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FLORISTIC RICHNESS, DIVERSITY, DOMINANCE AND SPECIES EVENNESS IN OLD-FIELD SUCCESSIONAL ECOSYSTEMS

ABSTRACT: The floristic composition of plant communities, their species richness, total diversity, evenness and dominance were studied in four uneven-aged old-fields (a Peucedano-Pinetum forest habitat) for three successive years. In the course of succession of the phytocoenoses the following were observed: (1) continuous directional changes in specific composition, (2) fluctuations of the values of the quantitative indices of structure, with a tendency towards lower levels of the indices of species richness, total diversity and evenness, a growth of the dominance index, (3) a fall of the rate of changes in the qualitative and quantitative structure characteristics, (4) a growing resistance of the communities to variable weather conditions.

KEY WORDS: Old-field succession, total diversity, evenness, dominance, species richness, floristic similarity, above-ground biomass, importance values of species.

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1. INTRODUCTION

The term "phytocoenosis structure", like the term "biocoenosis structure", covers a number of quantitative and qualitative features of the system, e.g., the list of species and their number, spectrum of living forms, size of minimum area, vertical and horizontal type of spatial distribution of vegetation (M a a r e l 1970, M ü l l e r 1970, T ü x e n 1970, K w i a t k o w s k a 1978). Many structure features of phytocoenoses can be specified precisely by means of indices characterizing the community as a whole and/or the relations between its components. These include, among other things, indices of species richness, similarity and diversity, calculated from frequency, density, and abundance or biomass of the populations of the particular species (P i e l o u 1966a, 1966b, W h i t t a k e r 1972, 1977, P e e t 1974, 1975, T e p e d i n o and S t a n t o n 1980).

Phytosociological papers as a rule take into account only a few of the structure features of phytocoenoses, and describe them with a varying accuracy and according to different criteria, which makes comparisons practically impossible. The weak point of these papers is that they provide a static, that is, made only once, description of the structure of phytocoenoses that are usually fully developed, whereas papers concerned with succession contain general data on the direction and rate of community changes. For this reason very little is known about the formation and structure dynamics of phytocoenoses.

The aim of the present study is to analyse changes in several structure elements of phytocoenoses in the course of a regenerative succession. The features studied included the number of species and floristic composition, as well as species richness (= species diversity), total diversity, evenness and dominance; the quantitative indices of the structure of phytocoenoses were calculated from the biomass of the above-ground plant parts. On account of the aim the object of the study was a simple, model object — uneven-aged old-fields located close to one another in the same type of habitat. The common origin of the systems compared and the almost identical environmental conditions were expected to minimize the risk of erroneous conclusions on temporal changes drawn from spatial changes. Another element diminishing the risk of error was the repeating of the analysis for three successive years, thereby keeping track also in a direct way — in addition to indirect inferring — of changes in the phytocoenoses. Furthermore, the three years' series of studies was expected to show a possible effect of weather conditions on the community structure at different stages of succession.

This paper is the first publication of a proposed series devoted not only to formal descriptions of the particular structure elements of phytocoenoses in a successional series, but also to the causes responsible for the direction and rate of changes, and to the results they bring about in the biotope.

2. STUDY AREA AND OBJECTS

The investigations were carried out at the south-western edge of the Białowieża Primeval Forest within its historical boundaries of the 16th century. As a result of an

intensified settlement in the second half of that century, the forests had partially been dug up and turned into arable fields (Wiśniewski 1964). After nearly 300 years of cultivation, from 1917 to the middle 70s the local population left the villages, and in the abandoned fields there started the process of a spontaneous secondary succession and a gradual return of the forest. According to Faliński (1980a), the final community – medium-moist Peucedano-Pinetum Mat. (1962) 1973 – forms there, about 70 years after the abandonment of cultivation, in a series consisting of eight successional phases.

Table I. Description of the vegetation and soil of old-fields I–IV in the first study year

Characteristics	Old-field			
	I	II	III	IV
Age (years)	6	10	16	25
Community physiognomy	herbaceous sward; single-layered community; juniper beginning to settle	first juniper specimens growing out of the herbaceous sward	two-layered community; shrub layer made up of juniper	two-layered community; shrub layer made up of juniper and pine; high percentage of mosses and lichens
Plant cover:				
total (%)	95	90	60	95
vascular (%)	80	75	45	20
mosses and lichens (%)	15	20	15	85
Number of species	39	30	22	27
Species dominant in respect of biomass	<i>Hieracium pilosella</i> , <i>Corynephorus canescens</i> , <i>Polytrichum piliferum</i>	<i>Hieracium pilosella</i> , <i>Corynephorus canescens</i> , <i>Polytrichum piliferum</i>	<i>Cladonia</i> sp., <i>Polytrichum piliferum</i> , <i>Corynephorus canescens</i>	<i>Polytrichum piliferum</i> , <i>Cladonia</i> sp.
Soils:				
pH (H ₂ O)	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 per 100 g 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
hydrolytic acidity (H)	7.15	7.15	6.51	6.77

The study covered the vegetation of four uneven-aged old-fields located near the road Jelonka-Kleszczele, about 2.5 km from the nearest human dwellings. The individual old-fields designated in the paper with I, II, III and IV represent the 3rd, 4th, 5th and 6th succession phase, respectively, as distinguished by F a l i ń s k i (1980a); the old-fields differ in vegetation properties and soil chemistry (Table I).

3. METHODS

The investigations presented in this paper were carried out in the years 1980–1982 during which the weather conditions in the plant growth period varied considerably (Table II). The species composition and biomass level were analysed in July when most of the species making up the communities were fully mature. Samples were collected

Table II. Description of weather conditions in the period of intensive plant growth and development (March–July)

The data have been received from nearest meteorological station in Białowieża

Characteristics	Month	Year		
		1980	1981	1982
Mean monthly air-temperature (°C)	March	−3.4	2.1	2.3
	April	6.4	5.2	6.0
	May	10.0	15.6	14.9
	June	16.7	18.1	16.0
	July	17.2	19.5	19.3
Maximum air-temperature (°C)	March	0.3	6.0	6.7
	April	10.6	10.2	10.7
	May	13.9	20.1	19.1
	June	20.5	22.3	19.8
	July	20.9	23.9	23.1
Minimum air-temperature (°C)	March	−8.1	−2.3	−2.3
	April	0.3	−1.6	0.1
	May	2.6	7.6	7.5
	June	10.2	11.2	8.1
	July	12.4	12.2	11.7
No. of days with mean circadian temperature $\geq 15^{\circ}\text{C}$	March	0	0	0
	April	0	0	0
	May	4	20	16
	June	22	23	16
	July	24	31	31
Total monthly precipitation (mm)	March	29.2	52.7	15.5
	April	49.3	19.8	30.5
	May	49.7	85.6	104.8
	June	108.7	64.2	58.4
	July	200.7	86.9	57.1

systematically over a grid of 100 shifted squares 1 m in side length; the centre of a square was at the same time the centre of a circle 0.1 m² in area, from which all above-ground parts of plants were cut off just above the soil surface. The plant material was sorted by species, dried at 105°C for 48 hours and weighed with an accuracy to the nearest 0.001 g; in the particular samples only the thalli of lichens of the genus *Cladonia* were treated jointly.

For each old-field the average biomass per 0.1 m² was calculated. The zero hypothesis of absence of significant differences between the means in the particular years was verified at the $\alpha = 0.05$ level of significance.

The floristic composition of the communities in successive years and succession phases was compared by using the coefficient of commonness (G_p) proposed by Ellenberg (1956):

$$G_p = \frac{P_c}{P_a + P_b + P_c} \cdot 100 (\%)$$

where P_c – number of species common to both communities (or to two successive years), P_a – number of species present only in one community (or in one year), P_b – number of species present only in the other community (or in the other year).

Species richness (= species diversity) of the communities was evaluated by the index (d):

$$d = \frac{S}{\sqrt{B}}$$

where S – number of species in the community, B – total biomass value per 0.1 m² area (Menhick 1964).

In a further elaboration of the results the importance values of the populations of individual species in the systems compared were calculated, the importance value being the ratio of the mean biomass of a species to the mean biomass of all species in a unit of area (0.1 m²). The distribution of the importance values has been presented graphically in a semilogarithmic scale, and the curves thus obtained have been interpreted according to Whittaker's (1965) method.

From the values of importance the following indices have been computed:

(1) Shannon's total diversity index (H'):

$$H' = - \sum \left(\frac{n_i}{N} \right) \log \left(\frac{n_i}{N} \right)$$

where n_i – importance value of each species, N – total of importance values (Whittaker 1977);

(2) Evenness index (J):

$$J = \frac{H'}{\log S}$$

where H' – Shannon's index, S – number of species in the sample for which H' is being evaluated (Pielou 1966a);

(3) Dominance index (C):

$$C = \sum \left(\frac{n_i}{N} \right)^2$$

where n_i — importance value of each species, N — total of importance values (S i m p s o n 1949).

4. RESULTS

In the course of a regenerative succession the floristic composition of the old-field vegetation undergoes significant changes. Only 35.9% of the species recorded in the youngest old-field (I) in the first study year persisted till the end of the period analysed. The list included: *Hieracium pilosella* L., *Corynephorus canescens* (L.) P. B., *Festuca rubra* L., *Agrostis vulgaris* With., *Hypericum perforatum* L., *Achillea millefolium* L., *Artemisia vulgaris* L., *Rumex acetosella* L., *Juniperus communis* L., *Jasione montana* L., *Centaurea rhenana* Bor., *Scleranthus perennis* L., *Polytrichum piliferum* Schreb. and *Cladonia* sp. The group of species retreating with the passing time includes primarily field weeds which are gradually replaced by pine-forest species. The retreating of populations from the community composition is faster than the settling of new species, hence the number of species that made up the phytocoenosis in the last year of the successional series under study represented as little as 69% of the total number of species recorded in the first year (Table III).

The distribution of the commonness coefficient values (G_p) indicates that in the early phases of succession (years 6 — 10) changes in the species composition of the old-field vegetation are relatively fast; later on the rate of changes drops, a clear quantitative jump being only seen between the 12th and 16th year of regeneration of the forest community. Twenty-four years after the cessation of cultivation the system attained a certain degree of stability: during three consecutive years only one species disappeared from the floristic list of the community in old-field IV (Fig. 1, Table III).

Subject to significant temporal changes are the quantitative ratios between the vascular plant populations and cryptogamous plant populations. In old-field I the contribution of mosses and lichens to the total biomass of the phytocoenosis on an average represents only 18.2% and in old-field IV — as much as 78.6% (Fig. 2). The cause of this reversal of proportions is both a growth of the absolute value of the biomass of mosses and lichens and a decrease in the frequency and biomass of the populations of flowering plants present in the communities of the whole period analysed, and notably *Hieracium pilosella*, *Corynephorus canescens* and *Festuca rubra* (Fig. 3). The role of the decrease in the total number of vascular plant species is considerably less important, because their total biomass is very small.

The remaining quantitative structure parameters of the phytocoenosis: species richness, total diversity, evenness and dominance are subject to irregular fluctuations in the course of succession. Generally, the variation amplitude of the particular indices is greater in the early succession phases than in the last three years of the study period.

Table III. Changes in the species composition of the phytocoenoses in the course of succession*

Species	Old-field no., succession year											
	I			II			III			IV		
	6	7	8	10	11	12	16	17	18	25	26	27
<i>Helichrysum arenarium</i> (L.) Moench	+	+	+	+	+	+	+	+	+	+	+	-
<i>Solidago virga-aurea</i> L.	+	+	+	+	+	+	+	-	-	-	-	-
<i>Convolvulus arvensis</i> L.	+	+	+	+	+	+	+	-	-	-	-	-
<i>Holcus mollis</i> L.	+	+	+	+	+	+	+	-	-	-	-	-
<i>Knautia arvensis</i> (L.) Coult.	+	+	+	+	+	+	-	-	-	-	-	-
<i>Euphrasia brevipila</i> Burn. et Grem.	+	+	+	+	+	+	-	-	-	-	-	-
<i>Euphorbia esula</i> L.	+	+	+	+	+	+	-	-	-	-	-	-
<i>Oenothera biennis</i> L.	+	+	+	+	+	+	-	-	-	-	-	-
<i>Viola tricolor</i> L.	+	+	+	+	+	+	-	-	-	-	-	-
<i>Cytisus ratisobnensis</i> Dschaeff.	+	+	+	+	+	+	-	-	-	-	-	-
<i>Hypochoeris radicata</i> L.	+	+	+	+	+	+	-	-	-	-	-	-
<i>Cerastium semidecandrum</i> L.	+	+	+	+	+	-	-	-	-	-	-	-
<i>Erigeron acer</i> L.	+	+	+	+	-	-	-	-	-	-	-	-
<i>Linaria vulgaris</i> (L.) Mill.	+	+	+	-	-	-	-	-	-	-	-	-
<i>Agrostis alba</i> L.	+	+	-	-	-	-	-	-	-	-	-	-
<i>Anchusa officinalis</i> L.	+	+	-	-	-	-	-	-	-	-	-	-
<i>Anthyllis vulneraria</i> L.	+	+	-	-	-	-	-	-	-	-	-	-
<i>Filago arvensis</i> L.	+	+	-	-	-	-	-	-	-	-	-	-
<i>Lupinus luteus</i> L.	+	+	-	-	-	-	-	-	-	-	-	-
<i>Medicago falcata</i> L.	+	+	-	-	-	-	-	-	-	-	-	-
<i>Silene otites</i> (L.) Wib.	+	-	+	-	-	-	-	-	-	-	-	-
<i>Teesdalea nudicaulis</i> (L.) R. Br.	+	+	-	+	-	+	-	+	-	+	+	+
<i>Cynoglossum officinale</i> L.	+	-	-	-	-	-	-	-	-	-	-	-
<i>Thlaspi arvense</i> L.	+	-	-	-	-	-	-	-	-	-	-	-
<i>Lotus corniculatus</i> L.	+	-	-	-	-	-	-	-	-	-	-	-
<i>Thymus serpyllum</i> L.	-	-	+	+	+	+	+	+	+	+	+	+
<i>Calluna vulgaris</i> (L.) Salisb.	-	-	-	-	+	+	+	+	+	+	+	+
<i>Carlina vulgaris</i> L.	-	-	-	+	+	+	-	-	-	-	-	-
<i>Spergula vernalis</i> Willd.	-	-	-	-	-	-	+	+	+	+	+	+
<i>Holcus lanatus</i> L.	-	-	-	-	-	-	+	+	+	+	+	+
<i>Astragalus arenarius</i> L.	-	-	-	-	-	-	-	-	+	+	+	+
<i>Cetraria islandica</i> (L.) Ach.	-	-	-	-	-	-	-	-	+	+	+	+
<i>Cornicularia aculeata</i> (Schreb.) Ach.	-	-	-	-	-	-	-	-	-	+	+	+
<i>Nardus stricta</i> L.	-	-	-	-	-	-	-	-	-	+	+	+
<i>Pteridium aquilinum</i> (L.) Kuhn	-	-	-	-	-	-	-	-	-	+	+	+

*Another constant component of the phytocoenoses under study was a group of 14 species (see the text).

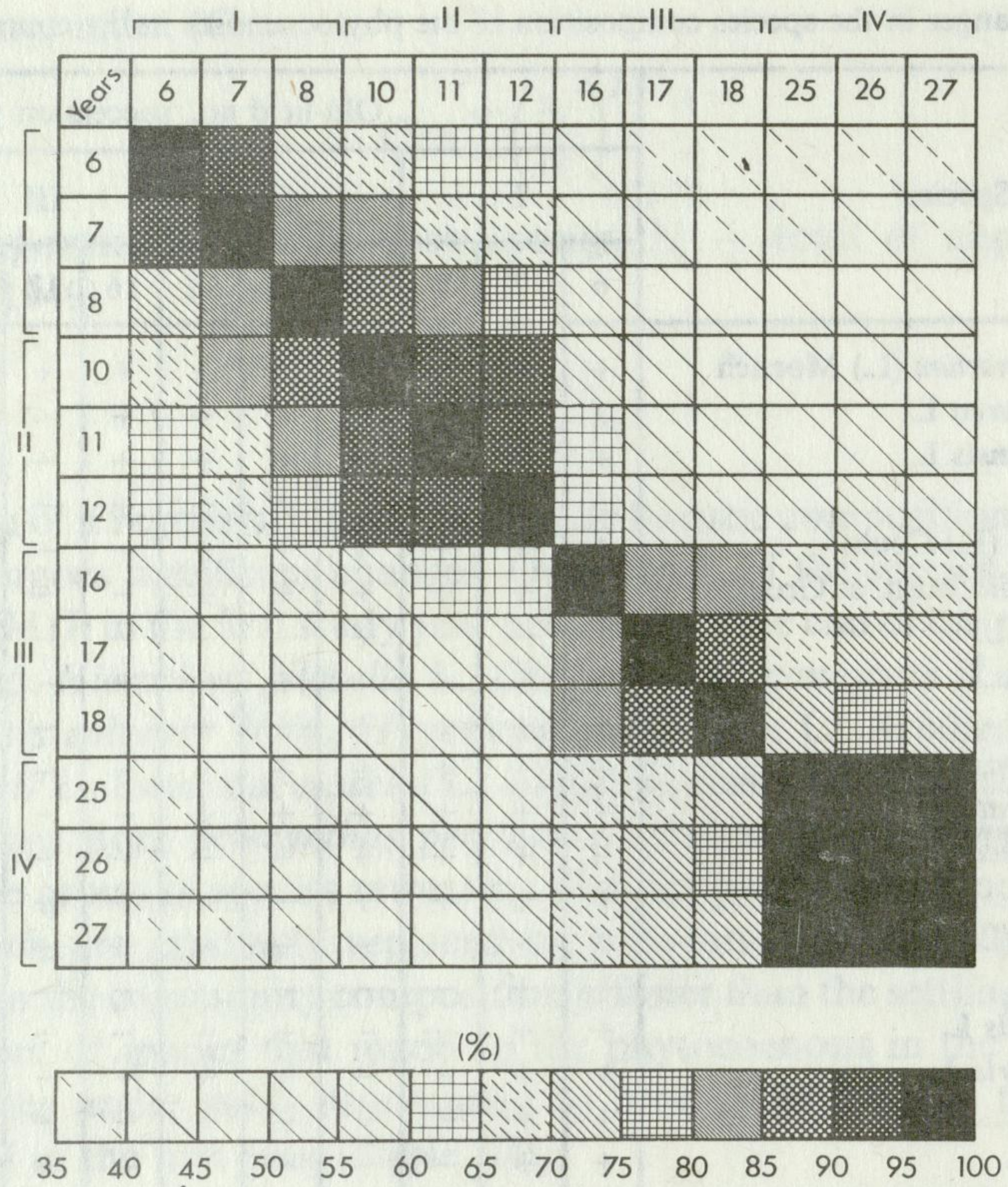


Fig. 1. Decrease of floristic-composition similarity of communities in the course of succession
Similarity index (G_d) calculated according to Ellenberg (1965)

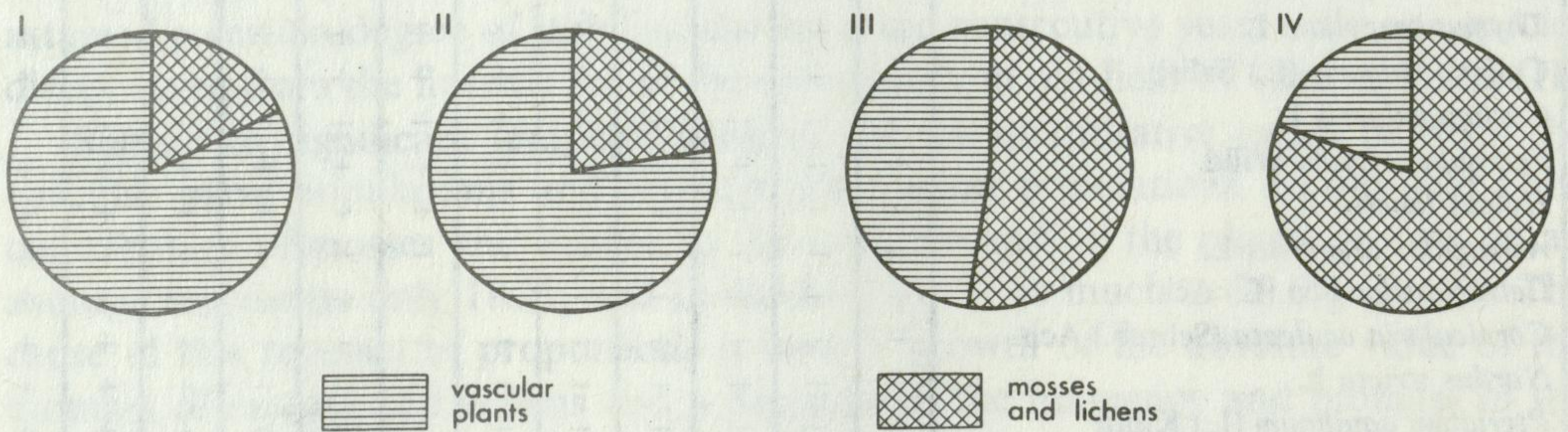


Fig. 2. Percentage of vascular plants, mosses and lichens in the total biomass of the communities in old-fields
I-IV

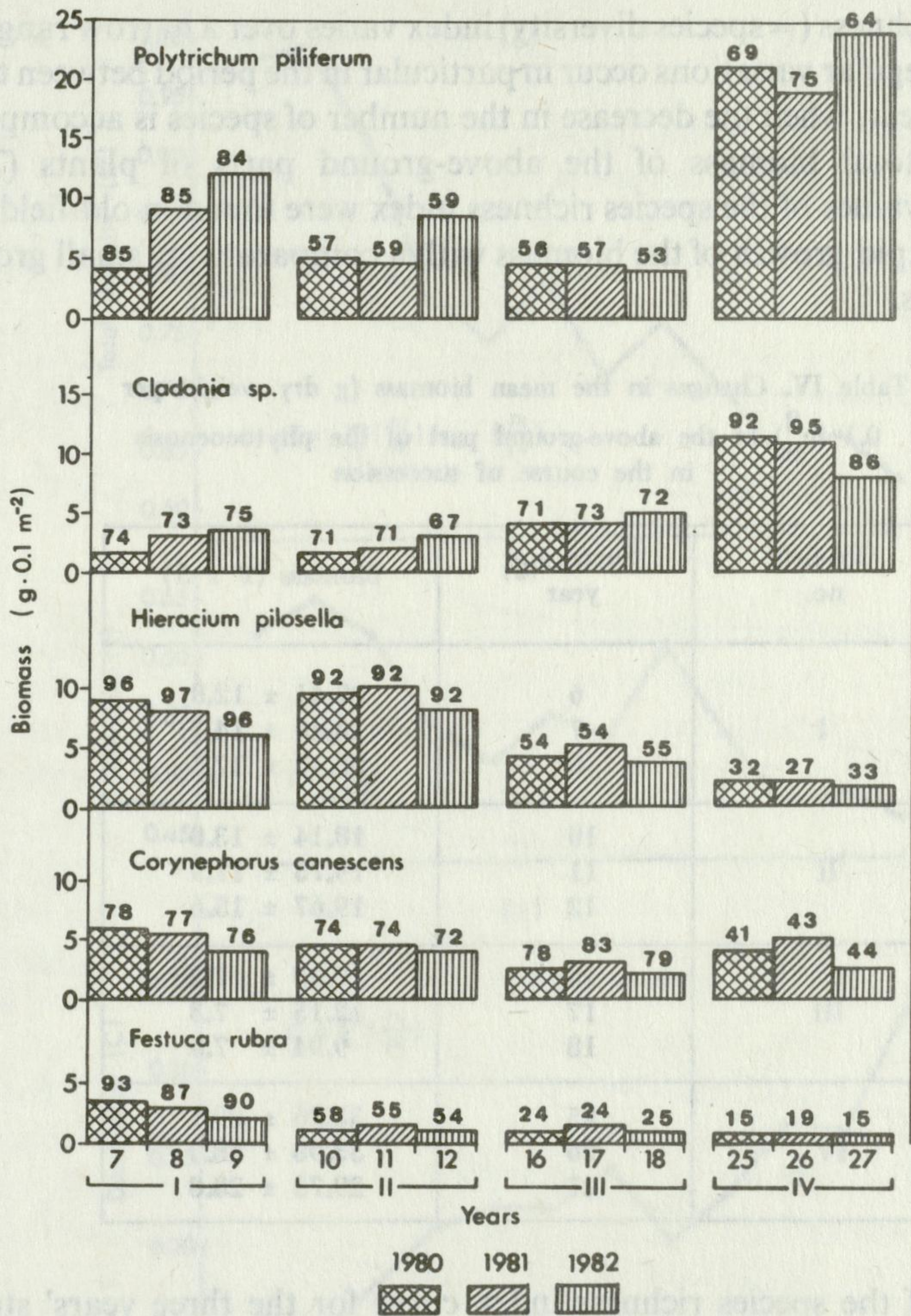


Fig. 3. Variations in the average biomass value of selected populations in the course of succession. The data concern samples with the respective species present; values above columns indicate frequency (%)

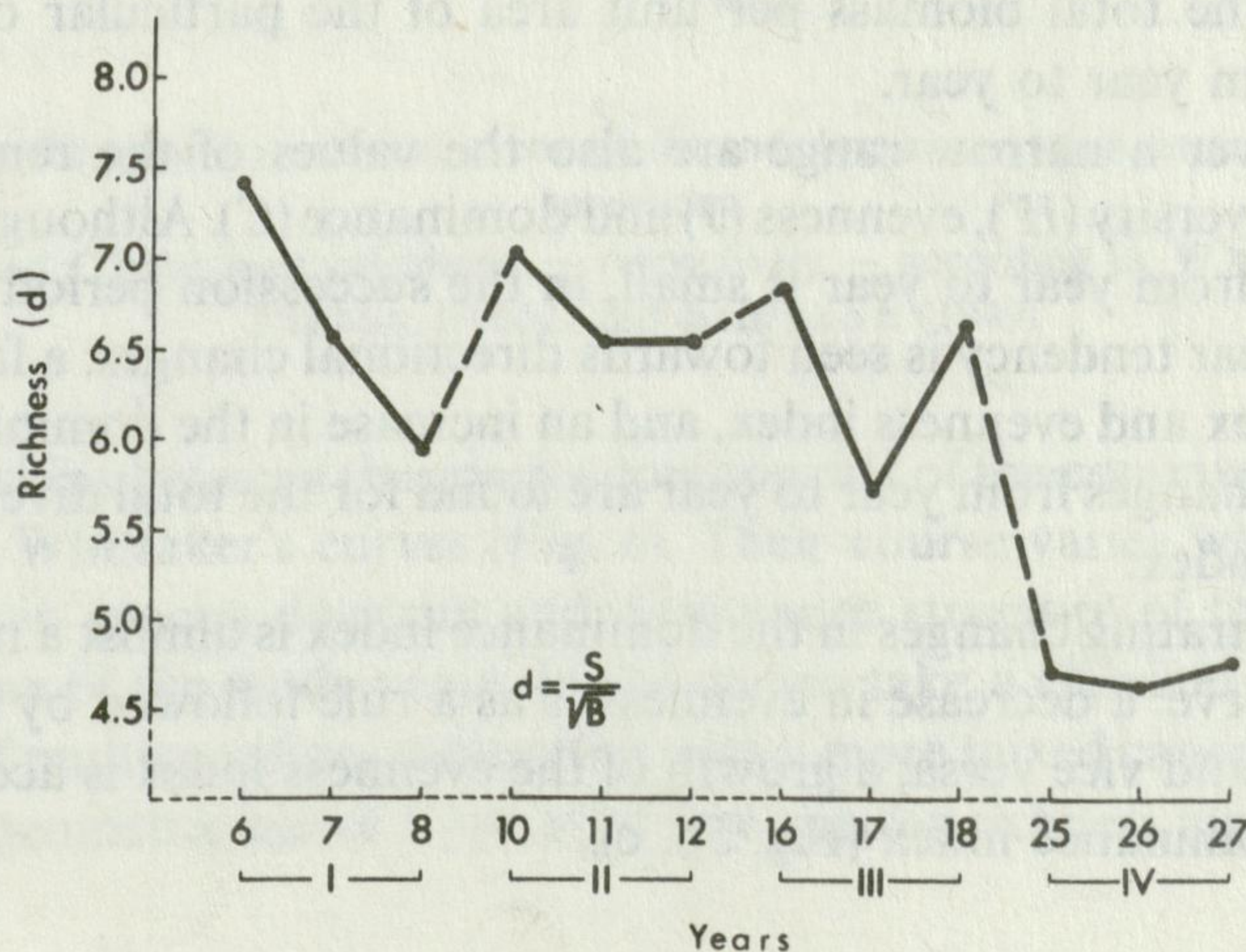


Fig. 4. Changes in the species richness of communities in the course of succession. *d* index has been calculated according to Menhinick (1964)

The species richness (= species diversity) index varies over a narrow range of values (Fig. 4). Small, irregular variations occur in particular in the period between the 6th and 18th succession year, when the decrease in the number of species is accompanied by a lower value of total biomass of the above-ground parts of plants (Table IV). Particularly low values of the species richness index were found in old-field IV, which resulted from a rapid growth of the biomass with a comparatively small growth of the number of species.

Table IV. Changes in the mean biomass (g dry weight per 0.1 m²) of the above-ground part of the phytocoenosis in the course of succession

Old-field no.	Succession year	Biomass ($\bar{x} \pm S$)
I	6	27.41 \pm 12.8
	7	28.46 \pm 14.7
	8	25.43 \pm 17.5
II	10	18.14 \pm 13.0
	11	19.73 \pm 11.9
	12	19.67 \pm 15.6
III	16	10.33 \pm 7.2
	17	12.15 \pm 7.3
	18	9.94 \pm 7.5
IV	25	33.26 \pm 29.1
	26	33.96 \pm 28.9
	27	29.73 \pm 28.8

The course of the species richness index curve for the three years' study in the individual old-fields is primarily the function of changes in the number of species, and to a lesser extent of the level of the biomass. At the level of the adopted error risk it has been found that the total biomass per unit area of the particular old-fields varied insignificantly from year to year.

Fluctuating over a narrow range are also the values of the remaining indices: Shannon's total diversity (H'), evenness (J) and dominance (C). Although the amplitude of their variation from year to year is small, in the succession period covered by the present study a clear tendency is seen towards directional changes: a fall of Shannon's total diversity index and evenness index, and an increase in the dominance index (Fig. 5a, b, c). Greater changes from year to year are found for the total diversity index than for the evenness index.

The curve illustrating changes in the dominance index is almost a mirror reflection of the evenness curve: a decrease in evenness is as a rule followed by a growth of the dominance index and vice versa; a growth of the evenness index is accompanied by a decrease in the dominance index (Fig. 5b, c).

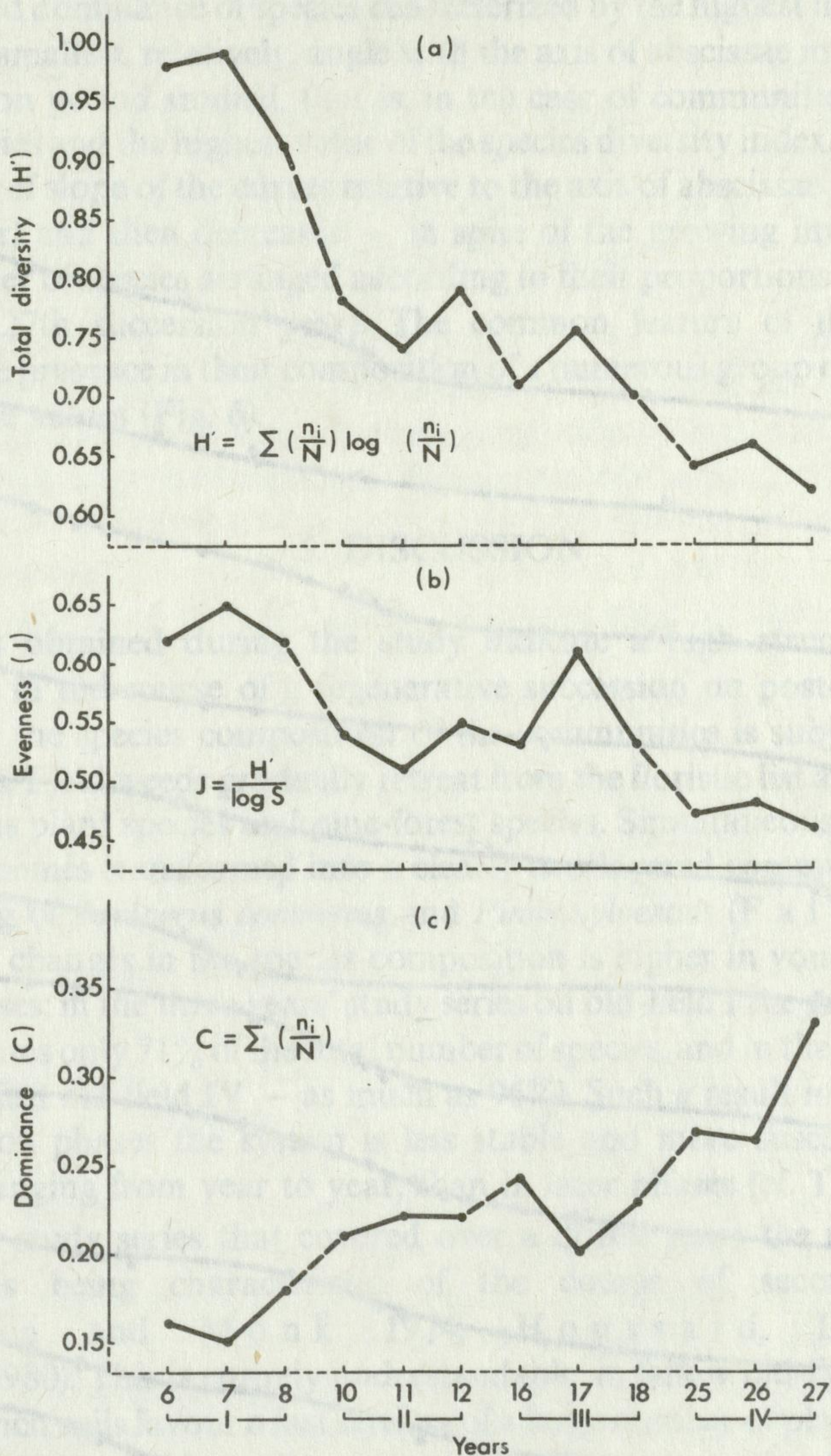


Fig. 5. Changes in the total diversity (a), evenness (b) and dominance (c) in communities undergoing succession

Indices H' , J and C have been calculated — respectively — according to Whittaker (1977), Pielou (1966a) and Simpson (1949)

The relationships between the species components of the communities under study are reflected by Whittaker's curves (Fig. 6). Their course varies with changes in the number of species, species diversity and dominance structure of the phytocoenoses. However, in none of the study years do the curves take a classical or sigmoid shape (characteristic of multispecific communities with a more mixed canopy dominance), or the shape of a geometric curve (typical of low species-richness systems with a very

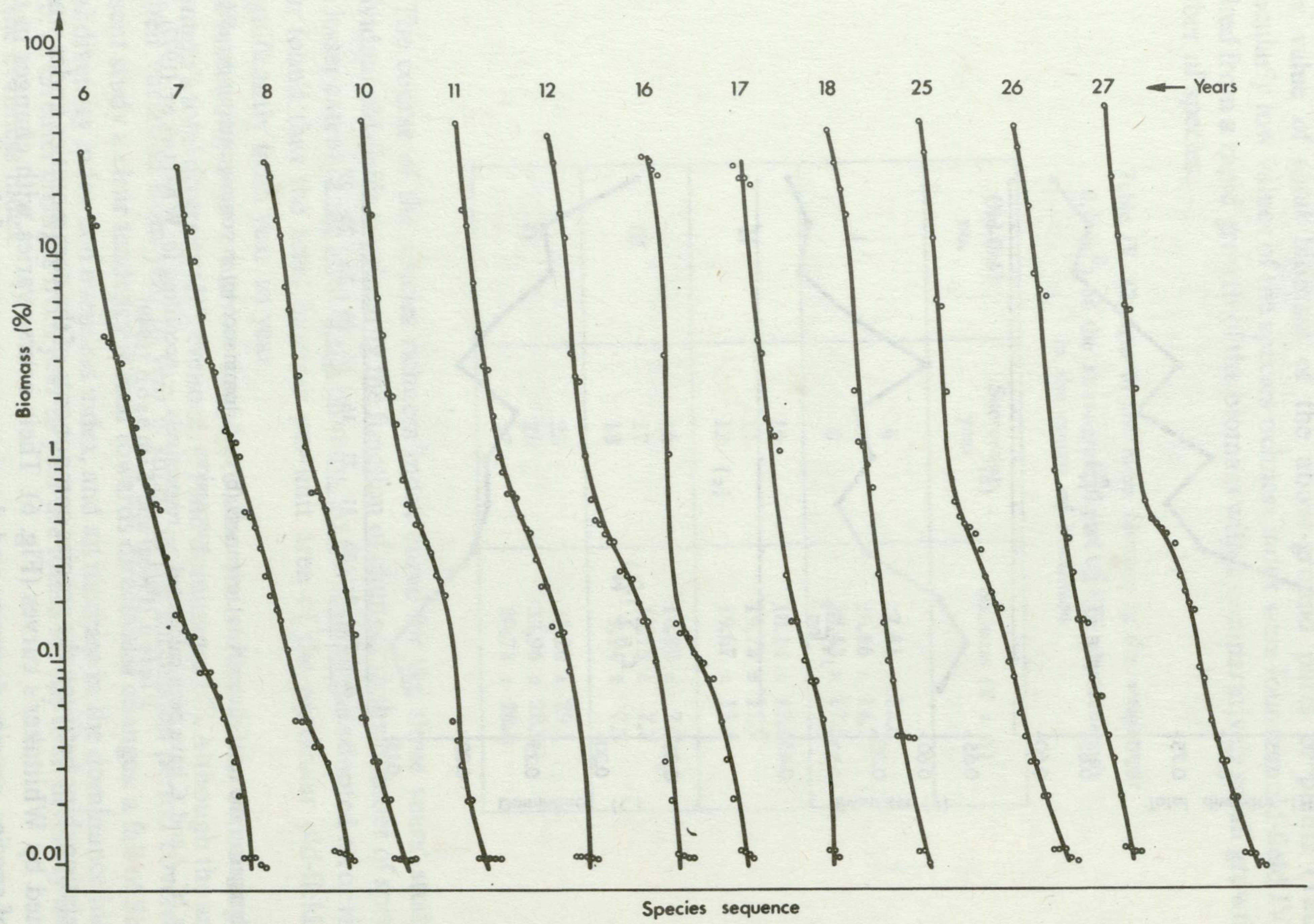


Fig. 6. Comparison of the importance-value curves for species in the communities during the succession
The curves have been drawn according to Whittaker's (1965) method

strongly marked dominance of species characterized by the highest importance values). They form the smallest, relatively, angle with the axis of abscissae in the first two years of the succession period studied, that is, in the case of communities with the largest number of species and the highest value of the species diversity index. In the subsequent years the angle of slope of the curves relative to the axis of abscissae increases (8 – 18th succession year) and then decreases – in spite of the growing importance contrast among a number of species arranged according to their proportions in the community biomass (25 – 27th succession year). The common feature of the phytocoenoses compared is the presence in their composition of a numerous group of species with very low importance values (Fig. 6).

5. DISCUSSION

The results obtained during the study indicate a high structure dynamics of phytocoenoses in the course of a regenerative succession on post-agricultural land. However, only the species composition of the communities is subject to continuous (linear) changes. Field weeds gradually retreat from the floristic list and are replaced by psammophilous plant species and pine-forest species. Simultaneously the one-layered community becomes transformed into a clearly two-layered community with a shrub layer consisting of *Juniperus communis* and *Pinus sylvestris* (F a l i ń s k i 1980b).

The rate of changes in the species composition is higher in younger than in older succession phases; in the three years' study series on old-field I the group of permanent species constitutes only 71% of the total number of species, and in the remaining – over 90% (in the oldest old-field IV – as much as 96%). Such a result indicates that in the initial succession phases the system is less stable and more susceptible to weather conditions, changing from year to year, than in later phases (cf. Tables II, III).

During the study series that covered over a dozen years the number of species decreased, this being characteristic of the course of secondary succession (N i c h o l s o n and M o n k 1974, H o u s s a r d, E s c a r r é and R o m a n e 1980). This is entirely understandable: in fallow old-fields the free space, and relatively rich soils favour a fast settling of a large number of plant species, some of which are later eliminated from the composition of the community (W e r n e r 1976, G r o s s 1980). A decrease in the number of species is probably caused by both the progressing soil depletion, connected with the mineralization of the arable layer, and intensified competitive relations in the community. However, after about 24 years of succession a clear remodelling of the community floristic composition can be seen, as well as a gradual increase in the number of species.

The diversity of the communities studied changes far less regularly than do the list and number of species. The diversity of ecological systems and the problem of their measurement have been dealt with in many studies (C o n n e l l and O r i a s 1964, P i a n k a 1966, 1969, P i e l o u 1966a, 1966b, H u l b e r t 1971, M a y 1975, 1976; W h i t t a k e r 1977 and others). Numerous empirical investigations have shown that the diversity of systems increases in the direction from the pole to the

equator (P i a n k a 1967), and in the temperate zone it grows with increasing continentalism (W h i t t a k e r and N i e r i n g 1965). Regardless of the climatic conditions, diversity is as a rule higher on rich than on poor soils (F r y d m a n and W h i t t a k e r 1968).

Changes in the diversity of a biocoenosis in the course of succession have also been discussed in the relevant literature, but the number of data documented so far does not permit unequivocal conclusions. J a c o b s (1975) maintains that in the early phases of a primary succession species diversity grows steadily, and it usually decreases only at the stage preceding the climax. According to O d u m (1969), in the course of a secondary succession a growth of diversity occurs only during the first several years. Later on, however, a gradual decrease can be seen as those species that are better adapted to the prevailing environmental conditions monopolize the available supplies. A decrease in diversity in the course of a secondary succession has been found by, for example, S h a f i and Y a r r a n t ò n (1973), N i c h o l s o n and M o n k (1974), B a z z a z (1975).

The results presented in this paper show that within the 21 years of succession analysed the species diversity increased and decreased several times; thus no continuous (linear) changes towards its growth or decrease have been found regardless of the kind of index considered. It is difficult, however, to compare the results with literature data, because of differences in the diversity measurement methods.

Of the many indices worked out for the assessment of diversity four basic ones have been used in the study. Other indices are their modifications; they are based on much more complicated mathematical functions, and since they require a complex computation, they are usually used only in theoretical considerations. In most empirical papers diversity indices are usually used alternatively. It seems wrong, because each of them has a different informative value.

The species richness index (d) describes a system as a whole; it does not, therefore, show relations between its components. Although the value of the index depends on two parameters: number of species and total biomass, it is a particularly sensitive index of variations in the number of species, because of the mathematical formula used, and to a considerably lesser extent — of variations in biomass. Hence in the three years' study period a great decrease in species richness was found in old-field I, where the number of species varied from year to year, and an almost identical index value in old-field IV, in spite of the fact that there occurred relatively great changes in biomass value.

The total species diversity index (H') is commonly accepted as the best measure of diversity (W h i t t a k e r 1977), because it takes into account both the species richness and an even sharing of the supplies of an environment among the populations of the individual species. Its value depends primarily on the importance of the species located in the middle of a series ordered according to their importance values; the more marked is the dominance of the first or of the first several species, and the more numerous are the species of a very low importance in respect of the criterion established, the lower the index value.

In old-field I — in the earliest succession phase of the period considered — the

relatively high H' value results primarily from the presence of a numerous group of species with similar biomass values, occupying the central segment of the series arranged in order of decreasing importance values, and to a lesser extent also from the relatively small number of species with a very low importance. A growth of the percentage of this species group in the phytocoenoses of the successive succession phases is the basic cause of the lowering of the value of Shannon's index (10–18th succession year). Its further fall in the last three years of the study series is in turn connected with a rapid growth of the biomass of the dominants: *Polytrichum piliferum* and *Cladonia* sp. All in all, in spite of the variation of Shannon's index from field to field during the three years' study, there is a clear tendency towards a decrease in the total specific diversity of the phytocoenoses in the course of succession. Thus the results in essence agree with the findings of Shafi and Yarranton (1973), Nicholson and Monk (1974) and Bazzaz (1975). At the same time they indicate a high sensitivity of Shannon's index even to small changes in the inter-species relations in a phytocoenosis, for its value fluctuated each year also in old-field IV, where the number and list of species were almost constant, and there was only a slight variation in the biomass of the individual species.

By contrast to Shannon's total diversity index, the value of the evenness index (J) depends on the total number of the species making up a community. For this reason, it is in the early succession phases (in old-fields I and II), when there occur relatively great changes in the number of species, that the evenness curve deviates most from the total diversity curve. In the last three years of the period analysed evenness, like diversity, stayed at a similar level, which indicates a relative stability of the system.

If the H' index value depends mainly in the importance values of the species in the middle of the series, then the dominance index (C) depends primarily on the importance of the first species, or the first group of species. That is why it takes the lowest values in the first three years of the period under study, when the predominance of the species that is dominant in the phytocoenoses (*Hieracium pilosella*) is fairly weak, and the highest values in the last three years — due to a positive dominance of *Polytrichum piliferum* and *Cladonia* sp.

Changes in the relations between the populations of the phytocoenoses compared are also indicated by the importance-value distribution curves. According to Whittaker (1965, 1977), they reflect the relationship between the biomass value and species diversity, and also the relationship between species richness and dominance in a phytocoenosis under study. In his interpretation of the shape of the importance-value curve Whittaker (1970) makes reference to the niche concept and the associated sharing of supplies among the populations of the different species in a community. According to the last-named author a lognormal distribution of importance values is characteristic of multispecific systems in supply-rich habitats, composed of species clearly differing in their importance; a geometric distribution of importance values relates to communities made up of a small number of species found in unfavourable environmental conditions (Whittaker 1970, 1972).

On account of the similarity of soil properties (identical habitat type) and a high value of the species commonness coefficient of the communities under study

(phytocoenoses of one successional series) it is understandable that the importance-value distribution curves obtained in the present study are fairly similar, and their interpretation according to Whittaker's (1970) concept would be risky. With great caution one could only speak of a growing tendency towards an uneven sharing of supplies among the populations of the phytocoenoses of the consecutive succession phases (cf. Housard, Escarré and Romane 1980). More complete data on the relations between populations, and between the biotic and the abiotic component of the system can be obtained from studies of the inter-species associations, spatial structure of the biomass as a whole, and of the biomass of the particular species, as well as of the spatial distribution of nutrients in the soil. These problems will be dealt with in separate studies.

When discussing the results it is necessary to consider the selection of the criterion on the basis of which the indices of species richness, total diversity, evenness and dominance have been calculated. As has been mentioned at the beginning, there is a lot of free choice in this area. A measure, often used, of species importance is the percentage of each population in the total number of individuals in a system under study. In the case of plant populations this is, however, an imperfect measure. Firstly, it makes it necessary in studies to leave out lower plants, especially lichens, because it is impossible to isolate an individual. Secondly, as there are a variable number of species propagating vegetatively, and a varied life form spectrum in the systems compared, an arbitrarily-established "individual" — shoot, tussock, leaf-rosette etc. — may become the source of a serious error. Finally, as a result of the high plasticity of plants, the population of a species may, depending on the environmental conditions, consist of very small and very big individuals, their number being the same; in such cases the numeric criterion is not correct.

According to Whittaker (1965), the best measure of the importance of a species in a phytocoenosis is its production (dry weight of organic matter produced in unit time per unit area). Since production assessment methods are laborious, more often an alternative measure — the population biomass is used, which according to many authors far better reflects the importance of a species in a phytocoenosis than does the number of individuals (Dickman 1968, Whilm 1968, Tramer 1975). Whittaker (1965) has in fact shown that importance-value curves for species in communities, worked out on the basis of production and biomass are similar in shape; this proves that the value of biomass is the right criterion to be used in comparative studies of the diversity of ecological systems.

To sum up, in the course of a regenerative succession in old-fields the following features have been observed: (1) a linear nature of changes in the floristic composition of the phytocoenoses, (2) fluctuations of quantitative structure indices, particularly wide in the case of species richness, (3) a tendency towards lower values of the indices of species richness, total diversity and evenness, and towards higher values of the dominance index, (4) a lower rate of qualitative and quantitative changes in the structure of the phytocoenoses, and (5) an increased resistance of the phytocoenoses — especially their species composition — to the effect of weather conditions, varying from year to year.

ACKNOWLEDGMENTS: I would like to thank Professor Dr. J.B. Faliński for the proposal of sharing the study area.

6. SUMMARY

The paper is devoted to an analysis of changes in the floristic composition, species richness, total diversity, evenness and dominance in a successional series of communities in old-fields. Field investigations were carried out in July 1980–1982 in four uneven-aged old-fields located in an area that was once at the edge of the Białowieża Primeval Forest (Table I). The quantitative structure indices of the phytocoenosis have been calculated from the biomass of the above-ground parts of plants (Simpson 1949, Menhick 1964, Whittaker 1965, 1977, Pielou 1966a). Samples were collected from 100 circles 0.1 m² in area in a grid system of shifted squares. The plant material was sorted out into species, dried at 105°C for 48 hrs. and weighed with an accuracy to the nearest 0.001 g.

It has been found that in the course of succession there occur significant qualitative and quantitative changes. The former are of a directional nature: field weeds gradually retreat and are replaced by psammophilous and pine-forest plant species (Table III). As indicated by the distribution of the commonness coefficients (Ellenberg 1956), the rate of changes is much faster in an early succession phase than in the oldest old-fields under study (Fig. 1). Analysed 25–27 years after the abandonment of cultivation, the phytocoenosis is characterized by an almost constant number of species and a constant composition. The proportion of mosses and lichens in the total biomass of the community clearly increases in the course of succession; at the same time there occurs a decrease in the frequency and biomass of vascular plant populations (Figs. 2, 3).

Odum (1969), Shafi and Yarranton (1973), Nicholson and Monk (1974), and Bazzaz (1975) report that in the course of a secondary succession the species diversity decreases. Since diversity is assessed by different methods, in the present study four basic indices were used simultaneously. It has been found, however, that the changes of all the indices are of the nature of irregular fluctuations (Figs. 4, 5a–c); the amplitude of their variations is wide in an early succession phase and only slight in the last three years of the series analysed. A similarly fluctuating course of changes is found for the distribution of the importance values of individual species in the phytocoenosis (Fig. 6). Apart from the yearly fluctuations of the particular indices, in the succession period analysed clear tendencies were found towards directional changes: a lowering of the indices of species richness, total diversity and evenness, and an increase of the dominance index. The results also suggest a gradual growth of uneven supply-sharing among populations making up the phytocoenoses of the consecutive succession phases (cf. Whittaker 1970, 1972). However, detailed information on the relations among species in a phytocoenosis and their connections with supplies can be obtained by analysing the inter-species associations and the correlation between the spatial distribution of biomass and the spatial distribution of nutrients in the soil. These problems will be dealt with in separate studies.

7. POLISH SUMMARY

Praca poświęcona jest analizie zmian składu florystycznego oraz bogactwa gatunkowego, ogólnej różnorodności, równomierności i dominacji w sukcesyjnej serii zbiorowisk na gruntach porolnych. Badania terenowe przeprowadzono w lipcu 1980–1982 r. na 4 różnowiekowych ugorach zlokalizowanych na skraju dawnej Puszczy Białowieskiej (tab. I). Ilościowe wskaźniki struktury fitocenozy obliczono na podstawie stanu biomasy nadziemnych części roślin (Simpson 1949, Menhick 1964, Whittaker 1965, 1977, Pielou 1966a). Próby pobierano w układzie sieci przesuniętych kwadratów ze 100 okręgów o powierzchni 0,1 m² każdy. Materiał roślinny segregowano na poszczególne gatunki, suszono w temp. 105°C przez 48 h i zważono z dokładnością do 0,001 g.

Stwierdzono, że w toku sukcesji zachodzą istotne zmiany zarówno jakościowe, jak też ilościowe. Pierwsze mają charakter kierunkowy: stopniowo wycofują się chwasty polne, na miejsce których wkraczają

gatunki roślin psammofilnych i borowych (tab. III). Tempo zmian, jak wynika z rozkładu współczynników wspólnoty (Ellenberg 1956), jest znacznie szybsze we wczesnej fazie sukcesji niż na najstarszym z badanych ugorów (rys. 1). W latach 25–27 od momentu zaniechania uprawy fitocenozę cechuje niemal stała liczba gatunków i stały ich skład. Wyraźnie w toku sukcesji wzrasta udział mchów i porostów w ogólnej biomacie zbiorowiska; równocześnie spada frekwencja i biomasa populacji roślin naczyniowych (rys. 2, 3).

O d u m (1969), S h a f i i Y a r r a n t o n (1973), N i c h o l s o n i M o n k (1974) oraz B a z z a z (1975) podają, że w toku sukcesji wtórnej następuje spadek różnorodności gatunkowej. Ze względu na różne sposoby oceny różnorodności w pracy zastosowano równocześnie 4 podstawowe wskaźniki. Okazało się jednak, iż zmiany wartości wszystkich wskaźników mają charakter nieregularnych fluktuacji (rys. 4, 5a–c); amplituda ich wahań jest większa we wczesnej fazie sukcesji i tylko nieznaczna w ostatnich 3 latach analizowanej serii. Podobnie falowy przebieg zmian charakteryzuje rozkład współczynników znaczenia poszczególnych gatunków w fitocenozie (rys. 6). Niezależnie od corocznych fluktuacji wartości poszczególnych wskaźników w analizowanym okresie sukcesji stwierdzono wyraźne tendencje do zmian kierunkowych: spadku wartości wskaźnika bogactwa gatunkowego, ogólnej różnorodności i równomierności oraz do wzrostu wartości wskaźnika dominacji. Wyniki sugerują także stopniowy wzrost nierównomiernego rozdziału zasobów środowiska pomiędzy populacjami budującymi fitocenozę kolejnych faz sukcesyjnych (por. W h i t t a k e r 1970, 1972). Szczegółowych danych o relacjach międzygatunkowych w fitocenozie oraz ich związkach z zasobami środowiska może jednak dostarczyć z jednej strony analiza sprzężeń międzygatunkowych, z drugiej zaś analiza korelacji między przestrzennym rozkładem wartości biomasy a przestrzennym rozkładem składników pokarmowych w glebie. Zagadnienia te będą przedmiotem osobnych prac.

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