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Changes in Phytocoenose Structure in Early Phases of Old-Field Succession in Poland

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ABSTRACT

The paper concerns the dynamics of phytocoenose structure in the early phases of secondary succession in four, spontaneously overgrowing old fields of different age in the *Peucedano-Pinetum* Mat. (1962) 1973 pine forest habitat (Poland). The studies were conducted during 1980-1982. It was concluded that the following phenomena are characteristic of the succession course:

1) wave-like changes in the number of species, state and spatial structure of biomass, minimum area size, species diversity and per cent of positive and negative interspecific associations;
2) tendency for decrease in species richness, total diversity, evenness and minimum area size;
3) tendency for increase in dominance;
4) directional changes in the floristic composition, i.e. decrease in the number of weed species and increase in the number of pine forest species;
5) gradual stabilization of the qualitative and quantitative structure characteristics.

ZUSAMMENFASSUNG

Gegenstand dieser Arbeit ist die Dynamik der Phytozönose-Struktur in den frühen Phasen der Sekundärsukzession. Die Untersuchungen wurden in den Jahren 1980-1982 auf vier spontan bewachsenen Brachfeldern verschiedenen Alters durchgeführt (potentieller Standortsraum des *Peucedano-Pinetum* Mat. (1962) 1973.

Folgende charakteristische Merkmale des Sukzessionsvorganges wurden festgestellt:
1) Artenzahl, Zustand und räumliche Struktur der Biomasse, Minimalraum, Artendiversität sowie der Prozentsatz positiver und negativer interspezifischer Korrelationen schwanken "wellenartig".
2) Artenreichtum, Gesamt-Diversität, Evenness sowie Größe des Minimalraumes zeigen abnehmende Tendenz.
3) Der Dominanz-Index zeigt steigende Tendenz.
4) Die Veränderung des Artenbestandes wird durch die Abnahme der segetalen Arten und die Zunahme der Nadelwald-Arten gekennzeichnet.
5) Die qualitativen und quantitativen Strukturmerkmale werden allmählich stabilisiert.

INTRODUCTION

Succession is a directional and irreversible process in which different phytocoenoses follow each other, and as such it has always belonged to the most discussed and studied phytosociological problems. Information on the direction and rate of changes in plant communities is found in most of geobotanical papers. Unfortunately, only some of them concern dynamics of the phytocoenose structure, although it enables us to understand the principles of plant aggregation and formation of phytocoenotic systems.

Investigations presented in this paper comprise detailed analysis of changes in the phytocoenose structure in the early phases of regenerative succession of *Peucedano-Pinetum* Mat. (1962) 1973 pine forest. The analysis has been carried out on the example of a simple model object - spontaneously overgrowing old fields of different age, located in the same habitat near each other. Common origin of the compared systems, nearly identical environmental conditions and 3 years' study were to minimize a risk of erronous conclusions on changes in time which have been made on the grounds of changes in space.

Some qualitative and quantitative characteristics of the phytocoenose structure have been taken into account, such as: number of species, floristic composition, state, species structure and spatial structure of aboveground plant biomass, minimum area size, and species diversity - measured by means of indices: species richness (d), total diversity (Shannon's index H), evenness (J) and dominance (C), as well as a number of positive and negative interspecific associations.

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The studies have aimed at answering the following questions:
1) whether changes in the individual structure elements of phytocoenoses in the course of their succession are directional and linear, or wave-like, only with a tendency for directional changes;
2) whether decrease in the total diversity of the phytocoenose followed by decrease in stability reflects succession progress;
3) whether in the course of succession the number of positive or negative associations between individual species populations increases.

STUDY SITE

The field study was conducted at the southwestern edge of Białowieża Primeval Forest (Poland) within its historical XVI century borders. In the second part of the XVI century, forests were partly cut down and replaced by arable fields. The process of village abandonment and reinvasion by forest into deserted fields started in 1917. According to FALIŃSKI (1980) a final community - *Peucedano-Pinetum* (1962) 1973 pine forest - developed in a series of 8 phases over the 70 years after cultivation was stopped.

The vegetation of four old fields (6, 10, 16 and 25 years old) was chosen for the studies. In this paper old fields were denoted I, II, III and IV, and these respectively correspond to phases 3, 4, 5 and 6 in the classification of FALIŃSKI (1980). Their short descriptions can be found in Table 1.

DATA COLLECTION AND ANALYSIS

Analysis of the species composition and biomass state was carried out in July of 1980-1982. Biomass samples were collected - 100 each year and in each old field - in a grid of shifted 1 m² squares; the middle of each square marked the middle of a 0.1 m² circle, where all above-ground plant parts were cut down. Plant material was segregated, dried at 105 °C for 48 h and weighed with an accuracy of 0.001 g. Only crisp and fragile thalli of lichens were treated jointly. In the old fields II-IV, big juniper specimens which grew above herb vegetation were not included in the biomass analysis.

The following indices were computed on the grounds of floristic composition, total biomass value in each point of the study area, mean total biomass value and mean biomass value of individual species (both for the unit area 0.1 m²):

1) coefficients of community similarity with respect to the floristic composition (G_p) and biomass state (G_m) (ELLENBERG 1956);
2) species richness index (b) (MENHINICK 1966);
3) total diversity index (H) (WHITTAKER 1977);
4) evenness index (J) (PIELOU 1966a);
5) dominance index (C) SIMPSON 1949).

Furthermore, interpolation maps were charted and serve to assign a type of the spatial biomass structure.

The criterion which provides a basis for the compution of diversity indices has to be discussed. Indeed, according to WHITTAKER (1965) the best measure of species importance in the phytocoenose is its production, but on account of high labour requirement of the production assessment its equivalent, the standing biomass of individual populations, has been used. This reflects the species importance in a phytocoenose much better than the population abundance (DICKMAN 1968, WIHLM 1968, TRAMER 1975). It is worth noting that WHITTAKER (1965) has proved high correspondence of the results when criteria of standing biomass state and biomass production were used.

The minimum area size of phytocoenoses compared was determined according to CALLÉJA's method (CALLÉJA 1962) modified by MATUSZKIEWICZ & WYDRZYCKA (1972), using random sampling within a permanent area of 64 m² divided into 256 basic units (each of 0.25 m²). In the same areas data on interspecific associations were collected. The analysis was performed using qualitative data by means of χ^2 independence test. All the species with a frequency higher than 95% and lower than 5% were excluded.
In all the statistical tests 5% error risk was used.

Table 1. Description of vegetation and soils in the I-IV old fields in the first year of studies

Characteristics \ Old field	I	II	III	IV
Age /years/	6	10	16	25
Community physiognomy	herb vegetation sod; one-layered community; juniper starts to settle down	the first juniper specimens grow above herb vegetation sod	two-layered community; juniper forms shrub layer	two-layered community; juniper and pine form shrub layer; high contribution of mosses and lichens
Plant cover /%/:				
total	95	90	60	95
vascular plants	80	75	45	20
mosses and lichens	15	20	15	85
Number of taxons	39	30	22	27
Dominants in respect of biomass	Hieracium pilosella	Hieracium pilosella	Polytrichum piliferum	Polytrichum piliferum
Soils:				
pH /in H_2O/	5.0	5.1	4.7	4.5
humus /%/	1.52	1.49	1.11	1.34
C /%/	0.88	0.86	0.65	0.78
exchangeable cations /mg/100g of soil/:				
Ca^{++}	0.24	0.14	0.07	0.06
Mg^{++}	0.016	0.008	0.005	0.041
K^{+}	0.08	0.05	0.03	0.04
Na^{+}	0.016	0.016	0.021	0.016
hydrolitic acidity	7.15	7.15	6.51	6.77

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RESULTS

Comparison of the phytocoenoses in the consecutive years and phases of succession indicates significant qualitative and quantitative transformations of the structure characteristics.

The floristic composition is subject to significant directional changes. Only 14 taxa (i.e. 35.9% of the total number of 39 taxa) noted in the youngest old field in the first year of studies survived till the end of period analyzed. These are: *Hieracium pilosella* L., *Corynephorus canescens* (L.) P.B., *Festuca rubra* L., *Artemisia vulgaris* L., *Agrostis tenuis* Sibth., *Hypericum perforatum* L., *Achillea millefolium* L., *Jasione montana* L., *Centaurea stoebe* L., *Rumex acetosella* L., *Scleranthus perennis* L., *Juniperus communis* L., *Polytrichum piliferum* Schreb. and *Cladonia* sp. A group of species which retreat in the course of succession comprised mostly field weeds which are gradually replaced by pine forest plant species (Table 2 and 3).

Table 2. List of the species retreating in the course of succession

Species	Old field /I - IV/ and year of succession										
	I			II			III			IV	
	6	7	8	10	11	12	16	17	18	25	26
Helichrysum arenarium /L./ Moench	+	+	+	+	+	+	+	+	+	+	+
Solidago virgaurea L.	+	+	+	+	+	+	+	-	-	-	-
Convolvulus arvensis L.	+	+	+	+	+	+	+	-	-	-	-
Holcus mollis L.	+	+	+	+	+	+	+	-	-	-	-
Knautia arvensis /L./ Coult.	+	+	+	+	+	+	-	-	-	-	-
Euphrasia stricta Wolff ex Lehm.	+	+	+	+	+	+	-	-	-	-	-
Euphorbia esula L.	+	+	+	+	+	+	-	-	-	-	-
Oenothera biennis L.	+	+	+	+	+	+	-	-	-	-	-
Viola tricolor L.	+	+	+	+	+	+	-	-	-	-	-
Chamaecytisus ratisbonensis /Schaeff./ Rothm.	+	+	+	+	+	+	-	-	-	-	-
Hypochoeris radicata L.	+	+	+	+	+	+	-	-	-	-	-
Cerastium semidecandrum L.	+	+	+	+	+	-	-	-	-	-	-
Erigeron acris L.	+	+	+	+	-	-	-	-	-	-	-
Linaria vulgaris /L./ Mill.	+	+	+	-	-	-	-	-	-	-	-
Agrostis stolonifera L.	+	+	-	-	-	-	-	-	-	-	-
Anchusa officinalis L.	+	+	-	-	-	-	-	-	-	-	-
Anthyllis vulneraria L.	+	+	-	-	-	-	-	-	-	-	-
Filago arvensis	+	+	-	-	-	-	-	-	-	-	-
Lupinum luteus	+	+	-	-	-	-	-	-	-	-	-
Medicago falcata L.	+	+	-	-	-	-	-	-	-	-	-
Silene otites /L./ Wibel	+	-	+	-	-	-	-	-	-	-	-
Cynoglossum officinale L.	+	-	-	-	-	-	-	-	-	-	-
Thlaspi arvense L.	+	-	-	-	-	-	-	-	-	-	-
Lotus corniculatus L.	+	-	-	-	-	-	-	-	-	-	-

Table 3. List of the species encroaching in the course of succession

Species	Old field /I - IV/ and year of succession									
	I	II			III			IV		
	8	10	11	12	16	17	18	25	26	27
Thymus serpyllum L.	+	+	+	+	+	+	+	+	+	+
Calluna vulgaris /L./ Hull	-	-	+	+	+	+	+	+	+	+
Spergula morisonii Boreau	-	-	-	-	+	+	+	+	+	+
Holcus lanatus L.	-	-	-	-	+	-	+	+	+	+
Astragalus arenarius L.	-	-	-	-	-	-	+	+	+	+
Cetraria islandica /L./ Ach.	-	-	-	-	-	-	+	+	+	+
Cornicularia aculeata /Schreb./ Ach.	-	-	-	-	-	-	-	+	+	+
Nardus stricta L.	-	-	-	-	-	-	-	+	+	+
Pteridium aquilinum /L./ Kuhn.	-	-	-	-	-	-	-	+	+	+

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From the distribution of floristic similarity coefficients it may be shown that the rate of qualitative changes, very high at first, gets lower with time. The system attains relative stability 24 years after cultivation was given up. Mutual similarity of the phytocoenoses compared (biomass contribution of individual populations) is much higher (not lower than 70%), whereas the change rate - at first minimal - grows only in the last three years (Fig. 1).

Differences in the values and distributions of similarity coefficients, using qualitative (species presence) and quantitative (contribution of their biomass) criteria, are fully understandable. In spite of significant changes in the floristic composition in the course of succession, 92.5% - 82.7% of the total biomass is contributed by the same species group. Within this group, *H. pilosella* gradually looses its status as dominant in favour of *P. piliferum* (Fig. 2).

In the analyzed series of communities the same aggregated type of spatial biomass structure holds on. This is evident both in the period of very low and very high biomass state (Fig. 3). Instead, the intensity of the structure changes, i.e. degree of contrast between the densed aggregation zone and the thinning zone which separates individual aggregations. Histograms of the distribution of biomass per unit area illustrate the course of changes in a simple way. In 6-17 years of succession simplification of the structure takes place, i.e. decrease in the number of biomass classes and consequently decrease in the degree of clustering occur. After 18-27 years the number of the classes increases, thereby intensity of the spatial biomass structure grows again (Fig. 4).

The course of changes in the other quantitative parameters of phytocoenose structure is also non-linear (Fig. 5). The more advanced the successional process, the smaller the fluctuations of their values. These fluctuations do not depend directly (except species richness index) on changes in the number of species that build up a phytocoenose. Generally, in the course of succession studied, some clear tendency for directional changes occurs - decrease in the minimum area size, value of species richness index, value of total diversity index and value of evenness index, as well as decrease in the value of the dominance index.

On the other hand, part of the intrinsic integration of phytocoenose (expressed as per cent rate of the significant interspecific associations to the total number of theoretically possible associations) is subject to non-directional changes. In the period under study, the per cent of positive associations is higher than that of negative. Still, in both cases high oscillations from year to year have been observed, independent of the succession phase. Lack of negative interspecific associations in the youngest old field in the first year of studies is worth noting (Fig. 5).

DISCUSSION

The results testify to the high dynamics of phytocoenose structure in the course of succession. However, only floristic composition undergoes linear changes, the direction of which is determined from the beginning. Replacement of weeds by pine-forest plants indicates unequivocally that a ground layer of the final forest community is formed.

For a dozen or so years of the analyzed series, the number of species characteristic of early phases of secondary succession decreases (ODUM 1969, SHAFI & YARRANTON 1973, NICHOLSON & MONK 1974, BAZZAZ 1975, HOUSSARD, ESCARRÉ & ROMANE 1980). It probably results from continuing soil depletion preceded by mineralization of the arable layer (QUARTERMAN 1957), as well as intensification of the competition between species which colonize new old fields in mass (WERNER 1976, GROSS 1980). After 24 years of succession the number of species increases gradually.

Fluctuations in total standing biomass, which run similarly to fluctuations in the number of species (to some extent), depend on transformation of the phytocoenose floristic composition. Instead, changes in the phytomass of the populations of constant components of communities under study and quantitative relationships within the group of dominants determine them. After 25-27 years of succession, the value of the analyzed ground-layer biomass does not vary essentially from the ground-layer biomass of the other moist pine forests (*Vaccinio myrtilli-Pinetum* Kobendza 1930, Tüxen, Vliegert 1959) at the climax stage, in a similar climatic region (DĄBROWSKI

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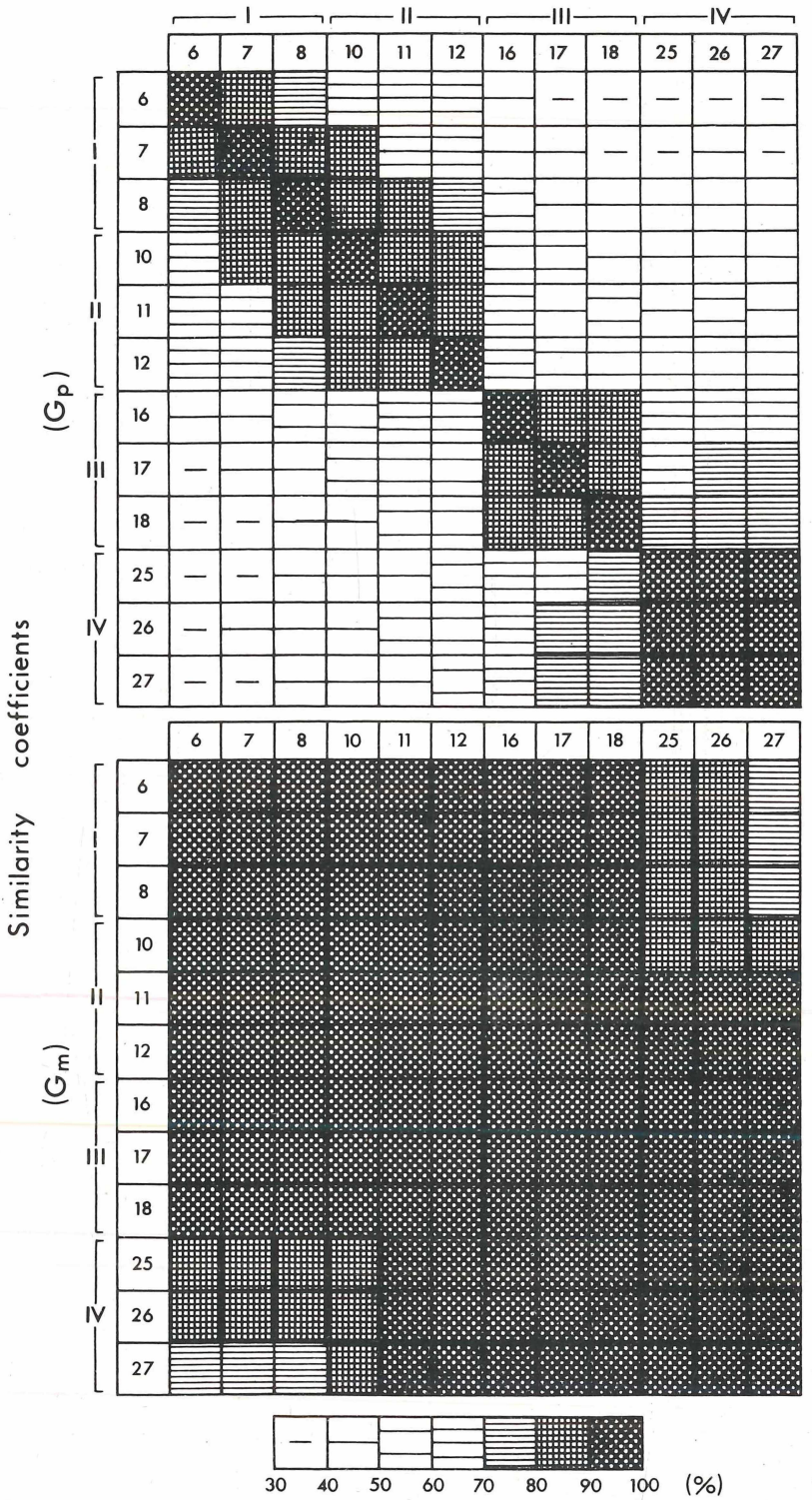


Fig. 1: Distribution of similarity coefficients of phytocoenoses in the course of their succession.
G_p - similarity coefficient in respect of presence
G_m - similarity coefficient in respect of biomass.

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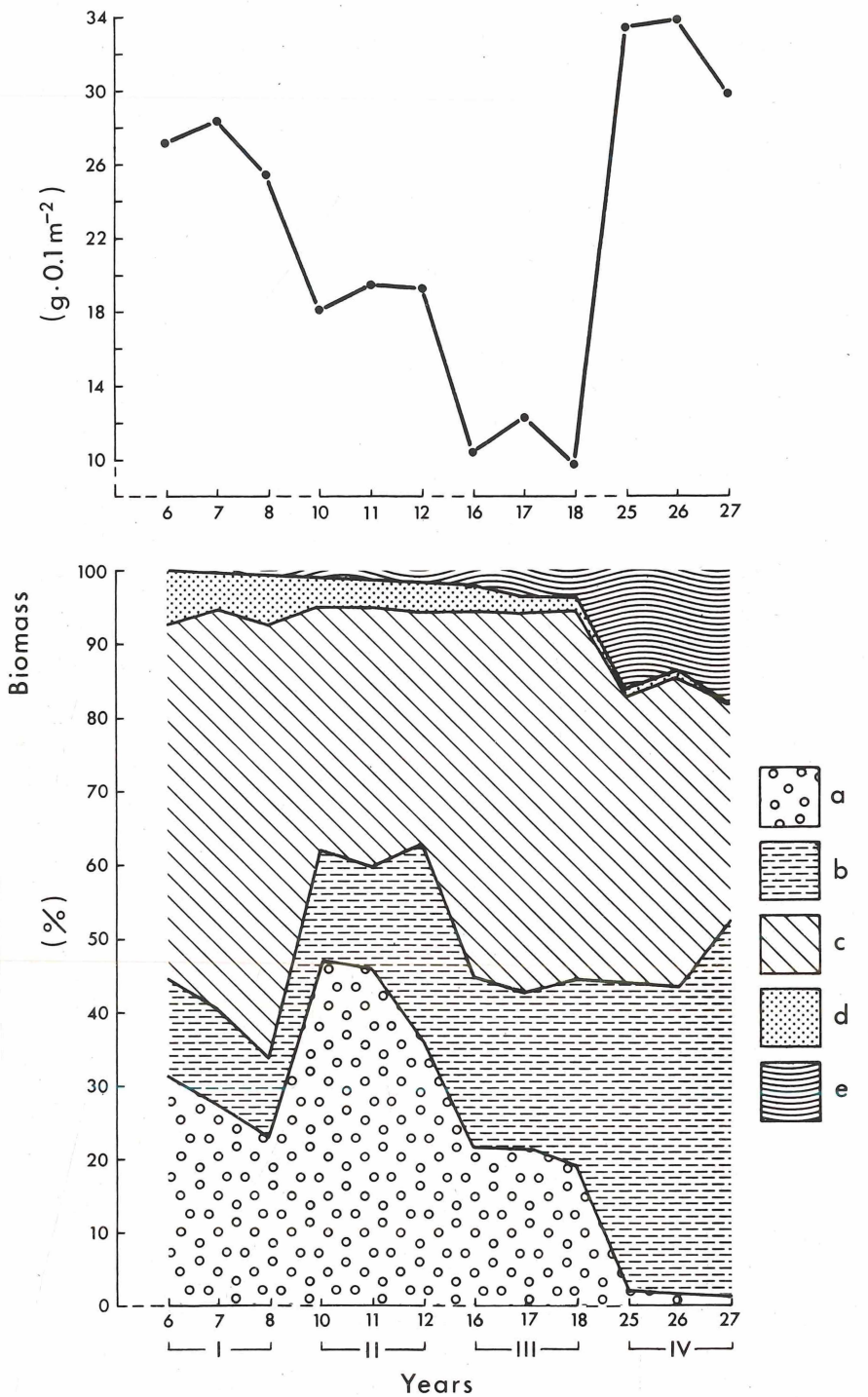


Fig. 2: Changes in biomass state (top) and species structure of biomass (bottom) in the course of phytocoenose succession.
a) *Hieracium pilosella*, b) *Polytrichum piliferum*,
c) group of constant species excluding dominants,
d) group of retreating species,
e) group of encroaching species.

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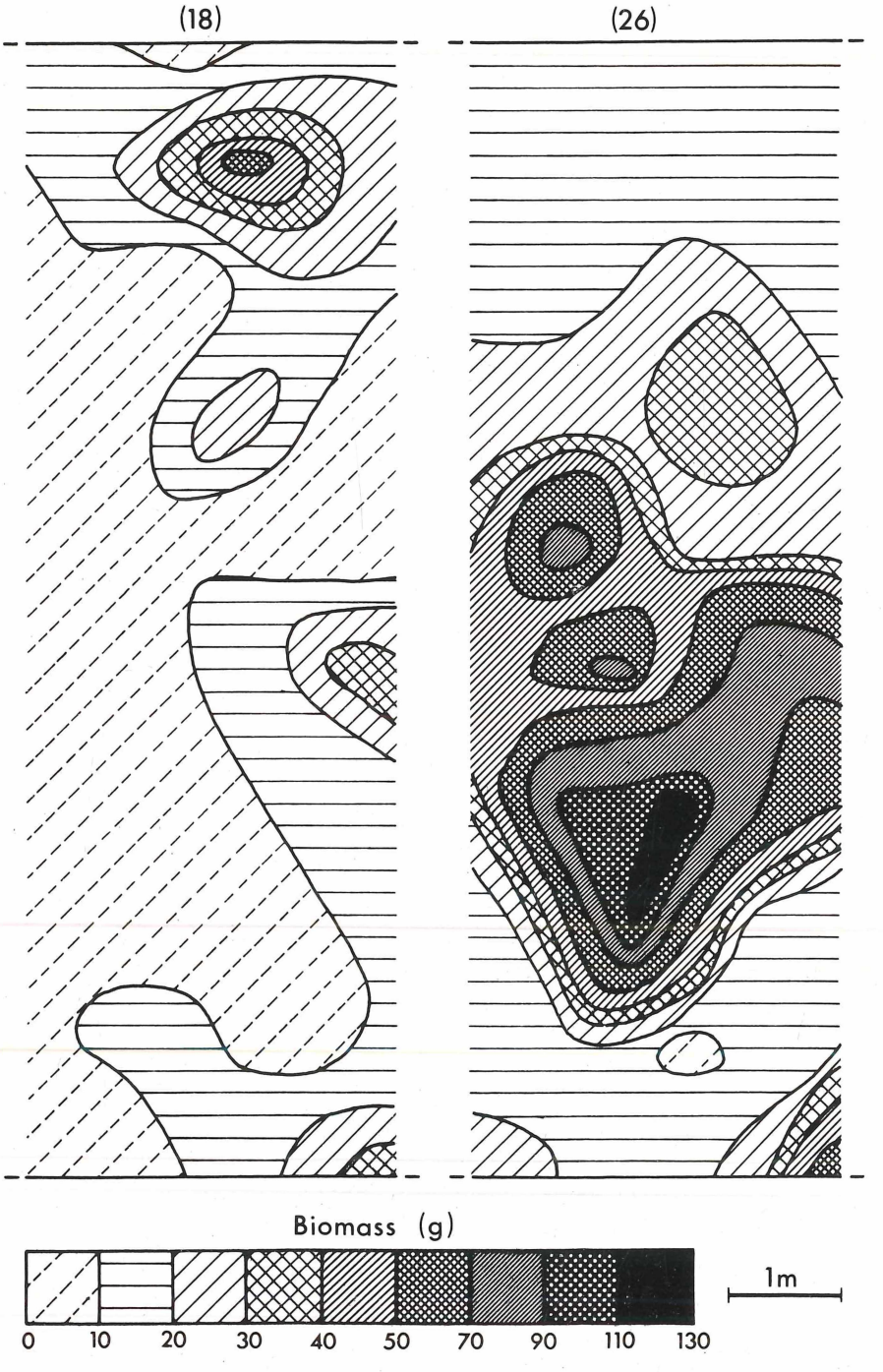


Fig. 3: Spatial biomass structure in year 18 (the lowest biomass state) and year 26 (the highest biomass state) of phytocoenose succession (fragment of the interpolation charts).

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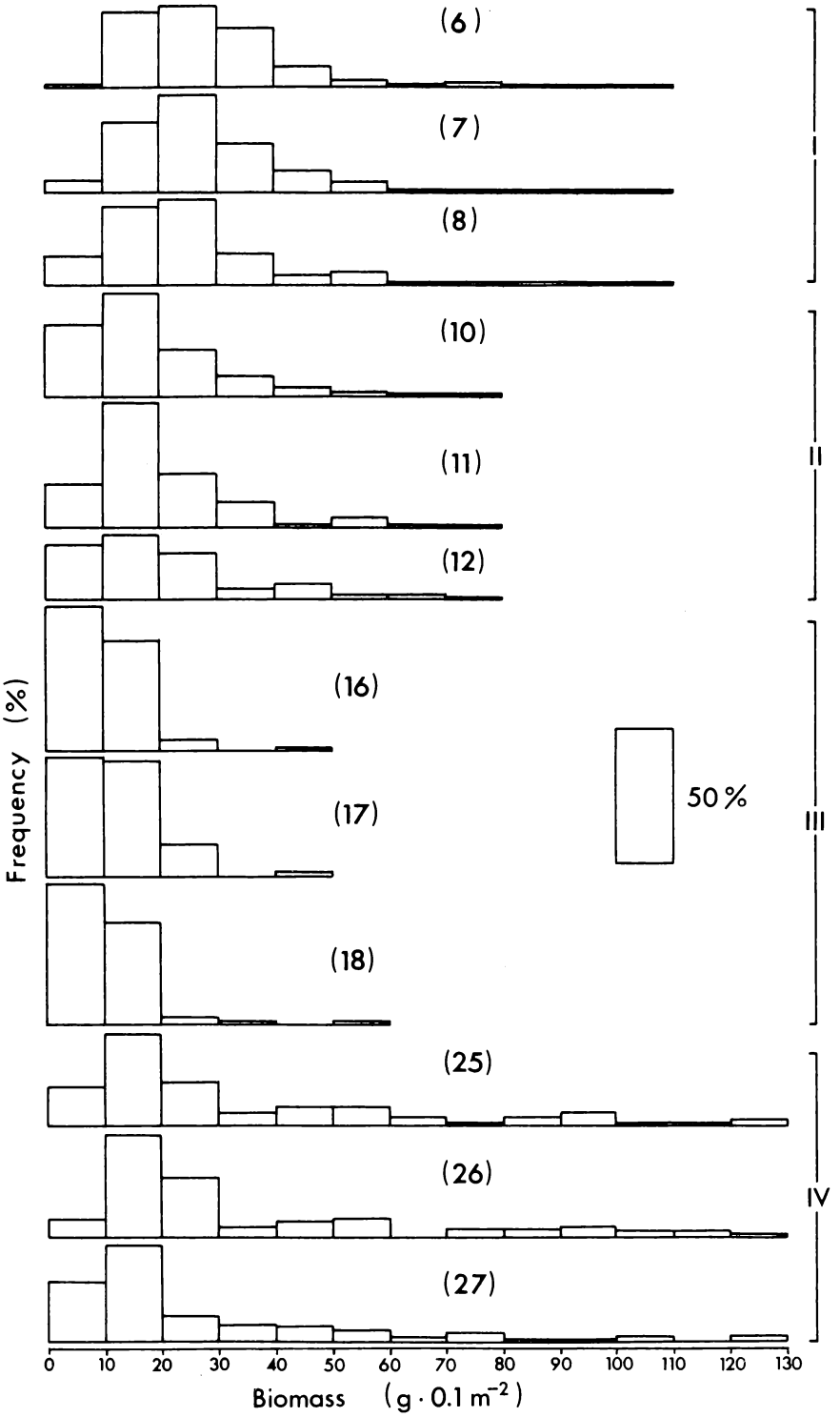


Fig. 4: Changes in biomass distribution in the consecutive years of phytocoenose succession.

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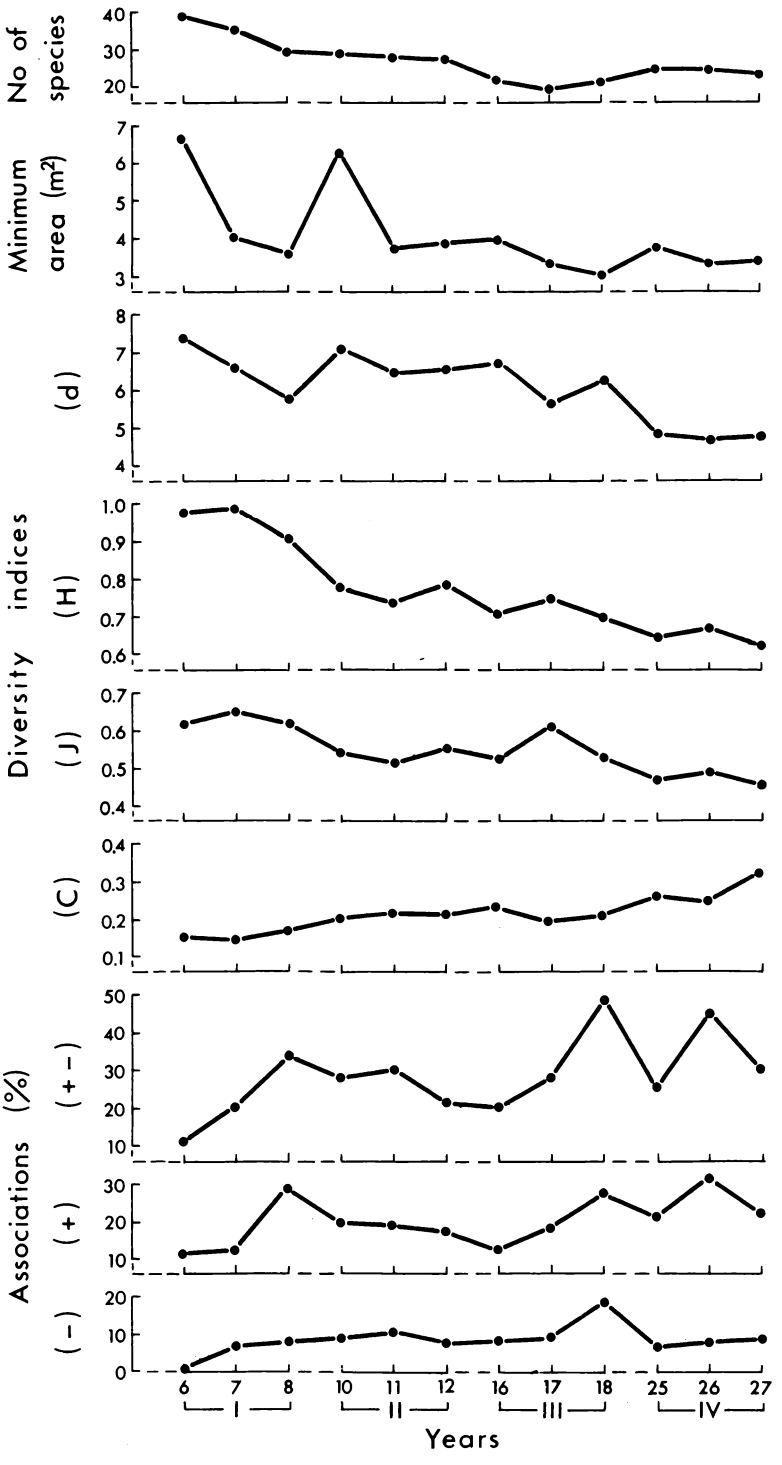


Fig. 5: Changes in some structure characteristics of phytocoenoses in the course of their succession.
Diversity indices: *d)* species richness index, *H)* total diversity index, *J)* evenness index, *C)* dominance index.

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1953, PUSZKAR, TRACZYK & WÓJCIK 1972). Given this, it may be concluded that after 25 years of succession the state of ground-layer biomass does not undergo significant changes; probably the contribution of sporogenous plants also does not change in substance.

Changes in the intensity of biomass spatial structure run in a similar direction as changes in the biomass state. Similarity of the biomass spatial distributions in the youngest and oldest old fields makes it very doubtful that biotope heterogeneity significantly affects formation of the plant aggregations within biochores (KERSHAW 1958, GREIG-SMITH 1961a, 1961b, HARPER, WILLIAMS & SAGAR 1965, BOORMAN & SICCAMA 1970). The degree of microhabitat diversification, low just after the cultivation was dropped, increases undoubtly with the old-field age. However, in the many-species phytocoenoses, simple correlation between the spatial structure of biomass and any soil factor does not exist (cf. KWIATKOWSKA 1978). From the results it may be inferred that growth forms of the plants dominating, with respect to their biomass state and interspecific associations, are superior to the spatial diversification of soil parameters. Still detailed studies are needed to solve this problem further.

In the course of succession the size of the minimum area (representative area) of the phytocoenose and its species diversity change considerably less regularly than the list and number of species. This problem has not been considered in a dynamic aspect till now, so it can not be discussed more widely. On the other hand, scanty data indicate that the minimum area of the forest ground layer is a dozen or so m² (CALLEJA 1962, MATUSZKIEWICZ & WYDRZYCKA 1972), that is much bigger than for the phytocoenoses under study. Probably, in the oldest old field in the further successional phases, the size of the representative area of phytocoenose will increase again.

During the analyzed period, the species diversity of the phytocoenose increases and decreases many times, similarly to changes in the minimum area size. However, the tendency for reduction of diversity with succession is beyond any doubt. Therefore, the author's results confirm results of others (ODUM 1969, SHAFI & YARRANTON 1973, NICHOLSON & MONK 1974, BAZZAZ 1975) but also stress the fluctuating and non-linear nature of diversity.

The problems of diversity of ecological systems and its proper measurement have been widely discussed (CONNELL & ORIAS 1964, PIANKA 1966, PIELOU 1966a, 1966b, HULBERT 1971, HILL 1973, MAY 1975, WHITTAKER 1977, ROUTLEDGE 1979, HUTCHINGS 1983). In most empirical papers, diversity indices are used interchangeably, although each has a different importance value.

The species richness index *(d)* characterizes a system as a whole and does not concern relationships between its components. On account of its mathematical formula, it is particularly sensitive to changes in the species number and, to a lesser extent, biomass state. That is why, in the three-year study period, a large decrease in the *d*-index value occurs in old field I (decrease in the species number, small oscillations in the biomass state), whereas in old field IV (nearly the same number of species, relatively high variations of the biomass state) practically no changes take place.

The total species diversity index *(H)* is generally accepted as the best diversity measure because it considers both species richness of the phytocoenose and evenness of the resource division between the populations of individual species (WHITTAKER 1977). The stronger the dominance of the first or several first species and the more the species with very small importance values (on account of a chosen criterion), the lower the index value. Relatively high *H* value in the earliest phase of a period under study results from presence of a large group of species with similar biomass state, as well as relatively few species with low importance values. Increase in the contribution of the last group of species causes (in 10-18 years of succession) decrease in the total diversity index value. Further reduction in the last three years is due to a rapid increase in the biomass state of dominants, especially *Polytrichum piliferum*.

On the contrary, the evenness index *(J)* value to a large extent depends upon the number of species that build up the community. Therefore the evenness curve deviates the most from the curve of total diversity in the early successional phases (old fields I and II), when relatively large changes in the number of species occur.

Whereas the *H* index value is determined mainly by the importance of species placed in the middle part of the series ordered according to the indices

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of species importance, the value of the dominance index *(C)* depends mostly on the importance of the first species or the first species group. The latter is lowest in the first three years, when predominance of the absolute dominant, *Hieracium pilosella*, is relatively weak, and highest in the last three years due to pronounced dominance of *Polytrichum piliferum*.

From the considerably smaller oscillations of most structure parameters in old field IV than in old field I and II, it can be inferred that stability of the phytocoenose structure increases in the course of succession, in spite of decrease in the number of species (cf. McNAUGHTON 1978, PIMM 1979). On the other hand the spatial relationships between individual species are unstable in the whole analyzed period. Irrespective of the successional phase the per cent of significant positive and negative associations fluctuates over a wide range. The nature and strength of the associations between individual species pairs, as well as the configuration of associated species, also varies. This problem is to be analyzed in a different paper.

Summing up, the questions in the introduction can be answered as follows:
1) in the course of succession most structure parameters change wave-like and not linearly, except floristic composition;
2) decrease in the total diversity of the phytocoenose and at the same time increase in the stability of synthetic structure indices testify to the successional progress;
3) in the early phases of succession a weak tendency for increase in the number of interspecific associations, positive as well as negative, occurs.

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