

Succession in urban habitats: an analysis of phytosociological data

Sukcese na ruderálních stanovištích - analýza fytoocenologických dat

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Phytosociological data from 46 permanent plots located in various urban habitats within the town of Plzeň, W Bohemia, were analysed. Differences between species occurrences in 1969 and 1974 were expressed as a shift in the values of the Braun-Blanquet scale. This method made it possible to distinguish among early, middle and late successional species. Changes in life forms, plant strategies as well as the representation of families and phytosociological units were discussed and found to be consistent with results reported by quantitative studies. The review of Central European phytosociological studies on succession in urban habitats is presented. Pros and cons of the phytosociological approach to study of succession are discussed.

Introduction

Within Central Europe, the vegetation in urban environment has been studied extensively for the last two decades (for review see Sukopp 1987, Klotz 1987, Mucina 1990). Descriptive phytosociological studies dominated this research field for a long time due to the strong Braun-Blanquetian tradition, influence of which is still apparent. However, similarly to other fields of vegetation ecology, the recent research is much more focused upon the vegetation dynamics. Succession is considered as one of the central points in ecology (e.g. Connell et Slatyer 1977, Prach 1985, Miles 1987).

The limitations imposed by approaches of the Central European phytosociological research school concern both the scale of the study (community approach based on the organismal viewpoint, Clements 1916) and the methods used (floristic composition recorded by vegetational relevé). Data sampled in this way hardly contribute to our knowledge of mechanisms that rule the vegetation dynamics. They are collected in the unified manner, however, and contain a great amount of information on vegetation and its relation to the habitat (Herben 1986). It seems thus plausible to use phytosociological material for further analyses.

Two main approaches may be applied in studies of succession: (1) snapshot records (Diamond 1986) of differently aged successional stages, and (2) repeated recording of vegetation in permanent plots (Schmidt 1974, Böttcher 1974, Eliáš 1990). Both approaches may be combined to provide a more complete picture of succession from the very start to the late successional stages (Pyšek 1977, Prach 1987, Lepš et Prach 1989).

This paper presents an analysis of species behaviour in succession based on the analysis of phytosociological data. Comparison of results with those based on other methodical approaches is presented as well.

Material and methods

Study site

The research was conducted in the town of Plzeň, West Bohemia (49.46 N, 13.24 E) which lies at the confluence of four rivers, 306-395m above sea level. Mean annual temperature is 7.8°C, annual precipitation is 495 mm. During the research period the town had 171,000 inhabitants and covered an area of 125 km².

The ruderal vegetation of this industrial town has been described in detail by Pyšek (1974, 1978). The phytosociological study of succession in the ruderal communities of Plzeň was published having brought the overall successional scheme as well (Pyšek 1977, 1978) and full data from several-years of observation in permanent plots (Pyšek 1978, 1984a).

Data analysis

Forty six permanent plots of approximately 10m² in size were established in 1967-68 by the latter author. The shape of plots differed with respect to the character of the community studied. Location of plots was based on the knowledge of the vegetation under study which made it possible to cover successional stages proportionally. Plots were located in the most frequent habitats occupied by ruderal vegetation: dumps (10 plots), organic waste deposits (8), soil heaps (2), ruins (4), deposits of manure and silage seepage (6), railway sites (8), village yards (3), banks of water courses (5). From 1969 to 1974, the latter author recorded the vegetation in plots using the seven grade scale of Braun-Blanquet (Mueller-Dombois et Ellenberg 1974). Six plots (13%) were destroyed during the research period. Full data are provided in Pyšek (1978:195-206).

For each species in each plot (n=40), the record from 1969 was compared with that from 1974. The Braun-Blanquet scale was transformed into numerical scale 1-7 which allowed expression of the differences between species occurrences in 1969 and 1974 in a simple numerical manner. Changes in representation of life forms (Rothmaler 1986, Grime, Hodgson et Hunt 1988), life strategies (Grime, Hodgson et Hunt l.c.), species groups with respect to immigration (Opravil 1980) and phytosociological units (Ellenberg 1979, Moravec et al. 1983, Rothmaler 1986) were analysed. Indicator values (Ellenberg 1979) were used to express the changes of environmental conditions in the course of succession. Nomenclature follows Rothmaler (1986) except as indicated.

The successional status (early, middle or late successional ones) of species and communities is understood here in accordance with the study of Pyšek (1977).

Results

Species exchange

The successional behaviour of individual species is expressed as a frequency distribution of shifts in the Braun-Blanquet scale over 6 years of spontaneous succession (Fig.1). In other words, -2 means retreat by 2 grades of the scale (e.g. the species was evaluated by the value "1" in 1969 and "1" in 1974, respectively) and so on. Presented histograms thus show the relative numbers of plots in which the species retreated (and how much it retreated) and, on the other hand, in which its abundance/cover increased (and how much it increased). The early successional species are characterized by concentration in the left part of histograms whereas the opposite pattern is typical of the late successional species.

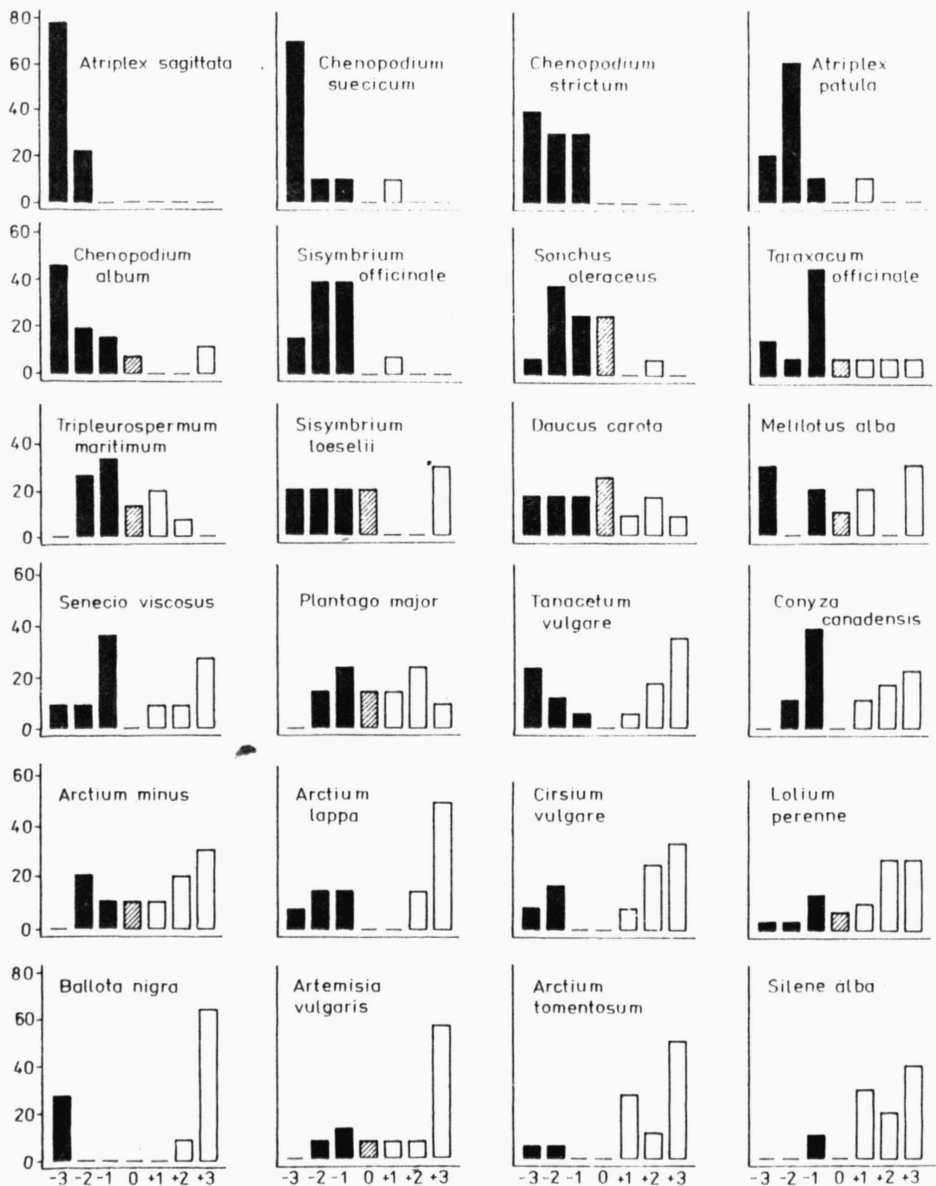
Changes in the occurrence of midsuccessional species are evenly distributed. This reflects that such species increase in plots originally established in early successional communities but decrease in those which were located in the middle and later successional stages. This may be exemplified by *Ballota nigra*. This species retreated from *Ballota*-dominated communities (*Lappo-Ballotetum nigrae*, *Ballota nigrae-Chenopodietum boni-henrici*) that have developed into more persistent *Arction*-communities (*Tanaceto-Artemisietum vulgaris*). The species invaded younger plots, however, that were originally occupied by *Malvetum neglectae* and some *Sisymbrium*-communities (Pyšek 1977, Kopecký 1986).

In Table 1, each species is characterised by the mean value of shift in the Braun-Blanquet scale. This value was calculated from all plots in which the species occurred. Ranking of species according to this characteristic roughly corresponds to our knowledge of their behaviour in succession.

Table 1 provides deeper insight into the exchange dynamics in the plots investigated. It reveals that although the number of species records did not change during the research period, at the end of succession the species may have occurred in different plots than at the beginning. During succession, *Senecio viscosus* either disappeared from or newly appeared in 90.9% of plots in which it totally occurred (*Plantago major* subsp. *major* 76.2%, *Arctium lappa* 71.4%, *Tanacetum vulgare* 64.7%, *Melilotus alba* 64.0%).

Persistence of species in permanent plots is shown in Fig.2. Comparison of Figs. 1 and 2 indicates that profound quantitative decrease of a species (Fig.1) does not necessarily mean its massive disappearance from the respective plots. In *Chenopodium album*, of 80.8% of plots where this species retreated, in only 47.8% it completely disappeared. Large soil seed bank (Kropáč 1966) can probably maintain the population of this species in the site for a longer period through continuing germination and seedling recruitment after the species has lost its dominance over the community.

Chenopodiaceae and *Brassicaceae* comprise mainly species of early successional stages, whereas the later successional species prevail in the *Poaceae*. Among the *Asteraceae*, the concentrations of both early/middle (*Tripleurospermum maritimum*, *Conyza canadensis*, *Lactuca serriola*) and late successional dominants (*Tanacetum vulgare*, *Artemisia vulgaris*, *Arctium* sp.div.) are reflected by distinctly two-peaked distributions (Fig.3). Rather similar situation seems to exist in the *Polygonaceae*, *Lamiaceae* and *Plantaginaceae* as well.



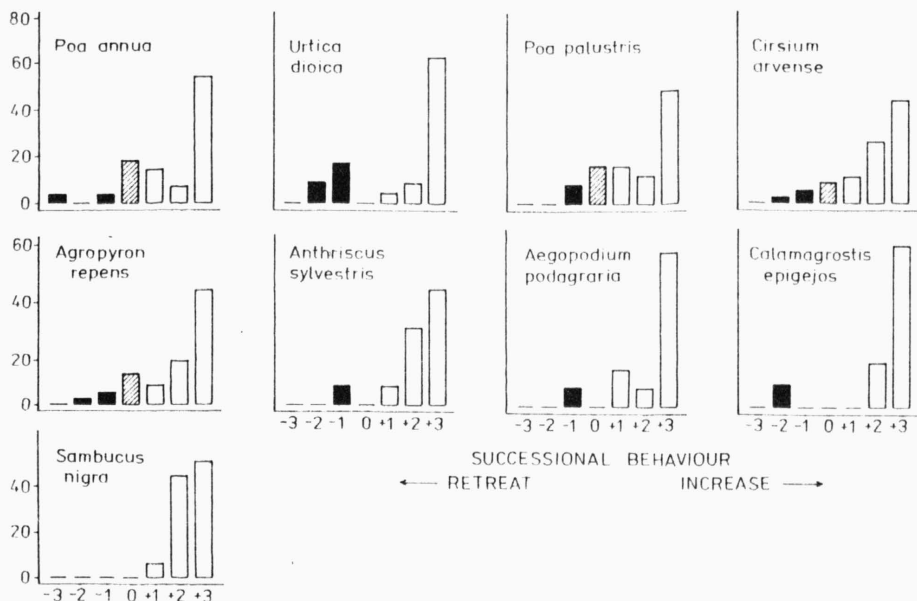


Fig.1. - Species behaviour in succession expressed as a frequency distribution of changes that the species showed during succession from 1969 to 1974. Type of changes (retreat or increase) and their magnitude (shift by 1,2 or more grades of the Braun-Blanquet scale) is shown. Species are ordered from early to late successional ones. Full bars indicate retreat, hatched bars indicate the same level of occurrence and empty bars are used for increase. Changes by 3 and more grades were summed up and presented together in the marginal bars.

Phytosociological units

A large number of species which decrease in succession may be found among diagnostic species of *Chenopodietea* and *Secalietea*. Species of *Galio-Urticetea* and *Agropyretea* clearly increased in most plots (Fig.4) which corresponds to the successional position of communities belonging to these units (Pyšek 1977).

Proportion of aliens

The replacement of alien species by native ones may be inferred from Fig.5. Most of the archaeophytes (59.0% of records) and neophytes (74.5%) decreased in succession. The corresponding value for the native species is only 34.0%.

Table 1. - Performance of the species in permanent plots (1969-1974). The "average change" represents the mean value of shift in transformed Braun-Blanquet scale, calculated from all plots the species occurred. Only species recorded in at least 25% of plots are included, those with 10-25% are listed below. D - disappeared, E - emerged.

	average change	%	total (n _{max} = 40)	number of occurrences			
				1969	D	E	1974
<i>Atriplex sagittata</i> Borkh.	-2.8	25.0	10	10	10	0	0
<i>Chenopodium succicuum</i>	-2.3	25.0	10	9	7	1	2
<i>Ch. strictum</i>	-2.1	25.0	10	10	8	0	2
<i>Atriplex patula</i>	-1.8	25.0	10	9	8	1	2
<i>Chenopodium album</i>	-1.6	65.0	26	23	11	1	13
<i>Sisymbrium officinale</i>	-1.5	32.5	13	13	12	0	1
<i>Sonchus oleraceus</i>	-1.1	40.0	16	16	10	0	6
<i>Taraxacum officinale</i>	-0.6	32.5	13	10	8	3	5
<i>Tripleurospermum maritimum</i>	-0.5	37.5	15	12	4	3	11
<i>Sisymbrium loeselii</i>	-0.3	27.5	11	10	6	1	5
<i>Daucus carota</i>	-0.3	32.5	13	10	5	3	8
<i>Melilotus alba</i>	0.0	27.5	11	8	4	3	7
<i>Senecio viscosus</i>	+0.3	27.5	11	7	6	4	5
<i>Plantago major</i> s.s.	+0.5	52.5	21	13	8	8	13
<i>Tanacetum vulgare</i>	+0.5	42.5	17	10	4	7	13
<i>Conyza canadensis</i>	+0.5	45.0	18	15	11	3	7
<i>Arctium minus</i>	+0.9	25.0	10	7	1	3	9
<i>A. lappa</i>	+1.1	35.0	14	8	4	6	10
<i>Cirsium vulgare</i>	+1.1	27.5	11	3	2	8	9
<i>Lolium perenne</i>	+1.3	67.5	27	19	0	8	27
<i>Ballota nigra</i>	+1.3	27.5	11	4	2	7	9
<i>Artemisia vulgaris</i>	+1.6	97.5	39	33	0	6	39
<i>Arctium tomentosum</i>	+1.7	45.0	18	5	2	13	16
<i>Silene alba</i>	+1.8	25.0	10	3	0	7	10
<i>Poa annua</i>	+1.8	70.0	28	15	1	13	27
<i>Urtica dioica</i>	+1.8	60.0	24	5	2	19	22
<i>Poa palustris</i> s.l.	+1.8	62.5	25	15	0	10	25
<i>Cirsium arvense</i>	+1.9	85.0	34	20	0	14	34
<i>Agropyron repens</i>	+1.9	90.0	36	19	2	17	34
<i>Anthriscus sylvestris</i>	+2.2	30.0	12	4	0	8	12
<i>Aegopodium podagraria</i>	+2.3	30.0	12	3	0	9	12
<i>Calamagrostis epigejos</i>	+2.3	25.0	10	2	1	8	9
<i>Sambucus nigra</i>	+2.4	40.0	16	6	0	10	16

Tussilago farfara : average change -2.8 (total number of occurrences 5), *Atriplex oblongifolia* -2.2(5), *Urtica urens* -2.2(5), *Polygonum monspeliense* -2.0(8), *Galinsoga parviflora* -1.8(5), *Plantago lanceolata* -1.7(6), *Carduus acanthoides* -1.5(6), *Solanum nigrum* -1.4(9), *Lapsana communis* -1.3(6), *Poa pratensis* -1.2(8), *Linaria vulgaris* -1.0(6), *Melilotus officinalis* -0.6(5), *Convolvulus arvensis* -0.5(6), *Stellaria media* -0.4(5), *Lactuca serriola* -0.1(7), *Dactylis glomerata* +0.3(8), *Echium vulgare* +0.4(5), *Malva neglecta* +0.8(5), *Chenopodium bonus-henricus* +0.8(8), *Arrhenatherum elatius* +1.1(7), *Galium aparine* +1.2(6), *Puccinellia distans* +1.6(9), *Rumex obtusifolius* +2.0(9).

Life forms and strategies

The analysis of life form spectra confirms the pattern that is generally recognized in ruderal succession. An increase of all groups to the debt of therophytes was found (Fig.6).

Fig.7 shows the changes in species groups delimited on the basis of Grime's strategies (Grime 1979). Retreat of R-strategists (or with R-type prevailing) as well as increase of C-strategists is documented.

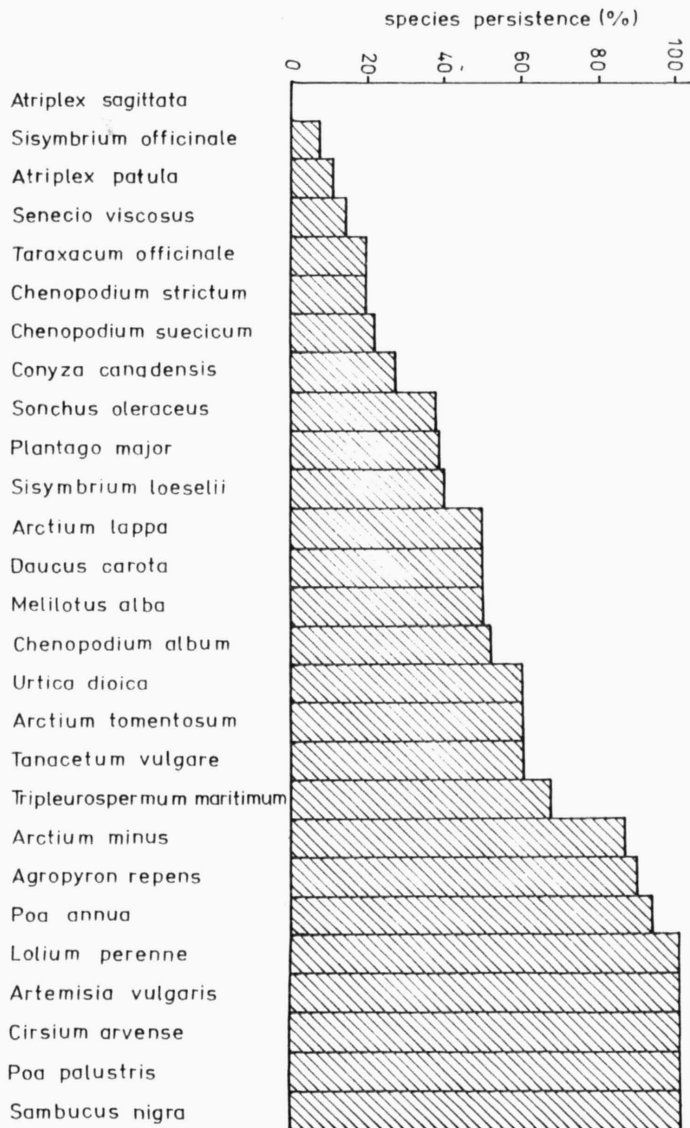


Fig.2. - Species persistence in succession expressed as a proportion of plots in which the species occurred in 1969 and persisted till 1974.

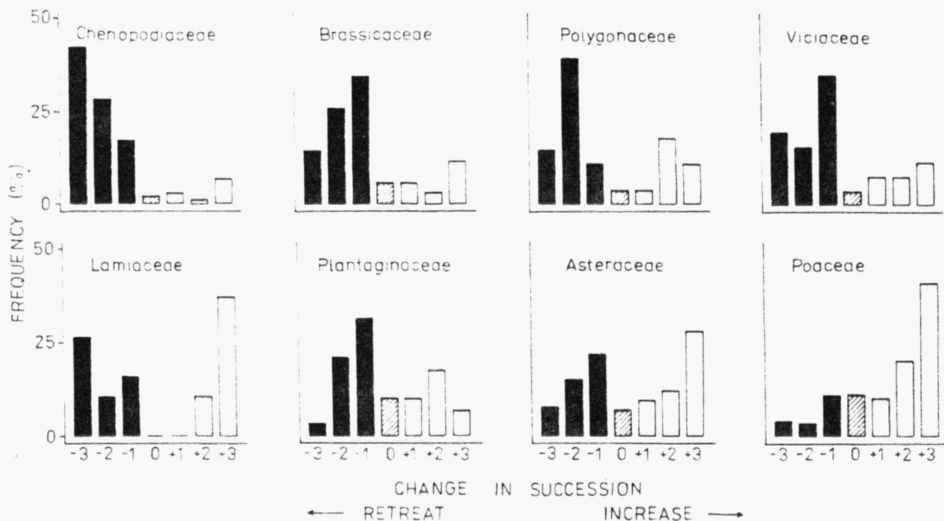


Fig. 3. - Changes in succession according to the families (for explanation see Fig. 1 and text).

Indicator values

The species whose occurrence increased in succession have higher nitrogen and moisture requirements (mean indicator value was used as a measure) than those that have retreated. Both regressions (Fig.8) were significant ($P < 0.05$). Concerning the light figure, no significant relation was found.

Discussion

Changes in vegetation characteristics usually estimated in phytosociological studies of succession in urban habitats are summarized in Table 2. The results obtained are mostly consistent with the pattern of changes reported from coal mining dumps (Prach 1982, 1987), old fields (Prach 1989) or other successional seres (Whittaker 1975, MacMahon 1980). General trends concerning life forms, participation of species groups, species diversity, as well as the pattern of species exchange relevant to the respective habitat may probably be satisfactorily described regardless of the method used. However, the detailed analysis and search for underlying mechanisms requires more exact results than the relevant method can provide (Prach et al. 1992).

None of the studies listed in Table 2 have dealt with the participation of aliens and native species in succession. Among aliens, there is a high proportion of annuals and R-strategists. These features are typical of early successional stages. Moreover, the alien species show generally higher requirements for temperature than do the native ones (Sukopp, Blume et Kunick 1979, Pyšek 1989). These requirements can be met in many settlement habitats such as dumps, industrial substrate deposits, manure deposit, and so on (Hejný 1971, Prach et al. 1992). The differences between both groups of aliens (Fig.5) may be

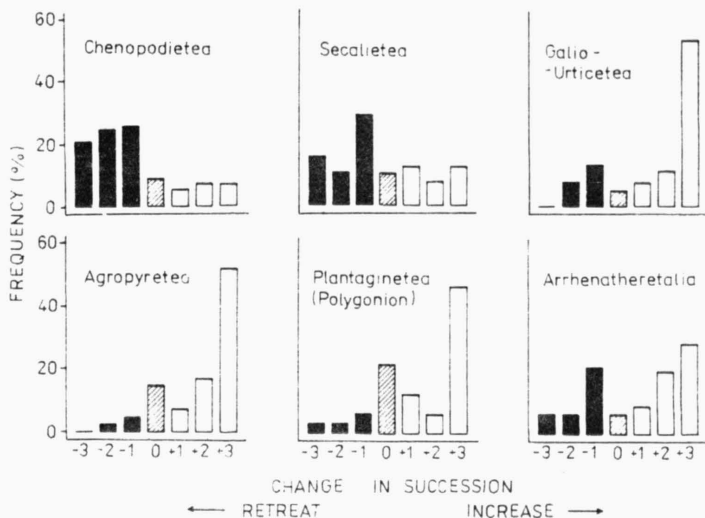


Fig. 4. - Changes in succession according to phytosociological units (for explanation see Fig. 1 and text).

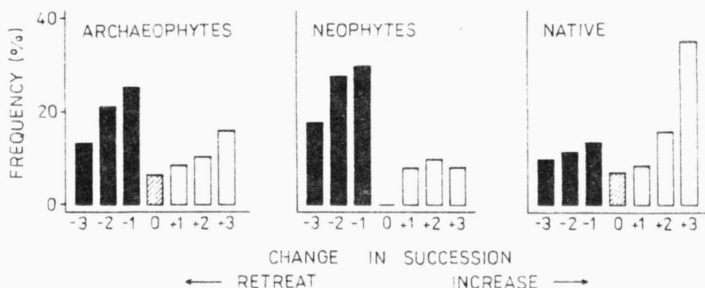


Fig. 5. - Behaviour of aliens and native species in succession (for explanation see Fig. 1).

partially explained by earlier immigration of archaeophytes which are thus better established in the Central European ruderal vegetation. Many archaeophytic species prevail in the midsuccessional communities (*Echio-Melilotetum*, *Descurainio-Atriplicetum oblongifoliae*, *Lappo-Ballotetum nigrae*, *Urtico-Malvetum neglectae*). Finally, as the spontaneous ruderal succession may be generally understood as a way back to the natural vegetation of a given area, an increase of native species may have been expected.

Unfortunately, only some studies concerning vegetation research in permanent plots contain the original relevé material (Table 2, for review see Böttcher 1974) and their subsequent reanalysis and mutual comparison among habitats is therefore not always possible. Moreover, we are aware of only two large data sets from permanent plots reported so far,

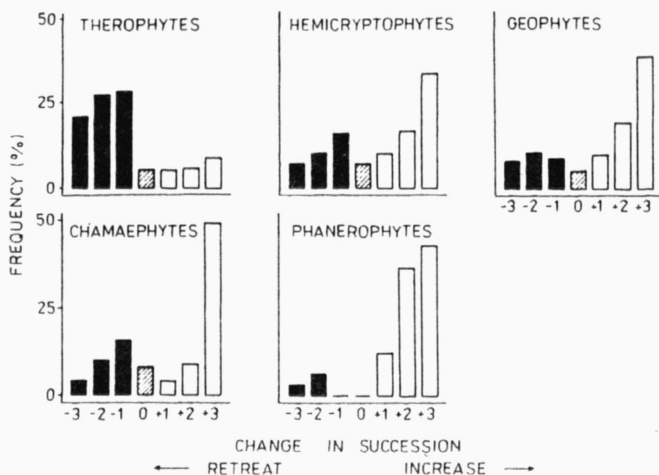


Fig. 6. - Changes in life forms during succession (for explanation see Fig. 1).

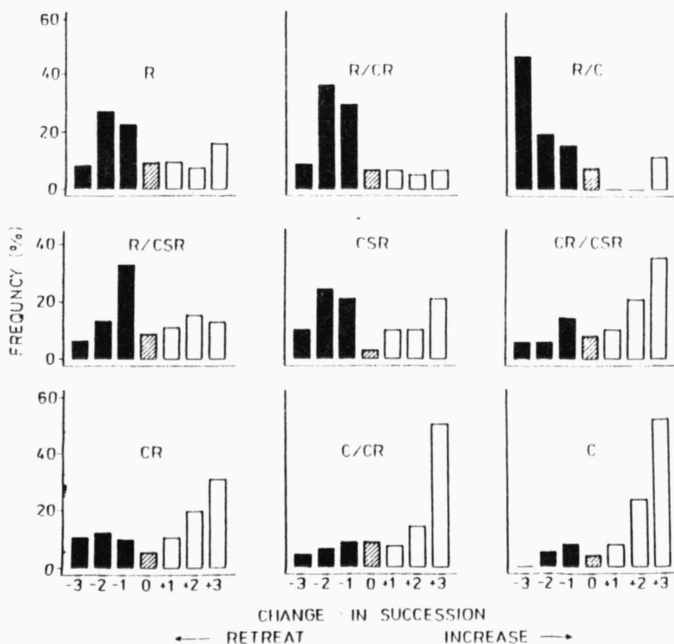


Fig. 7. - Changes in plant strategies in succession (for explanation see Fig.1). Classification of strategies was taken from the Grime, Hodgson et Hunt (1988).

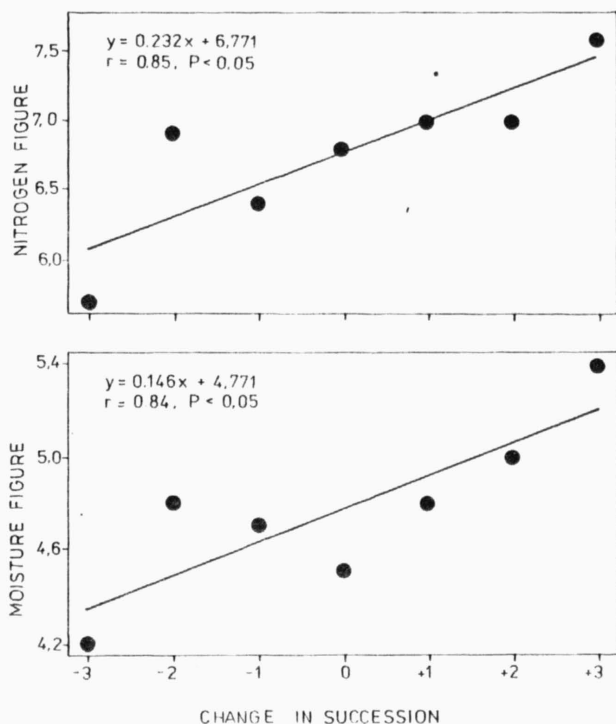


Fig. 8. - Changes in the nitrogen and moisture indicator values (Ellenberg 1979) during succession. Mean figures calculated from tabulated values of all species in which a given magnitude of shift was recorded are plotted against the shift in the values of Braun-Blanquet scale.

one of them being the data analysed in the present study and the latter one the data on succession in village settlements of the Bohemian Karst. Both are in manuscript (Pyšek 1978, Pyšek 1982). A sufficiently high number of plots is necessary if some kind of quantitative analysis is to be carried out.

Many phytosociological relevés have been recorded within the area of Central Europe so far. Provided that their localization is given with sufficient exactness, repeated investigations can be carried out after many years (Prach et al. 1992, for case studies see Hroudová et Prach 1986, Hadač 1990, Blažková 1991). Unfortunately, the plots located in settlement habitats, which are exposed to intense and frequent disturbances, are often destroyed soon after establishment (Pyšek 1984a, Prach et al. 1992).

The results presented in this paper are dependent on the time interval between initial and final records of permanent plots data. The six year interval seems to be appropriate for ruderal vegetation since within this period the succession may proceed (a) from the very

Table 2. - Vegetation characteristics investigated in phytosociological studies of succession in urban habitats within the area of Central Europe. Number of permanent plots for which the original relevé material was published in the respective study is indicated in the first column. A - species exchange, B - exchange of species groups (delimited on the basis of invasion time, phytosociological units etc., C - change in species diversity, D - change in life forms, E - exchange of communities, F - differences in succession due to habitats.

	A	B	C	D	E	F
Kreh 1935	+	+		+		
Kohler et Sukopp 1964	+					
Gutte 1971a	+2					+
Gutte 1971b	+2				+	+
Krippelova 1972	+10				+	
Kunick et Sukopp 1975		+		+		
Pyšek 1977			+	+		
Pyšek 1978, 1984a	+46			+	+	
Hilbert 1981		+		+		
Pyšek 1982	+42		+	+	+	
Bornkamm et Hennig 1982	+		+	+		+
Pyšek 1984b			+	+	+	
Bornkamm 1986	+9		+			+
Kowarik 1988	+1		+	+	+	+
Sauerwein 1988					+	+
Pyšek 1991			+	+	+	
this study	+	+		+		

start to the middle stages, and (b) from the middle stages to the later, relatively persistent ones, which are characterized by the forming of shrub layer. This makes it possible to record the midsuccessional species as well. However, suppose the longer time interval, e.g. 15 years: If the same method is used, then all the species will be considered as either early or late successional species. The midsuccessional species would appear in the former group as finally all the species originally present in the plots will be replaced by the late successional species.

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Shrnutí

Příspěvek se zabývá využitím fytoocenologických dat ke studiu sukcese ruderalní vegetace. V letech 1969-74 bylo druhým z autorů snímkováno celkem 46 stálých ploch rozmístěných na různých stanovištích. Výběr byl proveden tak, aby rovnoměrně pokrýval iniciální, přechodná a relativně trvalá sukcesní stádia.

Změna ve výskytu každého druhu na každé ploše byla vyjádřena jako rozdíl mezi transformovanými hodnotami Braun-Blanquetovy stupnice (1-7) v roce 1969 a 1974. Chování každého druhu v sukcesi je charakterizováno histogramem vyjadřujícím relativní podíl ploch, na nichž druh ustoupil, přibyl nebo zůstal zastoupen zhruba stejně. Podle těchto kritérií lze rozlišit druhy charakteristické pro jednotlivá stádia sukcese; toto vymezení odpovídá představám o ekologii jednotlivých druhů a jejich chování v sukcesi. Stejným způsobem je dokumentován ústup čeledí *Chenopodiaceae* a *Brassicaceae* a opačný trend u *Poaceae* a *Asteraceae*, dále zvýšení účasti všech ostatních životních forem na úkor terofytů během sukcese. Archeofyty a neofyty v průběhu sukcese většinou ustupují, i když mezi archeofyty je i řada druhů úspěšně rostoucích ve středních sukcesních stádiích. Původní druhy svoje zastoupení v průběhu sukcese výrazně zvyšují. Druhy s R-strategií (resp. s podílem R-strategie) ustupují, u C-strategie je trend opačný.

Výsledky získané fytoocenologickým přístupem odpovídají literárním údajům z jiných typů prostředí podloženým kvantitativními daty. Ke kvantitativní analýze fytoocenologických dat je potřeba jejich větší soubor. Těch však je ze stálých ploch k dispozici málo; mnohdy původní snímkový materiál vůbec chybí, což omezuje možnosti vzájemného srovnávání sukcesních řad. Fytoocenologická data lze využít k deskriptivnímu přístupu, nikoli pro studium mechanismů řídicích průběh sukcese; pro tento účel jsou nutná kvantitativní data a manipulativní experimenty.

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