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Statistical analysis of the phytocoenose homogeneity. III. Spatial distributions of species and their standing biomass as a function of the area size

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Abstract

Homogeneity of the *Leucobryo-Pinetum* phytocoenose was assessed on the grounds of species dispersal and spatial distribution of their biomass, determined with non-parametric runs test. It was confirmed that: 1) species dispersal and the type of spatial distribution of their biomass depended on the area size, 2) for analysed phytocoenose the area at which species dispersal and spatial sequence of the high and low standing biomass were random could be determined, 3) phytocoenose was homogeneous only under the difinite scale of its spatial differentiation, and 4) scale under which phytocoenose was homogenenous differed for qualitative and quantitative measures.

Key words: phytocoenose homogeneity, species spatial distribution, biomass

INTRODUCTION

Statistical analysis of the spatial dispersal of individuals of selected species has been one of the earliest and most common methods in the assessment of the phytocoenose homogeneity. According to Kylin (1926) a vegetation patch can be treated as homogeneous when its components — plant populations — are characterized by a random type of the spatial structure.

In the twenties Svedberg (1922) has proposed to assess randomness in plant dispersal on the grounds of agreement between the frequency distribution of density and Poisson's distribution. It has been analysed with the coefficient of dispersion (variance S^2 — mean $\bar{x}$ ratio). Coefficient of dispersion has been later frequently used (e.g. Blackman 1942, Archibald 1948, Dice 1952). Skellam (1952) has shown that its value depends on the quadrat size. It has resulted in the development of methods of the analysis of distribution type at the different quadrat size (Greig-Smith 1952, 1961a, 1961b, Kershaw 1957, 1958, 1959, 1960, 1963, 1973 and others). The spatial structure of a population has been also investigated with different indices and statistical tests (cf. Moore 1953, Greig-Smith 1957). Kwiatkowska and Symonides (1980) have given a wide survey on the methods of assessment of the type of plant population spatial structure.

The paper aims at: 1) analysis of the homogeneity of a model phytocoenose at the various quadrat size and on the grounds of spatial distributions of species, their standing biomass and the total biomass of ground layer; and 2) comparison of the results of homogeneity analyses based upon qualitative and quantitative measures. As the Kylin's (1926) criterion has been accepted, judgement on the phytocoenose homogeneity is the total of judgements on its components.

In the analysis of the spatial distributions of individual species non-parametric runs test has been used (Jones 1955, Gounot 1962, Kwiatkowska 1972). The test investigates into randomness of sequence of values in time or space and enables to analyse qualitative and quantitative measures. From the statistical point of view use of parametric tests when sampling is systematic is not correct, although it has happened before (Greig-Smith 1952, 1957, David and Moore 1954, Catana 1964).

The paper is the third in the series of works on homogeneity. Its aims and scope have been presented earlier in two first papers (Kwiatkowska and Symonides 1985a, 1985b). The studies were carried-out in the *Leucobryo-Pinetum* Mat. (1962) 1973 phytocoenose with the uniform physiognomy. It was composed of pure, even-aged, one-layered forest stand and floristicly poor ground layer (21 species of flowering and 7 of sporogenous plants), dominated by dwarf-shrubs. The full floristic composition of the ground layer and interpopulational quantitative relationships have been presented in the first paper (Kwiatkowska and Symonides 1985a).

MATERIAL AND METHODS

In sampling the Greig-Smith's (1952) grid was used. It was composed of 512 square quadrats (sample areas) of side 1 m each. In the period of maximum biomass of the ground layer (July) in each quadrat all species were recorded. Then, air-dry standing biomass of above-ground parts of all vascular plants in the ground layer was established. The data were arranged in plans of species occurrence and cartograms of their biomass in the successive quadrats. They served as basic data in the statistical analysis of phytocoenose homogeneity.

The type of spatial species distribution was tested for quadrat size ascending with geometric progression — from 1 m^2 to 32 m^2 (Fig. 1).

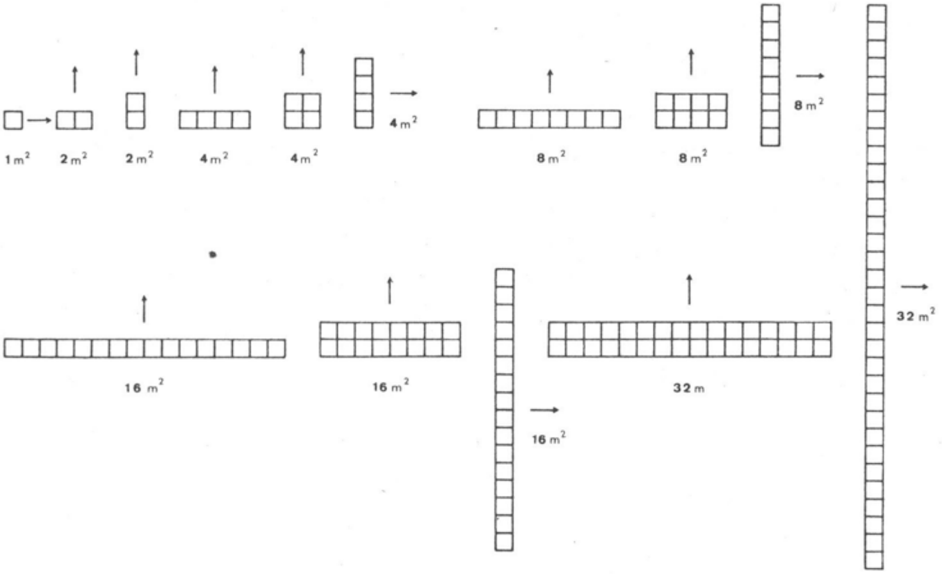

Fig. 1. Size and shape of quadrats. Arrows show the direction in which test was done

Due to the particular sensitivity of non-parametric runs test only such quadrat shape was used as to ensure runs size not smaller than 16 for each quadrat size. 14 species, i.e. 50% of the total species number were tested. Remaining species were not analysed due to their low frequency (less than 1%).

In further elaboration following fractions were obtained: 1) fraction of species with "contagious tests"[1], related to the total species number; and 2) fraction of the "contagious tests", related to the total number of "random" and "uniform" tests together[2]. Then, confidence limits were calculated (at the significance level $\alpha = 0.05$) for probability p determining fraction of species with "contagious tests" and that of "contagious tests"

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[1] Species with "contagious tests" are those which are characterized by contagious distribution.

[2] "Contagious tests", "random tests" and "uniform tests" are those which denote contagious, random and uniform distributions, respectively.

(Oktaba 1966). All quadrat sizes were taken into account. The significance of differences between fractions of "contagious tests" for 2 and 4 m^2 was verified with the significance test for the fraction difference (Greń 1980).

Runs test answers the question, whether chance of finding the species in different parts of investigation area is the same. When probability changes are directional, or aggregations are dispersed non-randomly result of test is the same — contagious dispersal. It does not show direction of clumping of the species individuals. Therefore, modification of the runs test was applied, where number of species occurrence were recorded in each "row" (sample runs amounted to 16) and "column" (sample runs amounted to 32) of the grid. Next, runs of number higher or lower than mean (established on the total of occurrences in "row" and "column") were tested.

Quantitative measures — the ground-layer biomass and those of individual species were elaborated analogously. Only fraction of "contagious tests" was related to the total number of tests possible for each quadrat size. Biomass values for the successive quadrats were transformed into plus, if they were higher than mean value, or minus — if they were lower. They were calculated for all square sizes, namely 1, 2, 4, 8, 16 and 32 m^2.

RESULTS

THE TYPE OF SPATIAL SPECIES DISTRIBUTION AS A FUNCTION OF THE AREA SIZE

From the results of non-parametric runs test it may be inferred that the type of spatial distribution of the majority of species depends on the quadrat size. Also fraction of the "contagious tests" and that of species with "contagious tests" are a function of the quadrat size (Fig. 2).

86% of tested species were characterized with "contagious tests" (Table 1). Random spatial distribution, independent of the quadrat size, was found only for two moss species: *Entodon schreberi* (Willd.) Mnhm. and *Pohlia nutans* (Schrebn) Lindb.

The number of "contagious tests" and the number of species with "contagious tests" decreased with increasing quadrat size. Also the total number of "contagious tests" and maximum number of tests possible for each quadrat size was reduced. The latter is a product of the number of tested species and the number of tests available for each quadrat size. Therefore, differences between successive quadrat sizes, with respect to the fraction of "contagious tests" related to "random tests", were analysed.

Table 1

Number of tests which denote random, contagious or uniform type of species spatial distributions, at the successive quadrat size

Species	F	1 m^2			2 m^2			4 m^2			8 m^2			16 m^2			32 m^2		
		a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	a	b	c
Entodon schreberi (Willd.) Mnkm.	509	0	0	48	0	0	24	0	0	20	0	0	10	0	0	5	0	0	2
Vaccinium vitis-idaea L.	459	14	7	27	6	3	14	3	1	16	0	0	10	0	0	5	0	0	2
Vaccinium myrtillus L.	451	10	10	28	3	6	15	0	4	16	0	0	10	0	0	5	0	0	2
Dicranum undulatum Ehrh.	442	2	30	16	0	5	19	0	0	20	0	0	10	0	0	5	0	0	2
Melampyrum pratense L.	245	12	35	0	6	16	2	6	12	2	1	4	5	0	0	5	0	0	2
Pinus sylvestris L.	225	2	46	0	3	19	2	1	14	5	0	2	8	0	0	5	0	0	2
Calluna vulgaris (L.) Salisb.	199	16	27	2	9	12	3	6	12	2	4	4	2	1	2	2	0	1	1
Molinia coerulea (L.) Moench.	105	10	27	0	7	13	0	5	14	0	3	6	1	1	3	1	1	0	1
Dicranum scoparium (L.) Hedw.	101	9	30	0	6	18	0	2	10	0	0	10	0	0	1	4	0	0	2
Quercus robur L.	96	2	43	0	2	22	0	1	19	0	0	8	2	0	2	3	0	0	2
Pohlia nutans (Schrehn) Lindb.	23	0	13	0	0	11	0	1	8	0	0	8	0	0	5	0	0	2	0
Frangula alnus Mill.	17	1	20	0	1	17	0	0	17	0	0	10	0	0	5	0	0	2	0
Sorbus aucuparia L.	14	0	10	0	1	12	0	0	14	0	1	7	0	0	5	0	0	2	0
Luzula pilosa (L.) Willd.	16	2	14	0	1	10	0	2	12	0	2	6	0	2	3	0	1	1	0
Total		80	312	121	45	164	79	27	137	81	11	65	58	4	26	40	2	8	18

F — species frequency, a — "contagious tests", b — "random tests", c — "uniform tests".

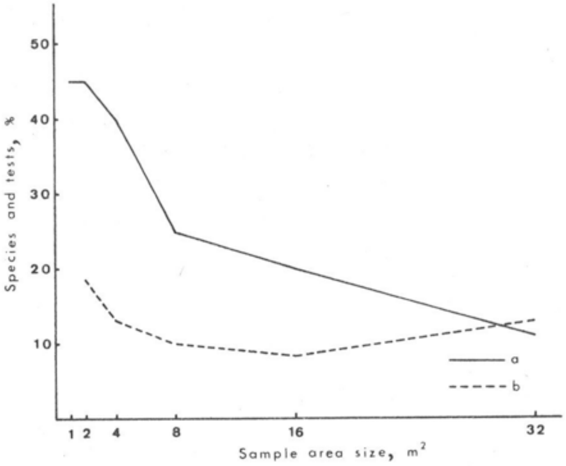

Fig. 2. Fraction of species with "contagious tests" (a) and fraction of "contagious tests" (b) as functions of the area size

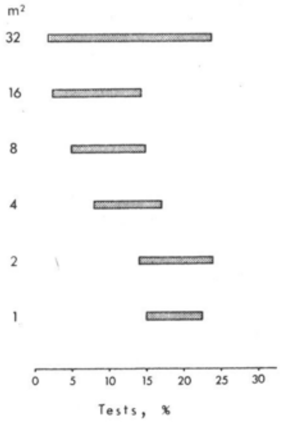

Fig. 3.

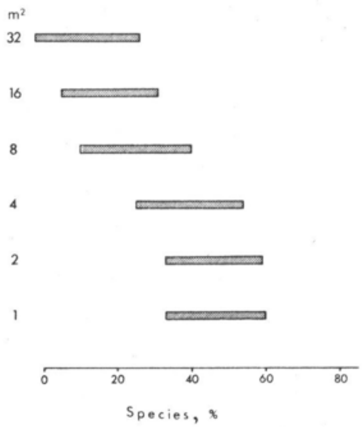

Fig. 4.

Fig. 3. Confidence limits for the fraction of "contagious tests". The fraction was calculated as the ratio of the number of "contagious tests" to the number of "random" and "uniform tests" at the successive quadrat size

Fig. 4. Confidence limits for the fraction of species with "contagious tests". The fraction was calculated as the ratio of the number of species with contagious distribution to the total species number at the successive quadrat size

This fraction informs how the number of tests denoting contagious distribution of species in the area under study is related to the number of tests which enable to consider this area as homogeneous.

The results indicated that fraction of "contagious tests" for 4, 8 and 16 m^2 was significantly smaller than that for 1 and 2 m^2 (Fig. 3). Also fraction of the species with "contagious tests" was significantly smaller for big (16 and 32 m^2), than for small quadrats (Fig. 4).

Due to the modification of non-parametric runs test it was possible to show that the chances of finding 6 species were different in various grid parts (Fig. 5). Those species tended to aggregate in some grid parts and to "avoid" the others.

Vaccinium myrtillus L. and *Vaccinium vitis-idaea* L. occurred mainly (with higher probability) in the eastern and north-eastern part of grid, whereas *Molinia coerulea* (L.) Moench — in the south-eastern part. The latter was also occupied by large aggregation of *Melampyrum pratense*. L. There was the second aggregation of this species in the north-western, opposite, end of the grid. *Calluna vulgaris* (L.) Salisb. was the most probable to find in the western and north-western area part, while *Luzula pilosa* (L.) Willd. — in the south-western (Fig. 5). For all these species "contagious tests" were found for middle-sized and large quadrats, i.e. 8, 16 and 32 m^2.

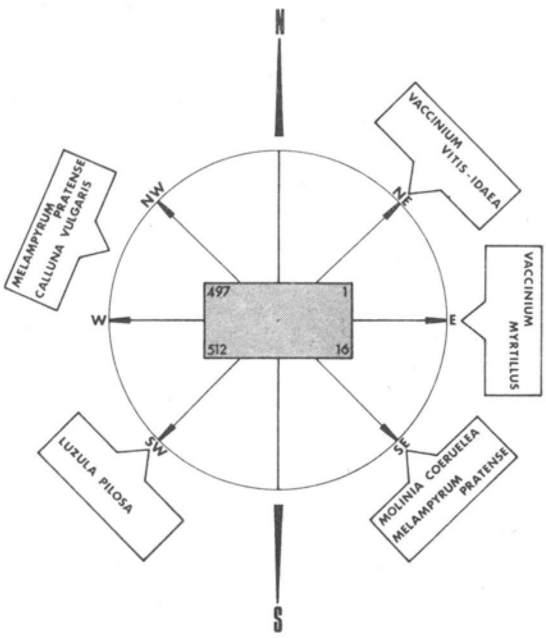

Fig. 5. Spatial location of the investigation area, and directions in which probability of finding individuals of each species and higher values of their biomass increases. 1, 16, 497, 512 — numbers of the initial grid quadrats

THE TYPE OF SPATIAL DISTRIBUTION OF THE BIOMASS OF GROUND LAYER AND THOSE OF INDIVIDUAL SPECIES AS A FUNCTION OF THE AREA SIZE

The results of runs test, with respect to quantitative measures, indicate that, as for qualitative measures, the type of spatial distribution of biomass depended on the scale of observations. Fraction of species with "contagious tests" and that of "contagious tests" are functions of the area size (Fig. 6).

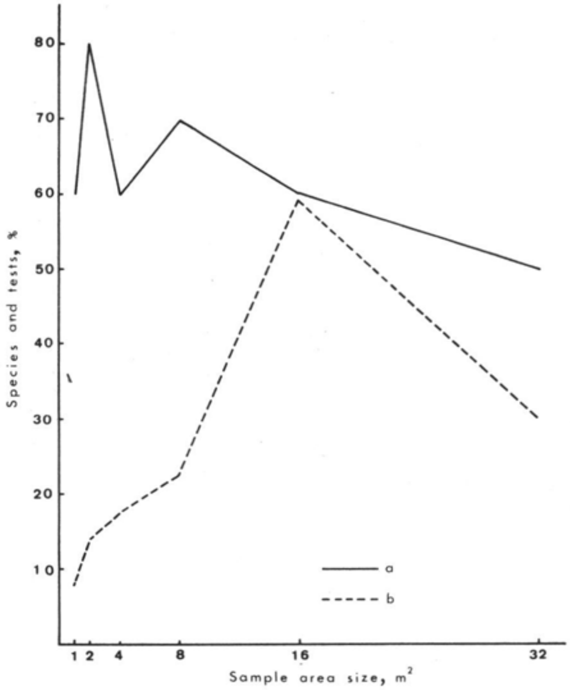

Fig. 6. Fraction of species with contagious biomass distribution (a) and fraction of tests denoting contagious biomass distribution (b) as functions of the area size

However, the course of curves which illustrate relation of quantitative measures to the area size is different than those typical of qualitative measures.

The test results and analysis of cartogramms showed that values of the ground-layer standing biomass were dispersed contagiously under the scale of 1, 2 and 4 m^2 (Figs. 6 and 7). Therefore, high biomass value (not lower than mean) in one quadrat increased probability of occurrence of other high values in the neighbouring quadrats. These elementary biomass aggregations were located randomly within aggregations of the second order, n.e. 16 m^2 each. This was illustrated through the test results which indicated

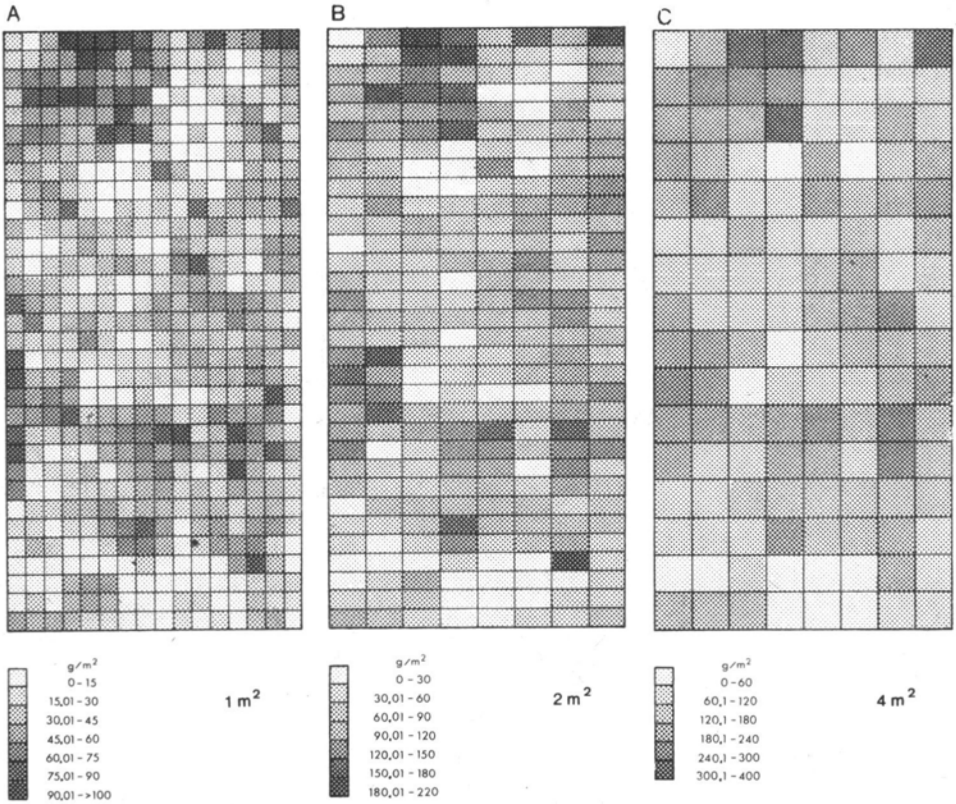

Fig. 7. Spatial differentiation of the ground-layer standing biomass under the scale of: 1 (A), 2 (B) and 4 m² (C)

random distribution for 8 m^2 and contagious distribution for 16 m^2. Afterwords, the chance of finding large aggregations within biochore was statistically the same, as for 32 m^2 distribution was again random (Figs. 6 and 8).

All analysed species, seedlings of trees and shrubs excepted, were characterized by contagious type of biomass distributions for 2, 4 and 8 m^2 (for qualitative measures — 1 and 2 m^2). The highest per cent of "contagious tests" was found for 16 m^2 (for qualitative measures — 1 and 2 m^2). Only for the larger quadrats decrease in the fraction of "contagious tests" was marked.

Calluna vulgaris, *Luzula pilosa*, *Melampyrum pratense*, *Molinia coerulea* and *Vaccinium vitis-idaea* were characterized by contagious distributions of their biomass, independent of the quadrat size. Biomass aggregations of *Vaccinium myrtillus*, which were found for 1, 2, 4 and 8 m^2, were located randomly under the scale of 16 and 32 m^2.

The type of biomass dispersal of seedlings of trees and shrubs was different. Biomass of *Pinus sylvestris* seedlings was dispersed at random with the exception of 8 m^2, where contagious distribution occurred. Seedling biomass distribution of *Quercus robur* L. and *Frangula alnus* Mill. were contagious only for two quadrat sizes: 2 and 16 m^2, as well as 1 and 2 m^2, respectively. Biomass values of *Sorbus aucuparia* L. seedlings were dispersed fully at random, independent of the quadrat size.

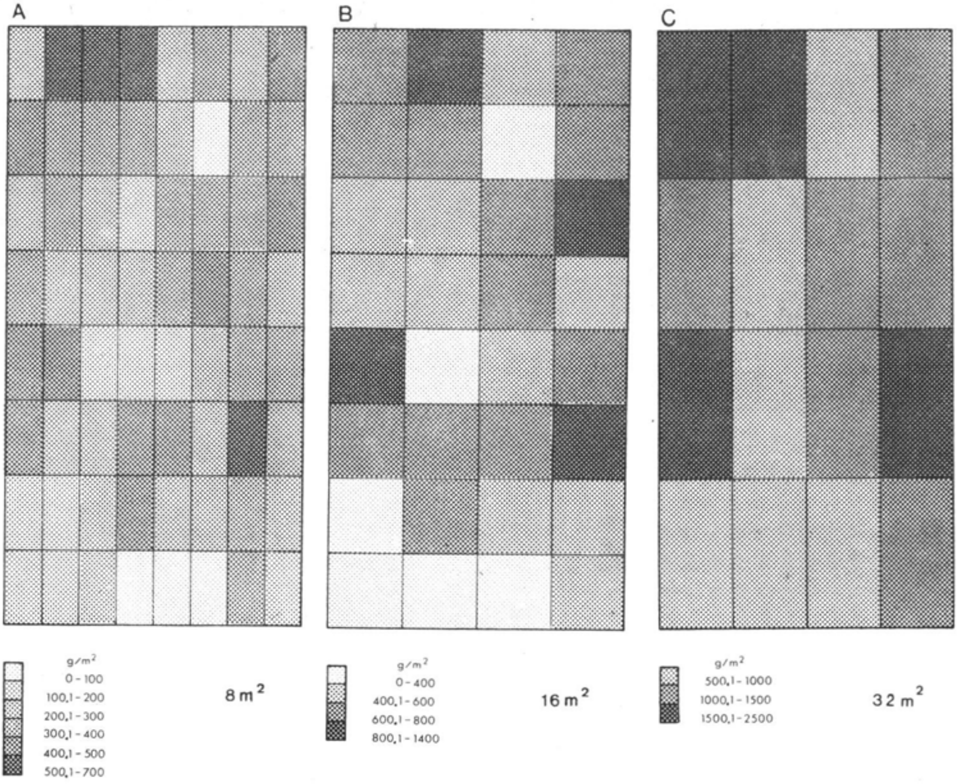

Fig. 8. Spatial differentiation of the ground-layer standing biomass under the scale of: 8 (A), 16 (B) and 32 m^2 (C)

Biomass spatial distributions of 6 species: *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, *Calluna vulgaris*, *Melampyrum pratense*, *Molinia coerulea* and *Luzula pilosa* were not the same within the grid. Changes in the probability of finding high biomass values of individual species took course in the same direction as changes in probability of finding their individuals (cf. Fig. 5).

DISCUSSION

Assumption of the statistical Kylin's (1926) criterion of homogeneity has to be followed by appropriate assessment of the type of species spatial distributions. In systematic sampling, e.g. Greig-Smith's (1952) grid, use of the non-parametric runs test is the most suitable from statistical point of view (Kwiatkowska and Symonides 1979). Unfortunately, as it has been rarely used so far (Gounot 1962, Kwiatkowska 1972) all comparison of results is difficult.

From the analysis it may be concluded that plant populations of the *Leucobryo-Pinetum* ground layer tend to aggregate. It has been proved by the relatively numerous "contagious tests". In the majority of species random distribution occurs only relatively, namely it is dependent on the area size. Under small scales (quadrats of 1 and 2 m^2) most populations are characterized by the contagious spatial distribution. In larger areas aggregations composed of individual species are dispersed randomly.

In some populations such aggregations formed also under macroscale (quadrats of 16 and 32 m^2). Such spatial structure has been characteristic of those species which tend to aggregate in various grid parts. They inhabit the patch in different ways so chances of finding individuals of these populations vary within biochore. When individual populations aggregate in different directions (with which probability of their finding increases), so when there is no common trend, phytocoenose can be spatially homogeneous under macroscale. Such as it has happened here.

For the analysed phytocoenose threshold area size, from which the fraction of "contagious tests" significantly decreases, equals 4 m^2. Afterwards most populations attain spatial distributions and the analysed patch can be considered homogeneous.

Results presented above and those of analogous studies with respect to the assumptions and methods, indicate that: 1) the type of spatial species distribution is a function of the area size (Gounot 1962, Kwiatkowska 1972), 2) a degree of the phytocoenose homogeneity, namely contribution of the species with random spatial distributions to all species composing phytocoenose, depends on the area size (Gounot 1962, Kwiatkowska 1972), and 3) for analysed phytocoenose the area size at which number of species with random spatial distributions is significantly higher than at any other area can be determined; that is the area above which number of "contagious tests" significantly decreases (Kwiatkowska 1972).

The phytocoenose homogeneity with respect to the biomass spatial distribution has been studied so far. There exist only some works concerning spatial differentiation of the standing biomass at the landscape level (Kwiatkowska and Dudziec 1974), spatial differentiation of the cormus volume in the phytocoenose ground layer (Faliński 1973), or changes in the type of biomass spatial structure in the succession series of plant communities (Symonides and Borowiecka 1985). Comparable date are available only for some indicators of the ground-layer standing biomass (Chojnacki 1974).

The type of spatial distribution of both qualitative and quantitative measures is a function of the quadrat size. For the total ground-layer biomass, as well as biomasses of the most species, the spatial distributions are contagious for small, and random — for large quadrats. Therefore, analysed phytocoenose is homogeneous with respect to the standing biomass only under the large scale of its spatial differentiation, namely 32 m^2. The fraction of "contagious tests" significantly decreases only for this and larger quadrats.

Decrease in the fraction of species with random biomass distributions and in that of "contagious tests", characteristic of quadrats not smaller than 32 m^2, is governed mainly by seedlings of trees and shrubs. Studies have indicated, that many herb species in the phytocoenose under study, as well as dwarf-shrubs, form non-randomly dispersed aggregations of high biomass values, even at such large quadrat size.

The phytocoenose homogeneity looks different with respect to the type of spatial distribution of the total ground-layer biomass, related to the area size. Then, phytocoenose can be considered homogeneous in the mean and large scales, namely 8 and 32 m^2. As the ground-layer biomass is organized spatially, probability of finding its high and low values differs within biochore.

Spatial distribution of the total ground-layer biomass and these of individual species result in a mosaic (Kwiatkowska and Symonides 1985a). Against the background of low values aggregations of high values occur. They are surrounded by transient values, and their mosaic on the cartogramms forms an arrangement with the spatial organization of values specific of the analysed populations.

Also some relationships, found earlier, indicate statistical non-homogeneity of the frequency biomass distribution. Frequency distribution of the ground-layer biomass and those of individual species do not fit the random distribution (normal distribution), independent of the area size. Symmetrical distributions have been found for the total ground-layer biomass and biomass of some populations only at the quadrat size of 8 and 64 m^2 (Kwiatkowska and Symonides 1985b).

The homogeneity analysis of phytocoenose under study shows that both for qualitative and quantitative measures analogous conclusions may be drawn: 1) homogeneity is always a function of the area size; 2) at least for the global measure, such as the total ground-layer biomass, condition of the patch homogeneity can be fulfiled under particular scale of the phytocoenose spatial differentiation; and 3) the specified scale of spatial differentiation of biomass values, related to the particular quadrat size, is homogeneous from the statistical point of view.

Summing-up, in the analysed *Leucobryo-Pinetum* phytocoenose the scale of spatial differentiation can be determined, at which species dispersal and spatial sequence of high and low biomass values are random. However, the area size at which phytocoenose is homogeneous with respect to qualitative measures differs from that at which it is homogeneous for quantitative measures.

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Statystyczna analiza jednorodności fitocenozy. III. Typ rozkładu przestrzennego gatunków i stanu ich biomasy jako funkcja wielkości powierzchni

Streszczenie

Praca jest częścią szerszych studiów nad problemem homogeniczności fitocenozy, mających na celu paralelizację wyników uzyskanych dla cech jakościowych i ilościowych, z zastosowaniem różnych wskaźników homogeniczności. W dwóch wcześniejszych opracowaniach za miarę jednorodności użyto typ rozkładu wskaźników ogólnej różnorodności gatunkowej i równomierności (Kwiatkowska i Symonides 1985a) oraz rozkład frekwencji i rozkład wartości stanu biomasy jako funkcję wielkości powierzchni (Kwiatkowska i Symonides 1985b). Do badań wytypowano fizjonomicznie jednorodny płat *Leucobryo-Pinetum* Mat. (1962) 1973. Szczegółowy opis fitocenozy oraz zakres i metody badań podano w pierwszej pracy prezentowanego cyklu (Kwiatkowska i Symonides 1985a). W niniejszej pracy analizę homogeniczności przeprowadzono na podstawie rozmieszczenia gatunków i rozkładu przestrzennego biomasy jako funkcji wielkości powierzchni. W obu przypadkach zastosowano nieparametryczny test serii (Jones 1955, Gounot 1962, Kwiatkowska 1972). Za kryterium jednorodności przyjęto losowy typ rozkładu wartości cech jakościowych i ilościowych.

Badania wykazały, że: 1) Typ rozkładu przestrzennego większości gatunków zależy od wielkości powierzchni podstawowej; skupiskowość rozkładu stwierdzono u 86% testowanych

gatunków (tabela 1); 2) Frakcja testów oznaczających skupiskowy typ rozkładu oraz frakcja gatunków, dla których stwierdzono rozmieszczenie skupiskowe maleją ze wzrostem powierzchni (rys. 2-4); 3) Prawdopodobieństwo znalezienia sześciu gatunków: *Vaccinium myrtillus, V. vitis-idaea, Calluna vulgaris, Melampyrum pratense, Molinia coerulea i Luzula pilosa* jest niejednakowe w różnych częściach biochory (rys. 5); 4) Typ rozkładu przestrzennego biomasy runa i większości gatunków są funkcją wielkości powierzchni (rys. 6); losowo, niezależnie od wielkości powierzchni podstawowej rozmieszczona jest tylko biomasa siewek *Sorbus aucuparia*; 5) Wartości biomasy runa i biomasy większości gatunków rozmieszczone są skupiskowo w skali małych powierzchni i losowo — w skali dużych powierzchni (rys. 7-8).

Reasumując, stwierdzono, że jednorodność jest zawsze funkcją wielkości powierzchni. W badanej fitocenozie można wskazać taką skalę zróżnicowania przestrzennego, w której rozmieszczenie gatunków oraz sekwencja przestrzenna wysokich i niskich wartości biomasy są losowe. Skala ta jest jednak różna dla cech jakościowych i ilościowych.