The structure of plant communities on the example of an oak-pine forest (*Pino-Quercetum*) in Ratanica Valley (Carpathian Foothills)

1. The homotoneity of a forest floor vegetation in terms of the frequency and co-occurrence of species

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Abstract

Mathematical methods of uniformity analysis were used to evaluate the results of classification of plant communities by the Braun-Blanquet method. This was done by both the frequency analysis method traditionally used in phytosociology and by the verification of the null hypothesis on the independent occurrence of species. The results obtained confirmed the validity of the following assumptions: 1) the number of high frequency species rises along with the decreasing rank of the syntaxon and 2) the proportion of species occurring interdependently (showing a positive or negative correlation) decreases.

Key words: homotoneity, interspecific association, syntaxa, Braun-Blanquet approach

INTRODUCTION

The Central-European phytosociology established mainly by Braun-Blanquet (1928, 1964) is, in a certain sense, in a paradoxical situation. Its methodological basis — the subjective criteria of selection, grouping and classification of sample plots, as well as its theoretical basis — the idea of associations and characteristic species — have for long been the subject of criticism (Gleason 1926, Goodall 1954, Poore 1955, 1956, Moore 1962, Kershaw 1973). In spite of this, it is undoubtedly the most wide-spread method of studying vegetation. This relatively exhaustive and universal system of identification and classification of most plant communities of Western and

Central Europe has been transferred to other continents as well. Due to its simplicity, it has been used in agricultural science and forestry in many countries.

Although diversity of scientific approaches is a natural trait of every branch of science, the future of phytosociology seems to lie in a well-understood compromise among and integration of its various trends and schools, aimed at developing a more universal method of vegetation analysis (Noy-Meir and Van der Maarel 1987, Róžański 1988). One of the more important factors of such integration is found in mathematical methods of data analysis, thanks to which it is possible to compare various results and its interpretation is more unequivocal.

It should be mentioned here that the precursor of these methods in phytosociology was the Polish botanist, Professor Stanisław Kulczyński, whose papers were used as standards for many years (Kulczyński 1928, 1940).

The objective of the series of papers entitled jointly "The structure of plant communities..." is to determine the relationship between the elements making up a phytocenosis or system of phytocenoses and to confront these results with the image of the vegetation obtained using classical Braun-Blanquet methods. The question of the degree to which these two pictures coincide, where they supplement each other and where they are in contradiction is of fundamental importance to the objective evaluation of the abundant production of the Central-European school of phytosociology.

This paper deals with the degree to which statistical analysis of uniformity can confirm the results of phytosociological classification.

ASSUMPTIONS

Central-European phytosociology is based on the statement that vegetation is made up of phytocenoses, e.g. sites covered by homogenous vegetation which may be grouped together on the basis of floristic similarities then classified and described as abstract entities, syntaxons. Because the Braun-Blanquet classification is hierarchical in structure, there is a relationship between the rank of a syntaxon and its floristic uniformity.

The question of uniformity is undoubtedly a key factor in studying vegetation, especially when the objective of the study is to produce a classification and systematics of communities. This concept is, however, often interpreted differently and sometimes ambiguously, depending on the methodological school and scale to which it is being applied. The terms homogeneity and homotoneity are associated with efforts to use more precise wording (Dahl 1960, Vasilevich 1969, Westhoff and Van der Maarel 1973). The proposition made by Westhoff and Van der Maarel (1973) seems to be relatively simple and logical. They associate homogeneity with analytical studies of single (individual) phytocenoses, while equating homotoneity with the synthetic approach to numerous phytocenoses representing the same community.

In this sense, the assessment of uniformity of an association by Central European phytosociology is a classical example of studying homotoneity,

although Braun-Blanquet himself (1964) does not distinguish between these concepts when using the term homogeneity. All of the measures of homogeneity used by this school (Raunkiaer 1934 cit. Braun-Blanquet 1964, Raabe 1952, Pfeiffer 1957, Moravec 1971, Westhoff and Vander Maarel 1973) are based on the same, fundamental assumption that the more uniform an association (or, more precisely, the phytosociological table that represents it), the greater the proportion of species occurring with high frequency.

Concepts of homogeneity based on various types of statistical analysis (Kyllin 1926, Dahl and Hadač 1949, Goodall 1954, 1961) may similarly be reduced to one null hypothesis that particular structural traits of phytocenoses have a random distribution. In agreement with such an approach, Goodall (1953) described as uniform, in the sense of homogeneity, those plant communities in which the species composing it occur independently, that is, randomly,

If, a set of random sample plots is classified according to Braun-Blanquet method, then frequency analysis and co-occurrence of species in the ordered sub-sets will be a way of verification of the classical phytosociological classification. Because the hierarchical Braun-Blanquet system assumes the increasing uniformity of increasingly lower syntaxons, such a verification must be founded on two basic assumptions:

1. The number of species occurring with high frequency rises with the decreasing taxonomic rank.
 2. The number of species occurring in a dependent manner, that is, showing a positive or negative correlation, decreases with decreasing taxonomic rank.
- These hypotheses need to be checked using sample plots of various sizes (Vasilevich 1969, Kershaw 1973, Podani 1984), although for our purposes, they should fit within the range of sizes generally used in phytosociological studies.

MATERIAL AND METHODS

STUDIES AREA

The study was carried out in the Wieliczka Foothills (Podórze Wielickie) in the Ratanica Stream watershed (49°51'N, 20°02'E) on an area of 2.412 km² and 50.4% forest cover at an altitude of 270-424 m above sea level. The study was localized in a forest complex with an area of 117.37 ha, in which pine and pine-beech dominated, classified in the most part as *Pino-Quercetum* Kozł. 1925 (Różański et al. 1987).

DATA COLLECTION

Two series of 116 phytosociological relevés were taken in July, 1987 of plots delineated by concentric squares having 10 or 16 m sides. In contrast with the Braun-Blanquet method, the relevés were not located subjectively, but in

a systematic-random way: the centers of the releves were placed in the intersections of the 100 x 100 m permanent grid. This material was expanded by data collected on the basis of this same grid in July, 1986 (D z i a s e k 1987). They contained information on the occurrence of species on every square meter of a square plot with a 5 m side. The data so compiled made it possible to analyze the frequency and co-occurrence of species in three series of 116 concentric sample plots, 25, 100 and 256 m² in size.

DATA SELECTION

On the basis of a phytosociological map made independently (R ó ž a ń s k i et al. msc) the plant association was determined for each of the 116 sample plots (Table 1). This made it possible to determine five sets from the analyzed samples having an increasing degree of syntaxonomic uniformity.

The forests of the Ratanica Valley are managed, due to which the tree cover, up-growth and undergrowth are subject to silvicultural practices. For this reason only the species of the forest floor vegetation were taken into account in the calculations. Seedlings with cotyledons were not taken into account because they are an ephemeral element of the phytocenosis.

The calculations on the co-occurrence of species were limited only to those species which occurred in the set under consideration at least 10 times. In cases of a lower frequency the use of tests of independence becomes inadequate (Vasilevich 1969, Kershaw 1973).

FREQUENCY ANALYSIS

The following measures were used to evaluate homotoneity:

1. The Raunkiaer constancy diagram (1934 cit. Braun-Blanquet 1964);
2. The Van der Maarel coefficient — CM (1972):

$$CM = \frac{S_{IV} + S_V}{S_{II} + S_{III}} ; \quad [1]$$

S_{II} ,, S_V — the number of species in the constancy classes II-V;

3. Pfeiffer's coefficient — H (1957):

$$H = \frac{n_1 + n_2 + \dots + n_N}{N \times G} 100\% ; \quad [2]$$

$n_1, n_2, \dots, n_N$ — the number of species on the sample plot; N — the total number of sample plots; G — the total number of species in a set.

The absolute values of the presented measures of homotoneity are significantly dependent on the total number of sample plots (Moravec 1971, West

Table 1
Selection criteria of sample plots (s.p.) in analysed data sets

Selection	Analysed set signature (number of s.p.)	Rejected sets (number of s.p.)
—	All s.p. in Ratanica valley R (116)	—
Association	<i>Pino-Quercetum</i> PQ (97)	<i>Tilio-Carpinetum</i> (5) <i>Luzulo nemorosae</i> - <i>Fagetum</i> (4) Alder, ash carrs (4) (Alliance <i>Alno-Padion</i>) Beechwoods (3) (Order <i>Fagetalia</i>) Mixed forests (Alliance <i>Pino-Quercion</i>)
Sub-association	<i>Pino-Quercetum</i> <i>rubetosum hirti</i> PR (81)	<i>Pino-Quercetum typi-</i> <i>cum</i> (16)
Variant	<i>P.-Q. rubetosum hirti</i> variant typical PT (38) <i>P.-Q. rubetosum hirti</i> var. <i>Fagus sylvatica</i> PF (43)	—

hoff and Von der Maarel 1973). In order to take this factor into account, frequency analysis was carried out in two calculation variants: in the first, all of the sample plots in a given set were used (Table 1) in the second, in order to guarantee an identical number of sets, 20 samples were drawn randomly.

ANALYSIS OF INTERSPECIFIC ASSOCIATIONS

The null hypothesis, according to which species occur on sample plots independently of each other, was verified at a level of significance of 0.05, by calculating the value of χ^2 according to the formula proposed by Yates for small samples (Sokal and Rolf 1981):

$$\chi^2 = \frac{N (|ad - bc| - N/2)^2}{(a+b)(a+c)(d+b)(d+c)} \quad [3]$$

a — the number of samples in which both analyzed species occur;
 b — the number of samples in which only the first species occurs;
 c — the number of samples in which only the second species occurs;
 d — the number of samples in which neither of the analyzed species occurs;
 N — the total number of analyzed samples $N = a + b + c + d$.

A measure of the relationship between two species was calculated according to the classical Pearson correlation coefficient, which has the following form for qualitative data (Cole 1949):

$$\Phi = \frac{ad - bc}{\sqrt{(a+b)(a+c)(d+b)(d+c)}} \quad [4]$$

(the letter designations are as above).

CORRELATION ANALYSIS BETWEEN SPECIES

The second stage of calculations also took into account quantitative factors of the sets under consideration. Only correlation analysis was done, based on the above-mentioned Pearson coefficient (Sokal and Rolf 1981):

$$\Phi_{xy} = \frac{\sum x_i y_i - \frac{1}{N} (\sum x_i) (\sum y_i)}{\sqrt{[\sum x_i^2 - \frac{1}{N} (\sum x_i)^2] [\sum y_i^2 - \frac{1}{N} (\sum y_i)^2]}} \quad [5]$$

x_i, y_i — are measures of the occurrence of species x and y on the sample plot i . For sample plots 100 and 256 m², the Braun-Blanquet cover-abundance scale was transformed according to the following principle: + — 1; 1 — 5; 2 — 10; ... 5 — 25, so that the numerical values corresponding to the particular Braun-Blanquet degrees fit in the frequency scale: 1–25 in 25 m² samples. The significance of correlation was evaluated at 0.05.

RESULTS

THE FLORISTIC COMPOSITION

The flora of the studied forest is rather poor. In the entire set of data, only 140 species were identified in the largest sample plots. This number consequently drops to 55 along with the lowering of the syntaxonomic rank of the analyzed sets and decreasing area of the sample plot (Table 2). The number of species occurring with a relatively high frequency (at least 10 occurrences) ranged from 12 to 36, but their fraction was maintained at a relatively steady level (Table 2). This means that the participation of species occurring with high frequency in sets containing fewer sample plots is distinctly higher (10 occurrences in 116 samples equals a frequency of 8.6%, while in 38 samples comes to 26.3%). This fact is the first confirmation of our hypothesis of the increasing floristic uniformity of the analyzed sets.

HOMOTONEITY AND SPECIES FREQUENCY

In general, all of the analyzed measures of homotoneity support the first assumption which states that along with decreasing syntaxonomic rank the proportion of species occurring with high frequency increases. The distribution of constancy (Fig. 1) changes from distinctly monoclinic for the whole set of data (when the sample size is 25 m² there is even no class V) to the expected J-shape in the sets representing variants, PT and PF. A similar picture of increasing homotoneity in the analysed series of subsets (Figs. 2, 3) was given by: the Van der Maarel coefficient [1] which is an attempt at a synthetic representation of Raunkiaer's Law and Pfeiffer's coefficient [2], which corresponds to the mean frequency of a species in a set.

These rules are broken by set R in the series representing the largest sample plots. It encompasses all of the samples and is undoubtedly the most differentiated, which is confirmed by Pfeiffer's coefficient (Fig. 3A, B) and the Van der Maarel coefficient, but only for a series of sample sizes of 25 and 100 m². For a size of 256 m² this coefficient is surprisingly high, and this in both series of calculations (Fig. 2A, B). The direct reason for such values of the Van der Maarel coefficient is the abrupt jump in the number of species in class IV (from 2 to 5 % A; from 0 to 4 — B) observable in the distribution of the constancy classes (Fig. 1A, B). Only ten-odd species (Table 2) commonly occur with high density on the studied area. They react with a distinct rise in frequency to an increase in sample size, and pass on to high constancy classes. The remaining species occur in low density and, in spite of increasing the sample size, they remain in lower constancy classes I and II. A gap arises in class III which becomes decisive for the results of the series of the series of sample plots 256 m² in size.

The results are less ambiguous for an analysis which takes into account all of the plots of a given set (Figs. 1A-3A). At a constant density of samples this guaranteed stratified, proportional to the area share of the individual communities, representation of the analyzed sets. When 20 samples are randomly chosen from each set (Figs. 1B-3B), the calculated measures of homotoneity are encumbered by a large scatter, but are not in contradiction with the first assumption. The substantial increase in the Pfeiffer coefficient seen in this calculation variant (Fig. 3B) is the effect of limiting the number of species in constancy class I (Fig. 1). In order for this coefficient to be more comparable, the computations should be limited to species from classes II-IV (Westhoff and Van der Maarel 1973).

This analysis brings out clearly visible differences between two communities representing the same syntaxonomic rank. The *Fagus sylvatica* variant of the sub-association *Pino-Quercetum rubetosum* is by such an evaluation less homotoneic than the typical variant for that same sub-association (Figs. 2, 3). It should be noted that the Van der Maarel and the Pfeiffer coefficients [1, 2] favorize communities floristically rich, which also becomes evident in the case of these two variants (Table 2).

<i>Pleurozium schreberi</i>	14	14	10	13	13	10	—	—	—	—	—	—	—	—	—
<i>Equisetum sylvaticum</i>	14	12	11	—	—	—	—	—	—	—	—	—	—	—	—
<i>Lamiastrum galeobdolon</i>	14	11	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Thelypteris limbosperma</i>	14	10	—	14	10	—	11	—	—	—	—	—	—	—	—
<i>Dryopteris filix-mas</i>	14	—	—	10	—	—	10	—	—	—	—	—	—	—	—
<i>Rubus idaeus</i>	12	11	—	11	10	—	—	—	—	—	—	—	—	—	—
<i>Molinia arundinacea</i>	11	—	—	11	—	—	—	—	—	—	—	—	—	—	—
<i>Salix caprea</i>	11	—	—	11	—	—	—	—	—	—	—	—	—	—	—
<i>Atrichum undulatum</i>	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Papulus tremula</i>	10	—	—	10	—	—	—	—	—	—	—	—	—	—	—
<i>Senecio fuchsii</i>	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Number of species occurring at least 10 times (A)	36	30	26	32	28	24	25	23	19	21	17	13	16	14	12
Total number of species in forest floor vegetation (B)	140	124	112	122	110	91	117	106	82	88	79	60	84	71	55
Ratio A/B	0.25	0.24	0.23	0.26	0.26	0.26	0.21	0.22	0.23	0.24	0.22	0.22	0.19	0.20	0.22

Nomenclature according to Tutin et al. (1980)

Fig. 1. The distribution of constancy classes. A — all samples in a given set are taken into account; B — twenty samples were randomly selected from each set. $0 < I \leq 20\%$, $II \leq 40\% < III \leq 60\%$, $< IV \leq 80\% < V \leq 100\%$ (see Table 1 for a description of the sets)

Fig. 2. Values of the Van der Maarels coefficient [1]. A — all samples in a given set are taken into account; B — twenty samples randomly selected from each set. (see Table 1 for a description of the sets)

Fig. 3. Values of the Pfeiffer [2] coefficient [1]. A — all samples in a given set are taken into account; B — twenty samples were randomly selected from each set. (see Table 1 for a description of the sets)

In light of phytosociological evaluations, even the most uniform of the analyzed subsets are not sufficiently homotoneic since in none of them do constancy classes IV or V reach a distinct advantage over class II or III (Fig. 1), and the Van der Maarels coefficient (Fig. 2) does not exceed the value of 1.5, which indicates a high degree of homotoneity (Westhoff and Van der Maarel 1973). This makes it possible to state that the phytosociological criteria of homotoneity are adapted to data collected in a selective manner, not randomly.

In summing up the picture of homotoneity obtained through the analysis of species frequency, it should be pointed out that the measures under consideration

depend to a high degree on the size and total number of sample plots and on the floristic richness of the community. The most homotoneic is the series containing the largest samples which, on random selection represent phytocenoses of the lowest homogeneity. This is, it seems, the weakest point of the evaluation of homotoneity based on frequency analysis.

HOMOTONEITY AND INTERSPECIFIC ASSOCIATIONS

In the entire studied complex (set R), depending on the size of the sample, the proportion of pairs of species occurring non-randomly was 30.2-34.8% (Fig. 4). Among these pairs, only 1/3 are species with a significant negative correlation. The size of the samples does not significantly affect the result also in the case of negative correlation (Fig. 4B). Both the predominance of independent pairs as well as the small percentage of negatively correlated pairs are a reflection of the small differentiation of the forests in the Ratanica Valley; only one type of vegetation is wide spread — that of a mixed forest.

Fig. 4. The proportion of pairs of species showing significant relationship. (Qualitative data). A — Joint relationships, positive and negative; B — negative relationships. (see Table 1 for a description of the sets)

Successive selections of material bring a distinct drop in the percentage of dependent pairs (Fig. 4). The relatively smallest changes were obtained by selecting the *Pino-Quercetum* association which dominate among the collected samples and is internally differentiated. Only on the level of the subassociation *Pino-Quercetum rubetosum hirti* did the percentage of correlated pairs fall by almost one-half — 14.7%-21%, with this drop being even more distinct in the negative correlations.

Further divisions into variants within a subassociation resulted in highly uniform systems because up to 90 and 95% of the pairs co-occurred with each other independently. In the variant with the beech dominating in the forest stand,

not one pair was significantly negatively correlated; 1 or 2 such pairs were found in the typical variant, depending on the size of the sample.

In spite of the fact that completely random systems were not obtained even in the lowest syntaxonomic ranks, the general direction of the changes support very well the second hypothesis of this study. The identification of units in the field and the classification of phytosociological relevés made using the classical method of comparison gave in effect the delineation of groups of phytocenoses ordered hierarchically from highly uniform to increasingly more floristically diverse.

HOMOTONEITY AND SPECIES CORRELATION

Introduction of information on the abundance of species into the calculations only slightly changes the overall picture of dependences described in the previous section (Fig. 5). This is, to a certain extent, the effect of the method of calculating the correlation coefficient which takes into account all of the samples of a given set, even those in which both of the species in question are lacking. Because of this, the same set of information was used in the analysis of qualitative and quantitative data. However, the fact that a plant was or was not present was the most decisive factor, the plant's abundance was only a modifying factor.

Fig. 5. The proportion of pairs of species showing significant correlations. (Quantitative data). A — correlations jointly, positive and negative; B — negative correlations. (see Table 1 for a description of the sets)

In comparison with qualitative analysis, the percentage of correlated pairs was somewhat lower in the whole set and their decreasing percentage is less marked in sets representing lower syntaxons (Fig. 5). More distinct and more irregular differences occurred between the results obtained for changing areas of sample plots. This is especially well visible for 25 m² plots; it must, however, be emphasized that in this case not only the size of the sample is significantly

decreased, but the species abundance was determined by the absolute frequency in the scale of 1-25, and not in the Braun-Blanquet abundance scale.

In spite of the general similarity of results of analysis of qualitative and quantitative data, significant differences also occurred. The "spectrum" of co-occurrence changed and only 23.5-60.1% of the pairs of species showed the same dependence — positive or negative (Fig. 6). Along with the decreasing syntaxonomic rank of the set the degree of agreement of the results also decreased. This result corresponds well with the criteria of the Braun-Blanquet classification, in light of which the abundance of species plays an important part only in the delineation of the lowest syntaxons — variants, facies.

Fig. 6. Agreement of results obtained according to qualitative and quantitative data. (see Table 1 for a description of the sets)

All of the changes of the relationship between species were limited to shifts in or out of groups of random pairs, which means that there was not one case of a pair that had been negatively correlated showing upon change in the nature of data (quantitative to qualitative or vice versa) a positive dependence. However theoretically impossible does the second case seem to be, the situation in which species negatively correlated quantitatively show at the same time a positive dependence in qualitative analysis, may take place. This would occur if similar habitat requirements caused species to meet more frequently than would result from random occurrences, however, one of them, the stronger one, would distinctly limit the quantity of its partner. This type of interspecific interaction requires analysis on smaller sample plots and the calculation of correlation only for those plots on which both species are found.

DISCUSSION

The development of phytosociology was accompanied by, on the one hand, sharp criticism of the basic methodological assumptions, on the other, by repeated attempts to objectivize the obtained results (see the works cited earlier).

In respect to the Braun-Blanquet school, the criticism was aimed at not only the collection of data, but at the manner of its classification as well. Modern numerical methods make it possible to order or classify relevés according to objective criteria (Westhoff and Van der Maarel 1973, Van der Maarel 1981), although the choice between the numerous different mathematical models which give significantly different results still remains the subjective choice of the investigator (Róžański 1988). It may therefore be said that numerical syntaxonomy has solved, in principle, the drawback of subjective classification of phytosociological relevés and that further progress in this respect will be aimed at determining the optimal mathematical model of numerical analysis for the Braun-Blanquet concept.

For this reason, the difficulties found in the collection of data become the main methodological problem. While not addressing the question of homogeneity of particular phytocenoses, which already has received much attention (Kwiatkowska and Symonides 1986 and ref. cit. therein), the objection that they are selected to fit a predetermined concept is hard to refute because the result depends on such intangible traits as the abilities of the investigator and his objectivism. The question to what extent can the random choice of data be reconciled with the theoretical principles of the Braun-Blanquet school begins to take on major importance.

Recently, attempts have been made to verify the results of synecological studies through the formulation and testing of the null hypothesis on the random nature of the phenomena under study (Wołek 1983, Noy-Meir and Van der Maarel 1987). The studies of Wołek on communities of pleustonic plants (class *Lemnetea*) seem to provide partial proof that the realities of nature and the achievements of phytosociologists do not always correspond. The hypothesis on the random distribution of the observed combinations of species could not be eliminated, therefore the entire material should be considered uniform, not permitting the delineation of numerous associations and higher taxonomic units. However, these results apply to very specific systems, especially prone to random disturbances (the translocation of plants by water currents). Phytocenoses of rooted plants, whose diaspores are also randomly translocated, do, however, undergo selection during early stages of development, have different sources and a more permanent structure, thereby the hypothesis about the random nature of groups of *Luzula* species has only in part not been abolished (Wołek and Pancer-Kotejowa 1988).

What is therefore the value of the huge mass of information contained in phytosociological studies? Pore (1955) was willing to accept the concept of an association and the usefulness of data collection in relevés, while decidedly rejecting syntaxonomic hierarchy.

The presented studies, based on a series of random samples, have to a significant extent confirmed the validity of phytosociological classification and this regardless of the size of the sample plots. Both frequency analysis and the

co-occurrence of species show that the successive, lower syntaxonomic ranks are increasingly more uniform. This upturns P o o r e 's criticism (1955) that the hierarchical classification is erroneous. However it should be emphasized here that analysis of the co-occurrence of species gave much more unambiguous results and a simpler interpretation than the results of frequency analysis of species. In contrast with the last one, the assumptions of co-occurrence analysis are adapted to the random method of data collection, and this is where the success of this method lies. The value of the conducted comparisons is raised by the fact that in the Ratanica forest, only those syntaxa were identified which were described on the basis of widespread studies of the forest communities of the Wieliczka Foothills (Podgórze Wielickie) (R ó ż a ń s k i et al. 1987), thanks to which this verification has a more universal application.

In summing this study up, we can ask if G l e a s o n was right when he wrote in 1926 "... definition and classification of associations... represent merely abstract extrapolation of the ecologist's mind."? Rather not. Phytosociology has accumulated a set of knowledge about vegetation which, to a significant extent, withstands the test of analytical-mathematical verification. It seems, however, that it is urgently necessary to further perfect the methods used, especially in the area of data collection, which will make it possible to apply to every case of vegetation description the entire mathematical apparatus which the science presently have at their disposal.

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Struktura zbiorowiska roślinnego na przykładzie boru mieszanego Pino-Quercetum w dolinie Ratanicy (Pogórze Wielickie).

1. Jednorodność zbiorowiska w aspekcie frekwencji i współwystępowania gatunków runa

Streszczenie

W pracy analizowano homotoniczność zespołu *Pino-Quercetum* zróżnicowanego na podzespoły i warianty. Na podstawie teoretycznych założeń szkoły Braun-Blanqueta sformułowano następujące hipotezy: 1) wraz z malejącą rangą syntaksonu liczba gatunków o dużej frekwencji wzrasta oraz 2) udział gatunków występujących zależnie (wykazujących dodatnią lub ujemną korelację) maleje. Materiał do weryfikacji statystycznej zebrano w zwartym kompleksie leśnym (ca 120 ha) ze 116 rozmieszczonych systematycznie prób o wielkości 256, 100 i 25 m². Na podstawie mapy zbiorowisk roślinnych tego terenu, z danych wyselekcjonowano 4 zbiory o różnej randze syntaksonomicznej (tab. 1). W analizie frekwencji wykorzystano rozkład klas stałości Raunkiaera oraz współczynniki Pffeifera i Van der Maarela. Do weryfikacji hipotezy o niezależnym występowaniu gatunków zastosowano statystykę χ^2 z poprawką Yatesa, zaś miarę zależności między nimi określono w oparciu o współczynnik korelacji Pearsona. Ogólnie wszystkie rozpatrywane kryteria homotoniczności potwierdziły przedstawione wyżej założenia. Miary oparte na frekwencji gatunków dają obraz mniej czytelny (rys. 1-3), ponieważ nie są dostosowane do danych zbieranych losowo, a ponadto na wyniki bardzo silnie wpływa liczba i wielkości powierzchni próbnych. Analiza współwystępowania gatunków dużo lepiej potwierdza hipotezę, że wraz z malejącą rangą syntaksonu zwiększa się jego homotoniczność i coraz więcej gatunków spotyka się w nim losowo (rys. 4 i 5). Prezentowane badania oparte na statystycznej analizie danych, w dużej mierze potwierdziły zasadność wykonanej tradycyjnymi metodami klasyfikacji fitosocjologicznej.