correlations with PC "plant density" were not significant.

Significant correlations were obtained with PC "type of landscape". They explained 34.3, 8.5 and 36.2 % of variance of *P. quatuordecimpunctata* population density in FL (in 1979–1981, resp.), but only 13.9 % in cereals, 1979 while in 1980 the correlation was not significant. The multiple correlation coeffi-

Table 3. Correlation (r) and regression (k) coefficients of (factorial scores of) principal components to CD

Principal component	% of variance absorbed	*C. septempunctata*		*P. quatuordecimpunctata*		*C. quinquepunctata*	
		r	k	r	k	r	k
Alfalfa and clover, 1979							
Type of landscape	50.0	.523[b]	2.4507[b]	.586[b]	2.0458[b]	–	–
Aphid density	17.0	.769[b]	4.5653[b]	.774[b]	3.2843[b]	–	–
Distance from field margin	11.9	–.357[b]	–1.4791[b]	–.461[b]	–1.4203[b]	–	–
Alfalfa and clover, 1980							
Type of landscape	43.9	–.154	–.4065	–.291[a]	–.2215[a]	–	–
Crop species	16.2	–.430[b]	–1.2476[b]	.006	.0045	–	–
Crop density	12.6	–.072	–.1891	–.139	–.1028	–	–
Alfalfa and clover, 1981							
Type of landscape	41.9	.682[b]	2.1602[b]	.602[b]	2.2682[b]	–	–
Crop and aphid density	15.1	.235	.4926	.318	.8879	–	–
Distance from field margin	14.0	–.519[b]	–1.2922[b]	–.566[b]	–1.9006[b]	–	–
Cereals, 1979							
Type of landscape	37.0	–.004	–.0014	.373[a]	.0661	–.192	–.0346
Aphid density	25.6	–.177	–.0650	.076	.0118	–.112	–.0189
Distance from field margin	10.0	–.176	–.0528	.004	.0005	.132	.0283
Cereals, 1980							
Type of landscape[c]	28.6	–.202	–.0791	.212	.0417	–.027	–.0057
Aphid density	19.2	.514[b]	.1512[b]	.426[b]	.0658[b]	–.194	–.0276
Crop density	15.5	.597[b]	.1837[b]	–.151	–.0189	.320[a]	.0462
Type of landscape[d]	14.8	.427[b]	.1443[b]	–.057	–.0088	–.167	–.0286

[a] $p < 0.05$. – [b] $p < 0.01$. – [c] orographic diversity. – [d] altitude and proportion of forests

cients with primary variables explained 31.9–71.0 % of variance of adult population density (tables 1 and 2). Aphid population density appeared the most important determinant of population density of *P. quatuordecimpunctata.*

3.4 Factors influencing population density of *C. quinquepunctata*

Population density of this species was analyzed only in cereals where it may become quite abundant in sparse stands. Plant density appeared as the most important determinant (and, in fact, the only one detected) of species' population density. This species occurred virtually only in very sparse stands with LAI < 1. The relation was quite obvious in both years of observation (fig. 2), though in 1980 it was not demonstrated by significant linear correlation due to non-linear relationship between LAI and CD. The correlation with PC "plant density" was significant and explained 10.3 % of variance in 1980. Preference of this species to sparse stands was confirmed by observations on a number of maize, sugar beet, potato, and rape stands with LAI < 1, where the species sometimes outnumbered the other ones. Direct insolation of a large proportion of soil surface within a stand appeared the prerequisite for the presence of this species.

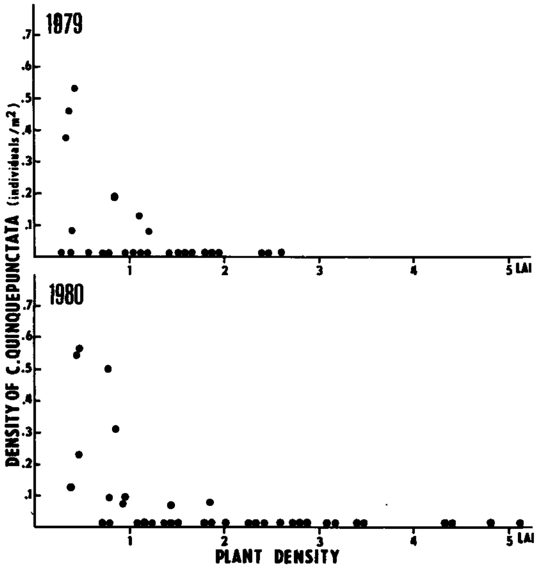

Fig. 2. Effect of plant density, expressed as leaf area index (LAI, i.e. leaf are per unit area of field surface), on population density of *C. quinquepunctata* in cereals

On the other hand, *C. quinquepunctata* had apparently low requirements for aphid density. No significant relation to this variable was revealed by our analysis, and abundant populations were frequently found in stands with minimum aphid density. Correlations with PC "type of landscape" were not significant.

The multiple correlation coefficients explained in total 51.3 % and 46.5 % of variance in species' population density in 1979 and 1980, resp. (table 2). Plant density appeared the only important determinant of *C. quinquepunctata* population density.

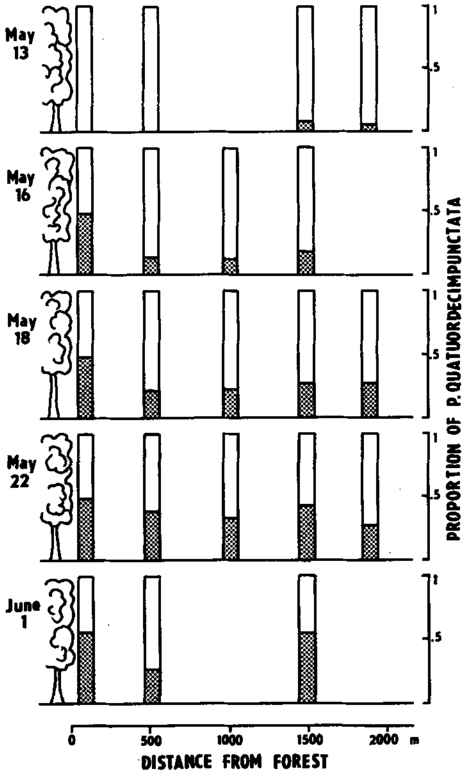

Fig. 3. Proportion of *P. quatuordecimpunctata* in communities of adult aphidophagous coccinellids in FL, in different distances from the nearest forest, between May 13 and June 1, 1979

3.5 Effect of migration from adjacent forests on the composition of coccinellid communities in FL

In years of study we observed no permanent influence of distance from forest on coccinellid communities in fields. However, at the period of formation of coccinellid communities by immigration a temporary effect of forest vincinity was observed. It appeared as different ratio of both dominant species, *C. septempunctata* and *P. quatuordecimpunctata*, at different distances from forest. This situation was most conspicuous on alfalfa in May, 1979 (fig. 3). The migration of *C. septempunctata* to field habitats preceded that of *P. quatuordecimpunctata*. The former species appeared in April, the latter around mid-May. On May 15, when massive migration of *P. quatuordecimpunctata* begun, the adults settled first at the FL stands adjacent to forest, while the remote stands were occupied only slightly. Thus the proportion of this species in coccinellid communities in about 50–100 m from forest edge was significantly higher than in 500–2,000 m. This situation persisted only for some 3–4 days, but disappeared completely after one week. Similar, although not so pronounced situations were observed also in other years.

4 Discussion

It appeared that population density of adults of three coccinellid species could be in some relation to aphid density, plant density, position of sample site, and type of landscape. In 1979–1981 the importance of these factors varied with coccinellid species, crop, season, and year. In explaining these variations we should consider the mechanisms and possible causal relationships between these determinants and CD.

The primary object of coccinellid interest in fields are aphids. Adults of two species, *C. septempunctata* and *P. quatuordecimpunctata*, accumulated at places where aphids were abundant. Such accumulation could be perhaps a consequence of cessation of searching movements, after frequent encounters with aphids (ROWLANDS and CHAPIN 1978; cf. GUTIERREZ et al. 1980), of otherwise randomly dispersing and searching coccinellid adults (ALI and AZAM 1977). Our results are in accordance with the results of several authors who succeeded to demonstrate similar density dependent responses (NEUENSCHWANDER et al. 1975; RADCLIFFE et al. 1977; TAMAKI and LONG 1978). However, the detailed study of SAKURATANI (1977) in maize revealed no such correlations in two coccinellid species. We also failed to demonstrate this relationship in *C. quinquepunctata* and even in two above species it was not significant in some crop × year sets of data. This fact signalizes the importance of further modifiers of adult CD.

At least in both species of genus *Coccinella*, density of crop stands was the most efficient modifier of population density in field biocenoses. Little systematic attention has been paid to this determinant. However, crop species, presence of weeds, plant spacing, sowing date etc. may influence CD (SMITH 1971; HORN 1981; TAMAKI et al. 1981). At least a part of these effects is perhaps due to differences in plant density. In cereals, thermophilic *C. septempunctata* (and still more *C. quinquepunctata*) preferred sparse stands while *P. quatuordecimpunctata* was more catholic in its requirements (HONĚK 1979). Plant density acts obviously through the change of microclimate within the crop stand. We suppose that in sparse stands coccinellids have an opportunity to warm up, in periods of sunshine, at directly insolated patches of soil surface, which is warmer than ambient air or plants. Thus on cool days or in early morning thermophilic species can increase body temperature to the level required for performance of vital activities.

The importance of above factors changes during the season, as the crop stands grow and aphid density increases. The different influence of plant density in FL and cereals may be explained in this way. Adult *C. septempunctata* migrated to FL stands when they were still sparse and low (from mid-April) and plant density had thus little importance in determining CD. As the FL stands became denser, the coccinellids did not leave them as long as trophic conditions were favourable. By contrast, immigration to cereal stands (late May) occurred at the time, when their density was largely diversified (winter and spring cereals). Coccinellids then preferred sparse stands. It appeared that conditions at the time of settling largely determine the acceptability of stands to coccinellids.

Area-specific differences in CD, specified as the effects of type of landscape, arose probably through interaction of several factors. The different timing of immigration of coccinellids to fields in lowland and submontane regions, and the fact that long-range migrations are perhaps not completed before late May, elicit the differences in May (FL) but are of less importance in late June (cereals). Some differences may be due to altitudinal variation in species abundance (HONĚK 1981), some represented local increases of CD dependent perhaps on better trophic conditions of previous year or other unidentified factors. The differences between subregions of an area so small as central

Bohemia may hardly represent consequences of clinal trends in abundance of species.

Similarly, the determinant "position of sample within a field" is perhaps the results of joint action of several factors directly influencing CD. It largely reflected differences between poorly developed stands of marginal parts of the fields and better central ones. Complex effects of differences in plant density and aphid abundance were perhaps the most important causative factors.

The importance of determinants varied between years from purely statistical reasons. In some years between-stand variation of plant density was far smaller than in others (cf. fig. 2). In others population density of aphids was generally low and even in all stands. Or coccinellids were extremely scarce so that little differentiation in CD may appear. Also some functional relationships between CD and environmental factors were apparently non-linear (see 3.4). Application of more sophisticated methods of mathematical analysis could result in a better prediction of CD from environmental data. Even so, the study revealed that large proportion of variation in population density of three coccinellid species in stands of agricultural crops may be explained in deterministic terms.

Zusammenfassung

Faktoren, welche die Zusammensetzung der Artengemeinschaften Blattlaus-fressender Coccinelliden (Coleoptera) bestimmen

1979–1981 wurden in Mittelböhmen die auf die Dichte adulter *Coccinella septempunctata, C. quinquepunctata* und *Propylaea quatuordecimpunctata* einwirkenden Faktoren untersucht. Die Käfer wurden durch Netzstreifen in Alfalfa- und Kleefeldern oder durch Handsammeln in Getreideparzellen gewonnen. Es wurden die partialen linearen Regressionen und Korrelationen zwischen der Coccinelliden-Dichte (CD) und 9–11 Parametern, die die Blattlausdichte, Pflanzendichte, Probenposition im Feld und den Biotop charakterisieren, sowie die aus diesen primären Variablen abgeleiteten Hauptkomponenten ausgerechnet.

Auf statistisch signifikante Beziehungen zu den primären Parametern der Blattlaus- und Pflanzendichte lassen sich 9,9–32,6 % der Varianz von CD zurückführen. Die Korrelationen mit den Hauptkomponenten, die die Blattlaus- und Pflanzendichte charakterisieren, erklärten 10,2–59,9 % der CD-Varianz. Auf Effekte der Hauptkomponenten, die die Probeposition im Feld und die Struktur des Biotops charakterisieren, ließen sich 8,5–46,5 % der CD-Varianz zurückführen. Die Bedeutung aller CD-Determinanten unterschied sich nicht nur in bezug auf Marienkäferart, sondern auch auf Jahr und Feldfrucht. Die Pflanzendichte war innerhalb der Gattung *Coccinella* von großer Bedeutung, besonders zur Zeit der Migration der Vollkerfe von den Überwinterungsplätzen auf die Feldkulturen. *C. quinquepunctata* bevorzugte dünne Pflanzenkulturen. Die Blattlausdichte war vor allem bei *C. septempunctata* und *P. quatuordecimpunctata* wirksam. Der Charakter der Landschaft führte zu ortsspezifischen Unterschieden der Populationsdichte beider Marienkäferarten gegen Ende Mai, doch kam es später zu einer Angleichung. Die Nachbarschaft eines Waldes konnte kurzfristig und vorübergehend eine atypische Zusammensetzung der Marienkäfergemeinschaften auf dem Feld verursachen.

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