Change in the community of epigeal spiders and harvestmen (Araneae, Opiliones) with the age of an apple orchard

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ABSTRACT

Change in the community of epigeal spiders and harvestmen (Araneae, Opiliones) was studied in an experimental apple orchard for six consecutive years. Five plots were surveyed by pitfall traps. Four of the plots were young (1–4 years); one plot was older (15–20 years). The abundance of epigeal arachnids increased with the age on the young plots, while it was constant on the older plot. There were significantly more arachnids on the young plots than on the older one. In turn, the diversity was significantly lower on the young than on the older plots. Lycosidae, Phalangiidae and Tetragnathidae dominated the young plots. The older plots were richer in Agelenidae, Clubionidae, Dysderidae, Gnaphosidae, Linyphiidae, Pisauridae and Salticidae. Principal species of the young and older plots were identified using multivariate analysis.

Keywords: Araneae; Opiliones; succession; habitat age; epigeal; orchard

Spiders are one of the most abundant natural enemies in various agrobiocenoses. Their beneficial effect has been studied in cereals (Riechert and Lockley 1984) and recently in orchards (Olszak et al. 1992, Baert et al. 1997, Bogya et al. 1999, Pekár 1999a). The majority of these investigations dealt with spiders of tree crowns. Several other studies centred upon spiders of the understorey plants (e.g. Bogya et al. 2000) and only few papers dealt with epigeal community of arachnids in orchards (Holstein and Funke 1995, Bogya and Markó 1999, Pekár 1999b).

Majority of these studies were conducted only for a short period, 1–3 years, thus did not take in account changes of the fauna, which are a result of natural succession. In respect to the frequency of man-made disturbances, orchards are considered as an intermediate type of habitat. It is neither as ephemeral as crop fields on which a complex disturbance is carried out each season due to planting of new crop; neither as stable as a forest, for example, where no disturbance is usually performed (Fazekas et al. 1992). Majority of disturbances is in a form of pesticide applications or mowing the understorey vegetation, which will affect only a part of the spider community present in the orchard. Although we have no information on the succession of the spider community in orchards, it is expected that it follows a similar pattern as a secondary succession in other type of habitats. Generally, the density and the diversity of spiders change with the age (e.g. Purvis and Curry 1980, Madden and Fox 1997). As a result, a young orchard is inhabited by a different spider fauna than an old one.

The aim of this study was (1) to define assemblages of epigeal arachnofauna of a young and an older experimental orchard, and (2) to investigate development of changes of the assemblages during succession in these two habitats.

MATERIAL AND METHODS

The study orchard is located in Praha-Ruzyně (50°06' N, 14°15' E, grid no. 5951), the Czech Republic. The whole area (1.8 ha) was divided into 5 plots, assigned here with letters A, B, C, D and E (Figure 1). A brief description of plots is given in Table 1. Plots A, B, D and E were young while plot C was older. The young plots were established two (A, B) and three (D, E) years, prior to the end of the study, respectively. The ground cover on all plots consisted mainly of grass (*Festuca rubra* L.), which was mown three times each season. On the young plots, ev-

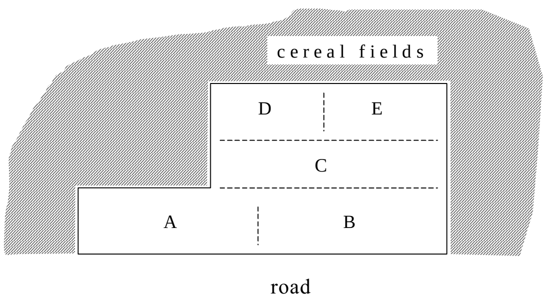

Figure 1. Map of the experimental apple orchard; letters identify position of the plots

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Table 1. Details of the study plots

Plot	Age (years)	Area (ha)	Year of sampling
A1	1	0.4	1995
A2	2	0.4	1997
B1	1	0.4	1995
B2	2	0.4	1997
C15–20	15–20	0.35	1992–1997
D2	2	0.3	1995
D3	3	0.3	1996
E2	2	0.3	1995
E3	3	0.3	1996

ery even strip between tree rows was cultivated (15-cm deep ploughing) three times each season. No pesticide was applied on the plots except for one application of an insecticide (Zolone WP) on crowns on plots D and E in 1996. The study plots are surrounded by a hedge belt about 3 m wide. Further from the study sites fields of corn, rape and wheat were maintained, each year a different crop.

Spiders and harvestmen were collected using pitfall traps. In each plot, five traps made of glass (volume 0.7 l, outlet 120 mm) were sunk into the ground in a line among trees, at 10m distances. The traps were put in the middle of the tree line in order to eliminate the effect of the border. The traps were one-third filled with 4% formaldehyde and over each, an aluminium cover was placed. During 6 years (1992–1997) the traps were sampled in two to three week intervals from spring until autumn as follows: May 21–October 8, 1992 (altogether 19 collections); April 28–October 21, 1993 (18 collections); March 30–October 14, 1994 (24 collections); March 24–September 4, 1995 (10 collections); April 24–October 4, 1996 (22 collections); April 1–September 3, 1997 (14 collections). Plot C was sampled for six, plots A and B for two, and plots D and E for three consecutive years.

Logarithmically transformed total annual abundance of spiders and harvestmen was compared between the study plots using 1-way ANOVA with the year of sampling as a covariable. Post-hoc comparisons between plots were done using Scheffe test. Shannon-Weaver diversity indices estimated from annual catches of arachnids on young plots (A, B, D and E) were compared with indices of the older plot (C) using two-sample randomisation test as the data did not follow a normal distribution (Manly 1992). There were 9999 random permutations generated using Resampling Stats (Simon 1997) and the significance level was determined from the number of randomised differences that were greater or equal to the observed mean difference. The same procedure was used to compare the mean annual abundance of the principal species between the young and older plots. Changes in the community of spiders and harvestmen due to the age of habitat were then studied by multivariate ordination methods, using CANOCO program (Ter Braak and Šmilauer 1998). The original data (mean annual abundance) were standardised according to the number of collections. At first, the data were processed by DCA (Detrended Correspondence Analysis) to find out the length of the first two axes. As these turned to be < 2, the linear method, redundancy analysis (RDA) was chosen for further analysis. In order to filter out the effect of the year of sampling it was set as covariable. The significance of the first axis was determined using Monte-Carlo permutation test (with 999 unrestricted permutations). Standard deviations are used to characterise variance throughout the text.

RESULTS

During 6 years, 3220 individuals of spiders and 1438 individuals of harvestmen belonging to 89 species were collected in total (Table 2). On all plots, lycosid spiders and phalangiid harvestmen were eudominant (Figure 2).

Comparison of the arachnid communities between young and older plots showed the following differences. Mean annual abundance changed dramatically with the age on some plots (Figure 3). On the young plots (A, B, D, E), the annual abundance was increasing from year to year, however significant difference was observed only

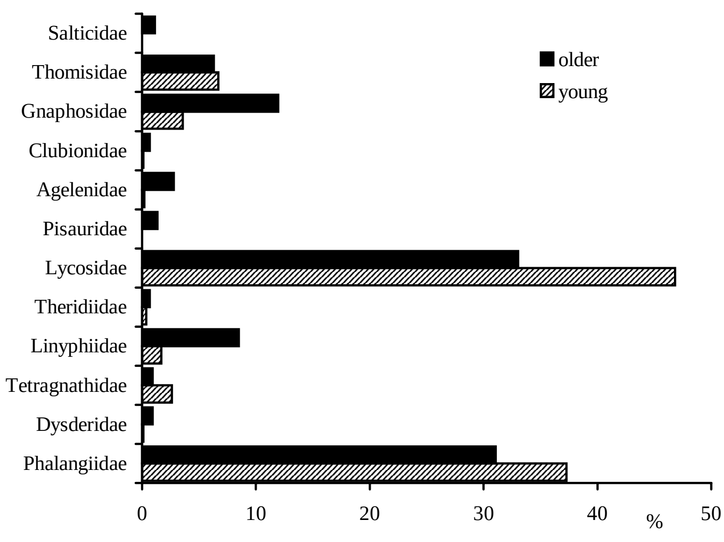

Figure 2. Family composition (%) on the young (D and E) and the older (C) plot; families that were represented by less than 1% are excluded

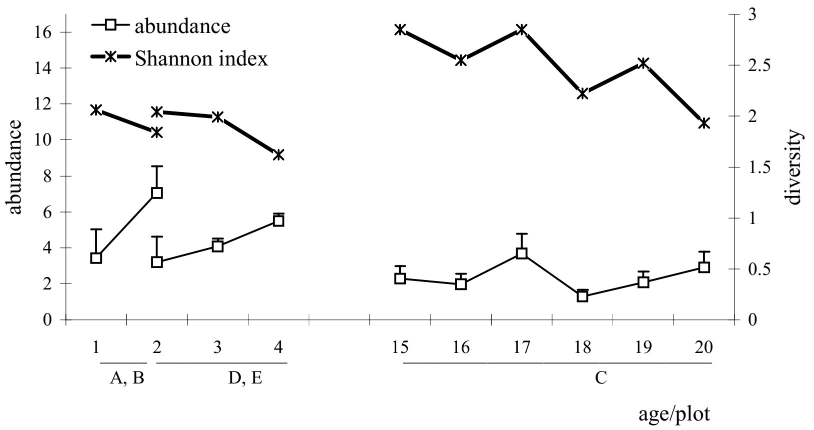

Figure 3. Comparison of the mean annual abundance and Shannon-Weaver indices of diversity on study plots; bars represent standard errors

between the first and the second year of A and B plots (P = 0.007, Scheffe test). The abundance on the older plots (C16–20) did not change significantly during study (*N.S.*, ANOVA). Comparison of annual abundances showed that there were on average almost twice as much arachnids on the young plots (4.7 ± 7.4) as on the older plots (2.5 ± 4.4) (P < 0.0001, ANOVA). As regards diversity, on all plots the diversity indices decreased from year to year (Figure 3) and the mean diversity value of the older plot was significantly higher than that of the young plots (P = 0.003, two sample randomisation test). This is because young plots were dominated by three very abundant species, *Phalangium opilio*, *Pardosa agrestis* and *Pardosa palustris*, whereas the older plots had several but less abundant spider species (Figure 4). The same pattern was apparent at the family level. While the young plots had more arachnids of the families Lycosidae, Phalangiidae and Tetragnathidae, older plots were richer in the families Agelenidae, Clubionidae, Dysderidae, Gnaphosidae, Linyphiidae, Pisauridae and Salticidae (Figure 2).

In order to find out the species-specific response to the age of plots, the abundance data were subjected to RDA with the variable AGE. This variable had significant effect on the distribution of arachnids (P = 0.001, Monte-Carlo permutation test). Based on the ordination diagram (Figure 5), principal species for the young and older stages were identified. Almost 30 species are displayed on the right side of the diagram, i.e. positively correlated with increasing age of habitat. This means that these species occurred exclusively or more abundantly in older plot. Among them the following ones were found to be principal for the older stage: *Opilio parietinus*, *Diplostyla concolor*, *Lepthyphantes alutacius*, *Oxyptila praticola*, *Pardosa lugubris*, *Pisaura mirabilis* and *Tegenaria agrestis* (Table 3). On the left side of the diagram there are almost 20 species suggesting that these ones were more abundant on the young plots. This is particularly true for *Phalangium opilio*, *Oedothorax apicatus*, *Pachygnatha degeeri*, *Pardosa agrestis* and *Xysticus kochi,* which were recognised as principal species for the young plots (Table 3). Several species, such as *Drassodes pubescens*, *Lepthyphantes tenebricola*, *Phrurolithus festivus* and *Tegenaria campestris* were similarly abundant in both stages. Ordination diagram of sites (Figure 6) revealed that there were marked temporal changes during study, particularly on the older plot. Dissimilarity between years on this plot was even larger than

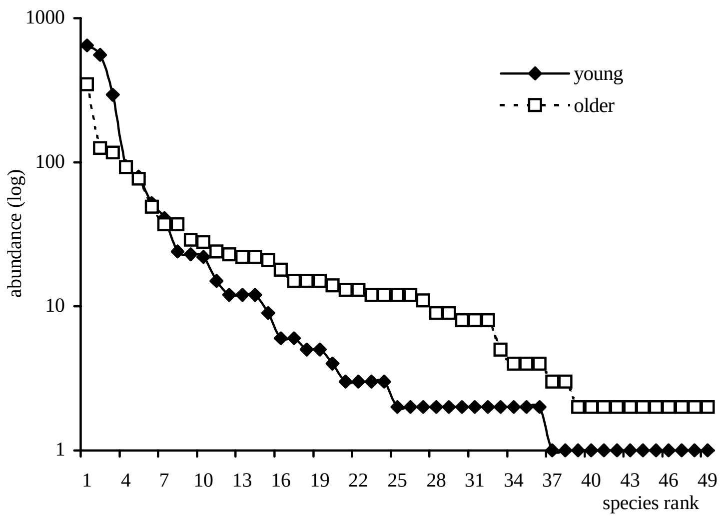

Figure 4. Comparison of the abundance curves of 50 most abundant species collected at the young (D and E) and older plot (C)

Table 2. The systematic list of species of harvestmen and spiders recorded on the studied plots of corresponding age; the numbers

No.	Plot	A + B		D + E			C					
	age	1	2	2	3	4	15	16	17	18	19	20
	Opiliones											
	Trogulidae											
1	*Trogulus tricarinatus* (L.)	1					1	1				
	Phalangiidae											
2	*Lacinius horridus* (Panzer)				77	3	11	2			2	
3	*Lophopilio palpinalis* (Herbst)		1	1					1			
4	*Oligolophus tridens* (C.L.K.)										1	
5	*Opilio parietinus* (DeGeer)	2	1	4	4	4	13	20	10		6	
6	*Phalangium opilio* L.	142	135	126	373	148	37	44	160	24	79	4
	Araneae											
	Pholcidae											
7	*Pholcus opilionoides* (Schrank)										2	
	Dysderidae											
8	*Dysdera erythrina* (Walckenaer)		1		1	1	1	2	9			
9	*Harpactea rubicunda* (C.L.K.)	1										
	Tetragnathidae											
10	*Pachygnatha clercki* Sundevall								1			
11	*Pachygnatha degeeri* Sundevall	2	23	6	17	29	3		5		1	2
	Araneidae											
12	*Aculepeira ceropegia* (Walckenaer)	1										
13	*Araneus quadratus* Clerck			1								
	Mimetidae											
14	*Ero furcata* (Villers)								1			
	Linyphiidae											
15	*Bathyphantes parvulus* (Westring)			1	1				2			
16	*Centromerita bicolor* (Blackwall)							1				
17	*Centromerus sylvaticus* (Blackwall)		1			1						
18	*Diplocephalus picinus* (Blackwall)								1			
19	*Diplostyla concolor* (Wider)				1	2	2	2	13	1	9	1
20	*Erigone atra* (Blackwall)	1	2	4			1					
21	*Erigone dentipalpis* (Wider)	2	5				6		5	1		
22	*Lepthyphantes alutacius* Simon						3		9		1	
23	*Lepthyphantes tenebricola* (Wider)	3		1			1	2		1		
24	*Meioneta rurestris* (C.L.K.)	4	1	1			1	3	9	2		
25	*Micrargus herbigradus* (Blackwall)								2			
26	*Micrargus subaequalis* (Westring)	3		2	1			4	17		1	
27	*Microlinyphia pusilla* (Sundevall)				1		1		1			
28	*Neriene clathrata* (Sundevall)									1		
29	*Oedothorax apicatus* (Blackwall)	1	2	4	11		1					
30	*Ostearius melanopygius* (O.P.C.)								1			
31	*Stemonyphantes lineatus* (L.)		2						3		2	
	unidentified	1	1	1					2			
	Theridiidae											
32	*Achaearanea riparia* (Blackwall)			1			2		2			
33	*Enoplognatha latimana* H. & O.				1						1	
34	*Enoplognatha thoracica* (Hahn)	4		1	1	1						
35	*Robertus* sp.									1		
36	*Steatoda phalerata* (Panzer)		1			1					1	
37	*Theridion bimaculatum* (L.)			1					1			
38	*Theridion impressum* L.K.								1			
39	*Theridion varians* Hahn	1										
	Lycosidae											
40	*Alopecosa accentuata* (Latreille)				2							
41	*Alopecosa aculeata* (Clerck)								14			
42	*Alopecosa cuneata* (Clerck)	3	1		3	2	3		2			3
43	*Alopecosa pulverulenta* (Clerck)	4	13			6	10	12		2	3	2
44	*Aulonia albimana* (Walckenaer)						1		1			
45	*Pardosa agrestis* (Westring)	62	333	74	136	85	3		12	3	14	45

represent total annual catches at particular plots

No.	Plot	A + B		D + E			C					
	age	1	2	2	3	4	15	16	17	18	19	20
46	*Pardosa lugubris* (Walckenaer)						3	2	1		3	15
47	*Pardosa palustris* (L.)	43	322	21	139	397	12			8	26	71
48	*Pardosa prativaga* (L.K.)	2	23		8	4	1		9		3	24
49	*Pardosa pullata* (Clerck)		7		3	3					1	
50	*Trochosa ruricola* (DeGeer)	1	34	4	9	10	23	12	17	3	16	22
51	*Trochosa terricola* Thorell							1				
52	*Xerolycosa miniata* C.L.K.	3	18	2	14	8	4	6	15	1	5	6
	Pisauridae											
53	*Pisaura mirabilis* (Clerck)				1		4		7	1	5	1
	Agelenidae											
54	*Agelena gracilens* C.L.K.			1			1		1			
55	*Cicurina cicur* (F.)	1	4				1		1			
56	*Tegenaria agrestis* (Walckenaer)	1			1		5	14	3	1		
57	*Tegenaria atrica* C.L.K.							1				
58	*Tegenaria campestris* C.L.K.	1	1					6			2	
59	*Tegenaria domestica* (Clerck)			1	1						1	
	Hahniidae											
60	*Hahnia nava* (Blackwall)	1							1			
	Dictynidae											
61	*Argaenna subnigra* (O.P.C.)			1								
	Liocranidae											
62	*Phrurolithus festivus* (C.L.K.)	1		4	1				1	1		
	Clubionidae											
63	*Cheiracanthium virescens* (Sundevall)										1	
64	*Clubiona neglecta* O.P.C.	1			1	1	2		5		1	
	Gnaphosidae											
65	*Drassodes pubescens* (Thorell)			2			1	2	1			
66	*Haplodrassus signifer* (C.L.K.)		2	4	4	1		4	2		3	
67	*Micaria pulicaria* (Sundevall)			1					1			
68	*Scotophaeus scutulatus* (L.K.)							1				
69	*Zelotes aeneus* (Simon)						2	1				
70	*Zelotes electus* (C.L.K.)			1	1							
71	*Zelotes latreillei* (Simon)	2		1		2			2			
72	*Zelotes lutetianus* (L.K.)	2	19	2	7	3			5		4	3
73	*Zelotes petrensis* (C.L.K.)			1								
74	*Zelotes praeficus* (L.K.)		1						1			
75	*Zelotes pusillus* (C.L.K.)	20	16	8	23	10	44	23	27	7	24	1
	Zoridae											
76	*Zora spinimana* (Sundevall)								1			
	Philodromidae											
77	*Philodromus aureolus* (Clerck)				2				1			
78	*Tibellus oblongus* (Walckenaer)				2							
	Thomisidae											
79	*Oxyptila praticola* (C.L.K.)						3	11	6		1	
80	*Oxyptila simplex* (O.P.C.)		2			1	1		8			
81	*Xysticus acerbus* Thorell				2						1	
82	*Xysticus audax* (Schrank)								15			
83	*Xysticus cristatus* (Clerck)	2	6	2	15	5	4		2	1	3	3
84	*Xysticus kochi* Thorell	24	17	26	35	33	3		9	5	4	1
85	*Xysticus luctuosus* (Blackwall)								3			
	Xysticus sp.		3	7		7						
	Salticidae											
86	*Euophrys frontalis* (Walckenaer)								12			
87	*Heliophanus cupreus* (Walckenaer)						1					
88	*Phlegra fasciata* (Hahn)						1					
89	*Synageles venator* (Lucas)										1	
	total individuals	343	986	320	899	768	217	177	442	64	228	204
	total species	32	29	32	34	25	38	24	52	18	33	16

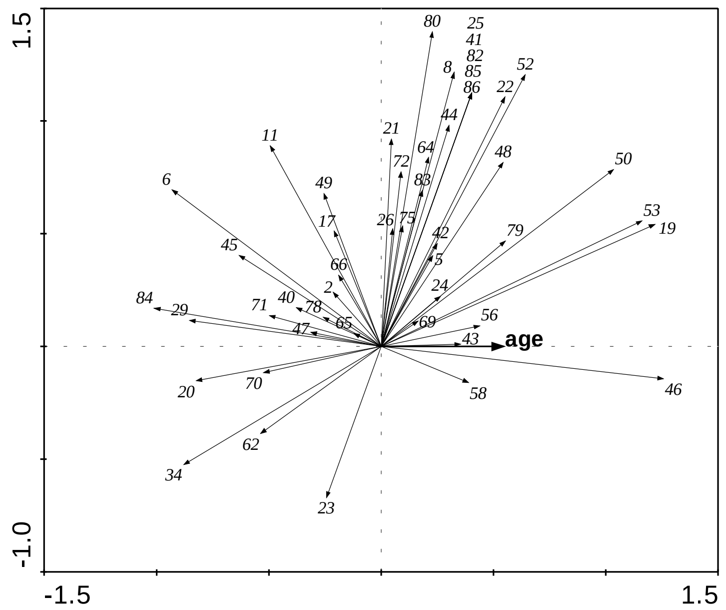

Figure 5. Ordination RDA diagram showing the response of selected arachnids to the age of the habitat; species with low abundance < 1% are excluded from the diagram

Species are represented by numbers as follows: 2. *L. horridus*, 5. *O. parietinus*, 6. *P. opilio*, 8. *D. erythrina*, 11. *P. degeeri*, 17. *C. sylvaticus*, 19. *D. concolor*, 20. *E. atra*, 21. *E. dentipalpis*, 22. *L. alutacius*, 23. *L. tenebricola*, 24. *M. rurestris*, 25. *M. herbigradus*, 26. *M. subaequalis*, 29. *O. apicatus*, 34. *E. thoracica*, 40. *A. accentuata*, 41. *A. aculeata*, 42. *A. cuneata*, 43. *A. pulverulenta*, 44. *A. albimana*, 45. *P. agrestis*, 46. *P. lugubris*, 47. *P. palustris*, 48. *P. prativaga*, 49. *P. pullata*, 50. *T. ruricola*, 52. *X. miniata*, 53. *P. mirabilis*, 56. *T. agrestis*, 58. *T. campestris*, 62. *P. festivus*, 64. *C. neglecta*, 65. *D. pubescens*, 66. *H. signifer*, 69. *Z. aeneus*, 70. *Z. electus*, 71. *Z. latreillei*, 72. *Z. lutetianus*, 75. *Z. pusillus*, 78. *T. oblongus*, 79. *O. praticola*, 80. *O. simplex*, 82. *X. audax*, 83. *X. cristatus*, 84. *X. kochi*, 85. *X. luctuosus*, 86. *E. frontalis*

on the young plots. Among young plots (A, B, D, E), the similarity between two plots of the same age (A:B and D:E) increased with age.

DISCUSSION

In general the epigeal arachnofauna of orchards is more diverse than that of cereals. For example, while in wheat only about 30 spider species are usually found (e.g. Pekár 1997) in older orchards the number doubles (Pekár 1999b) or triples (this study). This is a result of lower frequency of man-made disturbances performed in orchards. Older orchards thus may play an important role to surrounding intensively cultivated agrobiocenoses (as in this study) by providing a refugee to spiders. Particularly to such species whose phenelogy is not synchronised with the timing of the disturbing practices.

Table 3. Mean annual abundance (± *SD*) of the principal species for the young (i.e. A1, A2, B1, B2, D2–4, E2–4) and older plots (C15–20); abundances were compared by two-sample randomisation test (*$P < 0.05$; **$P < 0.01$, ***$P < 0.001$)

Species	Plot		*P*
	young	older	
Phalangium opilio	1.27 ± 0.57	0.57 ± 0.42	*
Oedothorax apicatus	0.02 ± 0.02	0.01 ± 0.01	*
Pachygnatha degeeri	0.12 ± 0.08	0.02 ± 0.02	*
Pardosa agrestis	0.99 ± 0.78	0.16 ± 0.24	*
Xysticus kochi	0.20 ± 0.10	0.04 ± 0.03	***
Opilio parietinus	0.02 ± 0.02	0.08 ± 0.09	*
Diplostyla concolor	0.01 ± 0.01	0.04 ± 0.04	**
Lepthyphantes alutacius	absent	0.02 ± 0.03	*
Oxyptila praticola	absent	0.04 ± 0.05	*
Pardosa lugubris	absent	0.05 ± 0.08	*
Pisaura mirabilis	0.01 ± 0.01	0.03 ± 0.02	**
Tegenaria agrestis	0.01 ± 0.01	0.04 ± 0.06	*

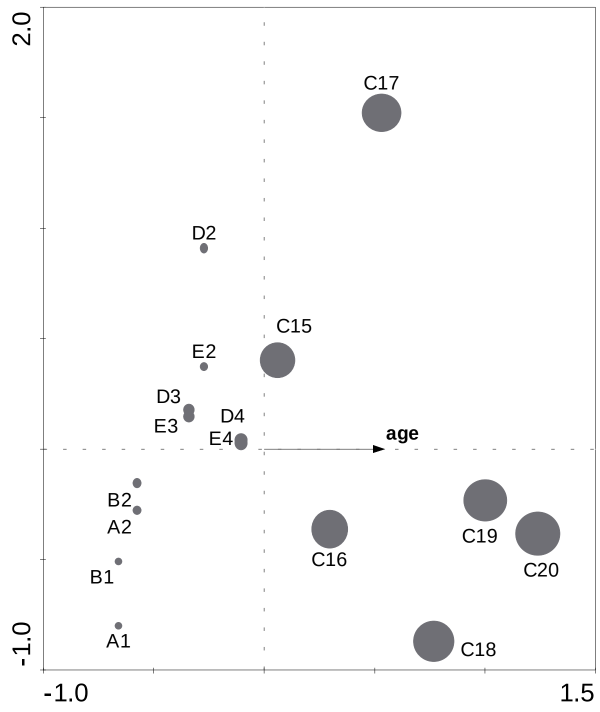

Figure 6. Ordination RDA diagram showing the similarity of study sites with respect to the age of habitat; a size of the circles represent age of the plot; values of the first two axes were 0.11 and 0.12, respectively

There are marked differences between orchards. A very young orchard (1–2 years old) is inhabited by a similar spider fauna as cereals. This means that it is characterised by a few very abundant spider species, particularly of the families Linyphiidae and Lycosidae. Surprisingly, in this study linyphiid spiders were less abundant. On the other hand, the community of an older orchard is similar to that of hedges (e.g. Pekár unpubl.) having many less abundant species of other families like Gnaphosidae or Thomisidae. This is in agreement with observations of other authors. Gack and Kobel-Lamparski (1986) surveyed succession in a vineyard in Germany. They observed greatest number of individuals, mostly linyphiids, in the first year, which decreased in the 2nd and 3rd year; in the 5th year these species were replaced by lycosids and gnaphosids. Very similar results were obtained by Nentwig (1988) who performed investigation of spider succession on a meadow. Růžička and Hejkal (1997) studied spider succession on spoil banks. Principal species of the young stages were mainly linyphiids, such as *Oedothorax apicatus* or *Meioneta rurestris*, and *Pardosa agrestis* or *Xysticus kochi*, whereas for the older (17 years) stage it was *Diplostyla concolor*, *Zelotes latreilei* or *Pardosa pullata*. This is in agreement with results of this study. Bogya et al. (2000) found higher diversity of spiders in older orchard but higher density of spiders in the young one. Hurd and Fagan (1992) compared density and diversity of cursorial spiders on several successional stages of pastures. They observed the greatest number of individuals on a 2-year old stage but the greatest number of species on a 15-year old plot. Similarly, Madden and Fox (1997) recorded a decrease of arthropod biomass with the age in a sand mine. Purvis and Curry (1980) reported increase in both the number of taxa and the density of spiders as the pasture aged from 1 to 3 years.

Buchs et al. (1995) and Hurd and Fagan (1992) found that there is a significant difference in the body size of spiders occurring at different successional stages. Large lycosid and gnaphosid spiders dominated older set-aside areas, whereas early stages with intensive management were rich in small linyphiid (pioneer) spiders. In this study, however, all plots either young or older were rather equally characterised by a guild of large spider species. It is possible that the fauna of young orchard was markedly affected by the spider assemblages of the previous old orchard, which was characterised by large spiders.

The development of species assemblages was found to be fastest in the early stages of succession. Blick (1995) documented marked change in the spiderfauna during the first two years. Similar pattern was apparent in this study. Both density and diversity changed with the age on the young plots. Although the older plot exhibited a considerable temporal change, it did not affect density or diversity of spiders.

It is not known whether the differences between spider fauna of the young and older plots were due to the age of habitat or due to the vegetation structure. It has been shown that there is a strong association between arthropod and plant succession (e.g. Murdoch et al. 1972, Duffy 1978, Haskins and Shaddy 1986) and that spider diversity and abundance is correlated with the physical structure of the litter (e.g. Uetz 1974, 1979). In a study designed to determine the crucial factor driving the change, Hurd and Fagan (1992) found that succession of spiders is influenced more by the habitat structure than by the age. As the vegetation changes with the age, the effects of these two factors are often confounded. In this study the vegetation cover (made of grass), was very similar on all plots, so both factors may had presumably a simultaneous effect.

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ABSTRACT

Změna společenství epigeických pavouků a sekáčů (Araneae, Opiliones) s věkem jabloňového sadu

Změna společenství epigeických pavouků a sekáčů (Araneae, Opiliones) byla studována v experimentálním jabloňovém sadu po dobu šesti let. Pět ploch bylo sledováno metodou zemních pastí. Čtyři z těchto ploch byly mladé (1–4 roky), jedna plocha byla starší (15–20 let). Hojnost epigeických pavoukovců se na mladých plochách zvyšovala s věkem. Na starší ploše byla hojnost během studia konstantní. Na mladých plochách byla zaznamenána výrazně větší abundance pavoukovců než na starší ploše. Naopak starší stadia měla větší druhovou diverzitu. Na mladých plochách dominovali pavouci čeledí Lycosidae, Phalangiidae a Tetragnathidae. Na starších plochách byly v porovnání s mladými plochami hojnější čeledi Agelenidae, Clubionidae, Dysderidae, Gnaphosidae, Linyphiidae, Pisauridae a Salticidae. Druhy charakteristické pro mladé i starší sukcesní stadium byly identifikovány s použitím mnohorozměrné statistické metody.

Klíčová slova: Araneae; Opiliones; sukcese; věk stanoviště; epigeický; sad

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