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STRUCTURAL CHARACTERISTICS OF HERB LAYER AND ITS PRODUCTION IN MORE IMPORTANT FOREST COMMUNITIES OF POLAND*

ABSTRACT: The paper indicates the relations and general regularities taking place between the production and structural characteristics of herb layer in different forest communities. Floristic richness, density, frequency and population production are otherwise reflected in the gradient of varying forest soil richness. Especially the dominance structure differs considerably between the oligo – and eutrophic environments. The significance of dominants in the structure and functioning of the ecosystem is pointed out.

Contents

1. INTRODUCTION

Plants, and especially their size, quality and production fluctuations, affect significantly other trophic levels and trophic connections of ecosystems. Nevertheless, the studies on populations and secondary production of heterotrophic organisms should be closely connected with simultaneous studies on plant systems. Therefore, the Laboratory of Plant Ecology, Institute of Ecology, Polish Academy of Sciences, always discusses the research projects and choice of environments with other organization units of the Institute which study the secondary production of various animals. The Laboratory of Plan Ecology cooperates with a group of zoologists examining the populations of small rodents. The biomass of herb layer and forest litter composed of leaf fall, bark, shoots, fruit of trees and shrubs are the main food base of several heterotrophic organisms. The formation of various properties of rodent populations depending on the structure of herb layer production and amount of plant fall, and also the gradient of environments of different forest communities — has been the working hypothesis in the cooperation of botanists and zoologists. This explains the genesis of a series of papers on the production of herb layer and the amount of plant fall. Several papers already been published and are quoted in references. They have been prepared mainly by the staff of the Laboratory of Plant Ecology at the Institute of Ecology and partly by people from other research centres participating in the cooperation.

These papers do not follow strictly the outline of primary productivity investigations recommended in papers of the International Biological Programme. These are not studies covering a range of fields, intense, long-lasting and situated on constant areas as, for example, the studies in the "Solling" project — E l l e n b e r g (1971), or in the "Ispina" project — M e d w e c k a - K o r n a ś (1971), M e d w e c k a - K o r n a ś, Ł o m n i c k i and B a n - d o ł a - C i o ł c z y k (1974), or the research work of D u v i g n e a u d nad F r o m e n t (1969). Our studies concern only chosen sections of the ecosystem — herb layer and plant fall. They were conducted only during one vegetation season. Still, this allowed to analyse the chosen parameters in a large gradient of forest communities and in the end provided a relatively abundant comparative material. The next assumption in these investigations was the use of a uniform method suggested by T. T r a c z y k (1967a) which allowed to obtain comparable material. Because not in all communities the amount of plant fall and production of ground layer were examined, therefore the estimates of these parameters are not given here. The research concentrated mainly on the analysis of herb layer. The main aim was to indicate the relations and general regularities taking place between the production and structural characteristics of the herb layer in and among different forest communities. The range of characteristics compared is given in the Contents.

2. FOREST COMMUNITIES

The communities discussed represent the gradient of environments with a high variation range, beginning from sallow scrubs and wet alderwoods, through alder-ash carr, acidophilous oak-pine forests, pinewoods and *Cladonia* pinewoods. A list of forest associations including their superior units of the phytosociological system (mainly after M a t u s z k i e w i c z 1967), locality and authors who provided the data, is presented below.

Class: *Alnetea glutinosae* Br.-Bl. et R. Tx. 1943. Order: *Alnetalia glutinosae* R. Tx. 1937. Alliance: *Alnion glutinosae* (Malc. 1929) Meijer Dress 1936.

1. Association: *Salicetum pentandro-cinereae* (Almg. 1929) Pass. 1961 (= *Salici-Frangu-*

letum Malc. 1929 pp) ("The Wild Apple-Tree Island" on Lake Bełdany, Masurian Lake District. From the paper by H. T r a c z y k 1971).

2. *Carici elongatae-Alnetum* Koch 1926 (Kampinos National Park. From the paper by T. T r a c z y k 1967b).

Class: *Querco-Fagetea* Br.-Bl. et Vlieg. 1937. Order: *Fagetalia silvaticae* Pawł. 1928. Alliance: *Alno-Padion* Knapp 1942 em. Medw.-Korn. ap. Mat. et Bor. 1957.

3. *Circaeo-Alnetum* Oberd. 1953 (Białowieża National Park. From the paper by A u l a k 1970).

4. *Circaeo-Alnetum* ("The Wild Apple-Tree Island" on Lake Bełdany, Masurian Lake District. From the paper by H. T r a c z y k 1971).

Alliance: *Carpinion betuli* Oberd. 1953.

5. *Tilio-Carpinetum* Tracz. 1962, subass. *stachyetosum* (Masurian Lake District. From the peper by H. T r a c z y k 1971).

6. *Tilio-Carpinetum*, subass. *typicum* (Masurian Lake District. From the paper by H. T r a c z y k 1971).

7. *Tilio-Carpinetum* (Kampinos National Park. From the paper by T. T r a c z y k 1967b).

Alliance: *Fagion silvaticae* R. Tx. et Diem. 1936.

8. *Dentario glandulosae-Fagetum* Klika 1927, em. Mat. 1964 (The Pieniny Mountains. T. Traczyk — unpublished data).

Class: *Vaccinio-Piceetea* Br.-Bl. 1939. Order: *Vaccinio-Piceetalia* Br.-Bl. 1939. Alliance: *Pino-Quercion* Medw.-Korn. 1959.

9. *Pino-Quercetum* Kozł. 1925 (Pisz Forest. From the paper by P l e w c z y ń s k a 1970).

10. *Pino-Quercetum* (Kampinos National Park. From the paper by T. T r a c z y k 1967b).

11. *Pino-Quercetum* („Las Piwnicki" (Piwnicki Forest) near Toruń. B. Moszyńska — unpublished data).

Alliance: *Dicrano-Pinion* Libb. 1933.

12. *Vaccinio uliginosi-Pinetum* Kleist 1929 (Kampinos National Park. From the paper by M o s z y ń s k a 1970).

13. *Vaccinio myrtilli-Pinetum* Kobendza 1930 (Kampinos National Park. From the paper by T. T r a c z y k 1967b).

14. *Vaccinio myrtilli-Pinetum* (Kampinos National Park. From the paper by T. T r a - c z y k, H. T r a c z y k and B. M o s z y ń s k a 1973).

15. *Vaccinio myrtilli-Pinetum* (Pisz Forest. From the paper by L. P u s z k a r, T. T r a c z y k and Z. W ó j c i k 1972).

16. *Vaccinio myrtilli-Pinetum* (Pisz Forest. From the paper by L. P u s z k a r, T. T r a - c z y k and Z. W ó j c i k 1972).

17. *Piceetum (excelsae) tatricum* (Szaf., Pawł., Kulcz. 1923) Br.-Bl. et Vlieg., Siss. 1939 (The Pieniny Mountains. T. Traczyk — unpublished data).

18. *Vaccinio myrtilli-Pinetum* var. *Calluna-Dicranum* (Kampinos National Park. From the paper by T. T r a c z y k, H. T r a c z y k and B. M o s z y ń s k a 1973).

19. *Cladonio-Pinetum* Juraszek 1927 (Kampinos National Park. From the paper by W ó j c i k 1970).

Altogether data from 19 forest communities have been used. This includes two papers on wet alderwood communities, two on alder-ash carr, four on oak-hornbeam forest and beechwood. The most abundantly represented are communities of the class *Vaccinio-Piceetea* (11 papers), i.e., three papers on oak-pine forests, six papers on pinewoods and two papers on *Cladonia* pinewoods. As regards the majority of characteristics examined an attempt was made

to describe them usually for communities within one alliance, although this has not been always possible. And so, e.g., because there has been only one table on beechwood (No. 8 in the list of communities) it was analysed together with oak-hornbeam forests (*Tilio-Carpinetum*), forming a group of communities of oak-hornbeam type and opposing it to the group of alder-ash carr, acidophilous oak-pine forests, coniferous forests, etc. Of the group of coniferous forests the two last communities were isolated as the so-called dry pine forests (*Cladonio-Pinetum*) – the poorest stands of pinewoods. Altogether six groups of communities were distinguished which most frequently correspond to the alliances. The groups are as follows:

1. wet alderwoods – alliance: *Alnion glutinosae*,
2. alder-ash carrs – alliance: *Alno-Padion*,
3. oak-hornbeam forests – alliance: *Carpinion + Fagion*,
4. acidophilous oak-pine forests – alliance: *Pino-Quercion*,
5. pinewoods and wet pinewoods – alliance: *Dicrano-Pinion*,
6. dry pine forests – close to association *Cladonio-Pinetum*.

3. METHOD

In all papers the method suggested by T. T r a c z y k (1967a, 1967b) has been used and it is briefly described below.

The method is based on two main field analyses. The first one concerns the determination of density (D) of individuals or shoots of particular plant populations, the second – the average individual growth (G_i) of each population separately at the maximum stage of its growth and development. Net primary production (P) of aboveground parts of a single species (population) equals the product of density and average individual growth: $P = D \cdot G_i$. Sum of production of particular populations gives the total production.

In the majority of species examined the aboveground parts die during the winter. For these species the maximum biomass in a given vegetation season will be simultaneously the maximum current growth. Species preserving partly their aboveground shoots over the winter and the following year (e.g., low shrubs) required a distinction between current and previous year's shoots (or increments). In such cases the individual growth has been usually calculated only according to current biomass. Thus, in this method, the production is not deducted from the difference among total biomass (regardless of age) but only with consideration to current biomass produced by particular populations.

A n a l y s i s   o f   d e n s i t y. In homogeneous herb layer stands 100—200 wire rings of a diameter 36.7 cm, i.e., 0.1 m^2 in surface area, are distributed in regular spaces (systematically) or at random (by throwing). In communities with distinct seasonal aspects (e.g., oak-hornbeam forests, beechwood) the analysis is made several times, for each seasonal aspect separately. In each sample the individuals (or aboveground shoots) are counted for each species and the total cover. The number of individuals is calculated per total surface area of samples and given for 1 m^2 or a hectare. The analysis of density also provides data on the frequency of particular species.

D e t e r m i n i n g   t h e   a v e r a g e   i n d i v i d u a l   g r o w t h   (G_i). In periods of maximum population development (blossoming – fructification) a number of individuals or shoots of each species (usually several tens or hundreds) was collected according to the results of density analysis. After drying and weighing the whole biomass of a given species, it was divided by the number of individuals, thus obtaining the average individual growth at maximum population growth.

Although the same method has been used, the variety of material compared is considerable. This was due to many factors: the structurs and productivity of herb layer were analysed in forest stands of different age, the canopy of tree layer varied which considerably affected the development of herb layer within the stand. There were several other causes such as drying, raking, etc. Nevertheless, the fact that there are some characteristics specific for a type (group) or all associations examined proves that they can be regarded as general ecological regularities and special attention will be paid to them.

4. RESULTS AND DISCUSSION

4.1. Frequency

Frequency expresses the probability of finding the species in a stand of a given association, regardless of its density. Therefore, it is not important whether the population of a given species is represented in the sample by 1 or, e.g., 100 specimens. The occurrence, presence of the species, is only significant. In the papers examined the frequency has been calculated from samples taken for density purposes (100—200 samples at random). The frequency is expressed in per cents and divided into the so-called frequency classes in intervals every 20%. For a more precise estimate of the number of sporadic species the class from 1—20% is divided into 2 subclasses; subclass "+" (1—10%) covering very rare, sporadic species with only few individuals in 100 samples, and rare species forming subclass I — frequency 11—20% (several individuals in 100 samples).

The results of frequency greatly depend on the size of main sample, the clumped distribution, size of individuals, etc. (Cain 1943, Oosting 1956, Greig-Smith 1964, Mueller--Dombois and Ellenberg 1974 and others). Of course, the size of main sample — 0.1 m², may be too small to estimate the frequency (even comparing data of Cain and Castro 1959), still, even the analysis of frequency shows some general regularities two of which shall be given:

Table I. Production (P), density (D) and number of species (N) in frequency classes (percentage)

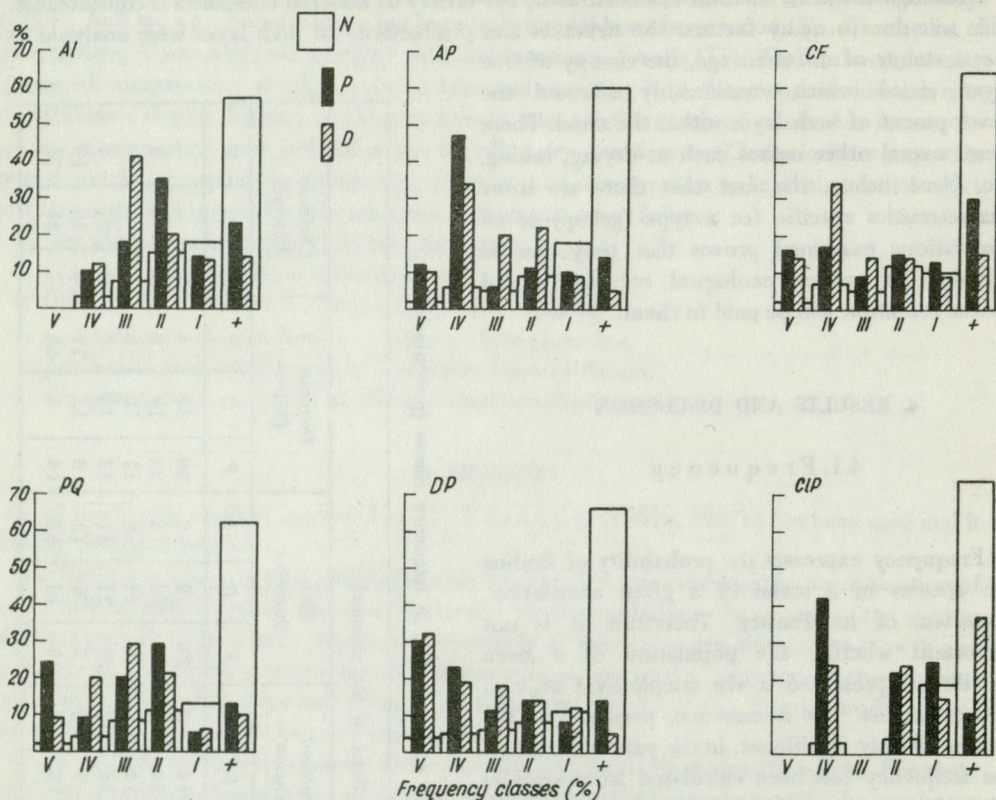| Frequency classes (per cent)		Alnion glutinosae			Alno--Padion			Carpinion + Fagion			Pino--Quercion			Dicrano--Pinion			Cladonio--Pinetum		
		P	D	N	P	D	N	P	D	N	P	D	N	P	D	N	P	D	N
81—100	V	—	—	—	12	10	2	16	14	2	24	9	2	30	32	4	—	—	—
61— 80	IV	10	12	3	47	34	6	17	34	7	9	20	4	23	19	5	42	14	3
41— 60	III	18	41	7	6	20	5	9	14	5	20	29	8	11	18	6	—	—	—
21— 40	II	35	20	15	11	22	9	15	14	12	29	21	11	14	14	8	22	24	4
11— 20	I	14	13	18	10	9	18	13	9	10	5	6	13	8	12	11	25	15	19
1— 10	+	23	14	57	14	5	60	30	15	64	13	10	62	14	5	66	11	37	74

Fig. 1. Percentage of the number of species — N, production — P, density — D in frequency classes
+, I–V — frequency classes, Al — Alnion glutinosae, AP — Alno-Padion, CF — Carpinion + Fagion, PQ —
Pino-Quercion, DP — Dicrano-Pinion, ClP — Cladonio-Pinetum

1. Regardless of the type of forest community the number of sporadic species in herb layer (1–20%) is undoubtedly the highest. This value ranges in particular associations from 66 to 93% of all species. On average, over 80% of herb layer species are either rare or rarely found. Sporadic species (several individuals in 100 samples) cover on average 64% of all species in the community.

2. Contrary to sporadic and rare species, the species belonging to highest frequency classes are not numerous — 1–2%. This means that in several tens of herb layer species only 1 or 2 species are more frequently found than 80 times per 100 samples. More detailed data in this matter are given in Table I and Figure 1.

4.2. Density

Density allows to estimate the number of individuals per surface area unit (m^2, ha). This value ranges considerably (Table I). When analysed in the gradient of soil fertility and abundance of species in communities, a general tendency may be observed, namely: total

density decreases parallelly to the change from fertile to poorer communities. On average the values are: 780 in alder-ash carr, 487 in oak-hornbeam forests, 331 in acidophilous oak-pine forests, 266 in pinewoods and 132 ind./m² in *Cladonia* pinewoods (Table II). This tendency has been observed despite the varying density within particular groups of communities. Density in the herb layer depends on several changing factors: mainly on total cover of herb layer in a given community and about this the canopy of tree and higher shrubs which had considerably changed, frequently decided. Another factor considerably affecting the density is the size of individuals or shoots. Having difficulties in distinguishing individuals, single shoots have been counted as basic units, e.g., *Oxalis* and some grasses, which considerably affects the density.

Table II. Total production, density, number of species and production per one individual
(P : D) and per one species (P : N)

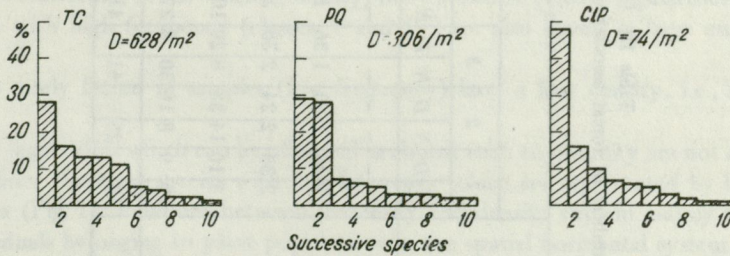| Parameters	Associations of the alliance:					
	Alnion glutinosae	*Alno- -Padion*	*Carpinion + Fagion*	*Pino- -Quercion*	*Dicrano- -Pinion*	*Cladonio- -Pinetum*
Production — P (g/m²)	133	166	45	33	36	15
Density (D/m²)	198	780	487	331	266	132
Number of species — N	21	41	38	30	20	13
P : D	0.67	0.21	0.09	0.10	0.13	0.11
P : N	6.3	4.0	1.2	1.1	1.8	1.2

Fig. 2. Dominance structure of 10 successive species in the densities of three communities
D — general density, $1-10$ — successive species according to decreasing percentage, TC — *Tilio-Carpinetum*,
PQ — *Pino-Quercetum*, ClP — *Cladonio-Pinetum*

Table III. Contribution of number of species and density in density classes
1–19 – numbers of forest associations according to the list in the paper, *N* – number of species, *D* – density (percentage)

Classes	Associations																																					
	1		*2*		*3*		*4*		*5*		*6*		*7*		*8*		*9*		*10*		*11*		*12*		*13*		*14*		*15*		*16*		*17*		*18*		*19*	
	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D
> 50%	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	52	–	–	–	–	–	–	1	67	–	–	–	–	1	72	1	55	–	–
25–50	1	46	1	33	1	36	1	32	1	28	1	28	1	36	–	–	2	57	–	–	2	66	1	46	1	38	–	–	2	62	2	66	–	–	1	39	1	48
10–25	2	35	2	24	2	36	3	34	2	27	4	53	1	33	3	58	–	–	2	29	1	12	3	45	2	32	1	18	–	–	–	–	1	10	–	–	2	26
1–10	5	10	14	33	8	20	10	25	11	36	6	15	5	23	9	22	13	36	5	13	7	19	3	8	7	28	3	9	7	30	9	28	4	12	2	5	6	24
< 1%	10	9	8	10	30	8	27	9	28	9	18	4	19	8	41	20	32	7	16	6	10	3	12	1	3	2	7	6	21	8	16	6	16	6	10	1	4	2
Σ	18		25		41		41		42		29		26		53		47		24		20		19		13		12		30		27		22		14		13	

The analysis of density, similarly as of frequency, has shown that the majority of species are of small value – the so-called sporadic species. Still, in each community there is a distinct dominance in the herb layer of individuals of one or several species (usually 2–4) which decidedly prevail over other species. In communities richer from the floristical and biocenotic point of view, for example, in oak-hornbeam forests, the dominance gradient is milder, whereas in floristically poor and oligotrophic communities (e.g., in coniferous forests) the differences in the density of dominant species (1–2 species) as compared to those with a low density are much higher. The contrast in domination is much higher then. This regularity is confirmed by the whole material examined. Figure 2 illustrates these relations by presenting histograms of densities in oak-hornbeam forests, acidophilous oak-pine forests and *Cladonia* pinewoods.

With consideration to the great differences in the density of particular species, several classes (groups) of species may be distinguished due to their percentage in total density. The suggested division is as follows:

Class V – the main dominant species (main dominants) with over 50% of total density.
Class IV – dominant species (dominants): 25.1–50% of total density.
Class III – frequent species (subdominants): 10.1–25%.
Class II – rare species (influents): 1.1–10%.
Clas I – sporadic species (accessory): less than 1% of total density.

Table III indicates the numbers of species in particular classes of density with the percentage of species in total density. Of 19 associations analysed only in four the main dominant species (main dominants) were found: *Oxalis acetosella* L., *Vaccinium myrtillus* L. and *V. vitis-idaea* L. (in floristically poor coniferous forest communities). Very few species are dominants and subdominants. The majority, over 80%, are the rare and accessory species which are of little significance in the total density. The quantitative aspect of the density of particular populations in a given system can be defined as the domination structure (T r o j a n 1975).

4.3. Frequency and density

Between the occurrence (number of finds) of species in a determined stand (frequency) and the number of individuals in the species (density) there are some general regularities.

1. Species with high frequency (classes V and IV) are also found in large numbers (high density).

2. Species rarely found in samples (low frequency) have a low density, i.e., are sporadic species.

These two regularities which can be observed in almost each community are not a rule for all cases. Sometimes there are species with low frequency which are represented by high density and vice versa (Fig. 1). Relations between frequency and density explain mainly the distribution of individuals belonging to plant populations in the spatial horizontal system, i.e., in the horizontal structure of the system. Four main relations can be observed:

1. If a species has a very high density and frequency it should be checked whether it occurs in the stand in large aggregations or in large clumps more or less evenly distributed as, for example, species forming facies.

2. Species of a low density (few individuals) and low frequency occur sporadically in the herb layer as single individuals.

3. Species of a relatively low density but high frequency are distributed more or less evenly and do not tend to agglomerate.

4. Species of a much higher density but low frequency have a clumped distribution, i.e., occur in bigger groups, hummocks which are unevenly distributed — mosaics.

This, of course, is a general approach. The spatial structure of communities is examined in detail by using special methods (M u e l l e r - D o m b o i s and E l l e n b e r g 1974 and the papers discussed in this work).

Figure 1 and Table I (columns *D*) present detailed data on the density in classes of frequency. Species which prevail (over 80% of all species) in low classes of frequency have a very low density as opposed to species with high frequency. The latter are very few (2—4% of all species), but their density is always much higher than that of numerous accessory and rare species.

4.4. Production in frequency classes

The production of species in particular classes of frequency varies. Species from low classes of frequency which markedly prevail in the floristic composition of the herb layer produce, in general, a relatively low biomass. For example, in acidophilous oak-pine forests the rare species (up to 20% of frequency) cover 75% of all species, although they only produce 18% of total production of the herb layer; analogously in pinewoods: 77 and 22% (Table I). Constant species, frequently found, although very few (usually 2—8% of all species) do not produce much less, sometimes even several times more than a large number of species with low frequency. But the production rate is not much related to the classes of frequency (Table I, Fig. 1). The frequency is an exponent of finding the species in the stand regardless of its density and individual size, and therefore it often happens that a species recorded in samples (V — IV classes) but having low density and small individual biomass does not give high biomass. This is even more complicated as usually in a determined class of frequency there are few or several different populations varying in density or individual size.

4.5. Relation between production and density

Together with the density the production of a given species increases. But in the analysis of production rate in the aspect of classes of frequency or density, where few or several species belong to one class, this obvious principle is not confirmed. This is mainly because of the size of individuals of particular species. If the density of species consists of very small individuals (e.g., *Oxalis*, *Trientalis*, *Majanthemum*), then despite of the high density of this group the production will be low. And the contrary, species represented by large individuals, such as: *Urtica dioica* L., *Cirsium oleraceum* (L.) Scop., *Filipendula ulmaria* (L.) Maxim., etc., despite of their rare occurrence, give high biomass and production. This may explain the lack of close correlation between production and density in Figure 1, where production increase is not always accompanied by proportional increase in density, sometimes it even visibly decreases. The production, therefore, is the result of density of individuals and the individual biomass they produce.

4.6. Index of individual production

This index is the quotient of total production and density $(P : D)$ and expresses the production rate of an average individual in a given community. As all mean values, it may also have a considerable range of data. This becomes especially significant in communities, where beside such giants as, e.g., in the herb layer of wet alderwoods: *Phragmites communis* Trin. or *Carex Hudsonii* Bennet, occur small plants like *Viola palustris* L. or *Hottonia palustris* L. Still, it can be said, that an average individual in wet environments (shallow scrub, wet alderwood) produces 6–7 times more than in other forests (Table II). This confirms the main principle that in moist environments, mesotrophic or eutrophic, there are many more bigger species than on soils with similar trophy, which are drier or periodically very dry.

4.7. Index of species production

Analogously to the production index per average individual in a given community the production index per 1 species per 1 population can be obtained by dividing the total production by the number of species in the herb layer $(P : N)$. However, on average, a species in the herb layer of wet alderwood type produces 6.3 g, in alder-ash carr – 4 g, and in the remaining 4 groups – 1 g, and thus the proportions are similar to the production index per 1 individual (Table II). Although these are not accurate indices they at least show the contrast between extreme environments.

4.8. Biocenotic and habitat-ecological optima

The material obtained in such broad site gradient, and quantitatively analysed, explains much of the ecology of species of the herb layer, the problems of ecological tolerance, and especially their ecological optima. The living conditions of the population are the best, where the individual size, density of individuals and production attain the highest values. The problem of species with narrow limits of ecological tolerance is relatively simple and easy to analyse even using simple phytosociological methods, for example, tabular comparisons. Not enough is known about the ecological preference of species with broad limits of ecological tolerance – "eury" species – and only population studies dealing with the broad aspect of environmental variation may give an answer. The material in 19 tables of cited papers|cannot|be presented in detail. Only general results will be presented. Among "eury" species, even occurring in several forest associations, the majority shows preference for one of the associations (sometimes 2–3). They obtain there the highest parameters of values examined – i.e., higher density, production, larger individuals which blossom and fructify better than in other communities.

Also, some species in a particular type of community have higher density at simultaneous small individual biomass, whereas in other communities their density is lower but the biomass is high. This means that in a particular environment the species population may find its "biocenotic optimum" – high density at lesser development of individuals, and in other – "habitat-ecological optimum", when the limited number of individuals is made up by their good development. But although the species may find good growing conditions it is driven out by other species, better adapted to this environment.

Quantitative indices of particular population characteristics prove the complex character of biocenotic influence on social systems of the ecosystem level. A very nice example of these
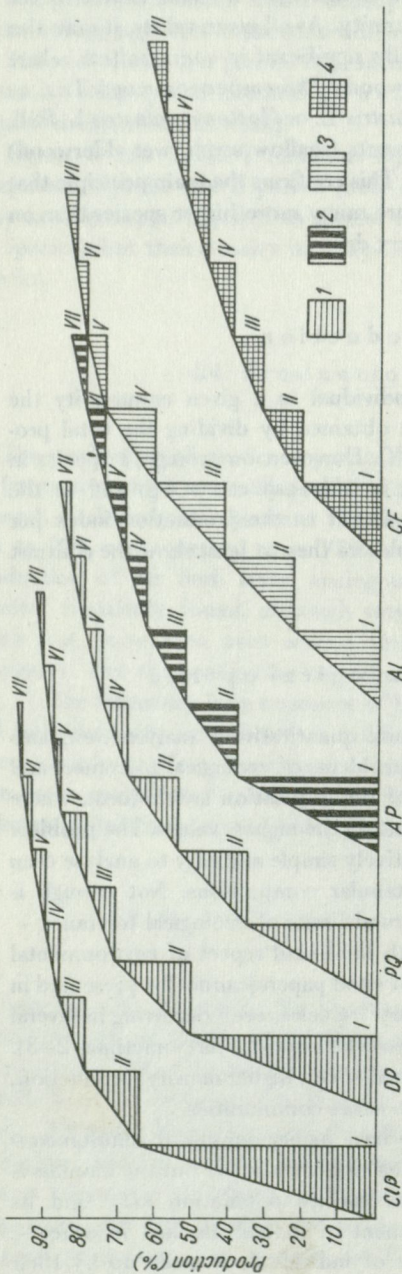
Fig. 3. Dominance structure of species in herb layer production of six types of communities I–VII – successive species according to their decreasing contribution to production, 1 – *Vaccinio-Piceetea:* CIP – *Cladonio-Pinetum,* DP – *Dicrano-Pinion,* PQ – *Pino-Quercion,* 2 (AP) – *Alno-Padion,* 3 (Al) – *Alnion glutinosae,* 4 (CF) – *Carpinion + Fagion*

relations is described by Paczoski (1925) when analysing the spruce population in the Białowieża Forest. This problem is generally discussed and no detail data are given. Those who would like to know more about it should study the material in 19 tables of the original papers, where it is easy to find the confirmation of these statements.

4.9. Distribution of production into species

Total production of a community or its layer, frequently used when describing particular communities, gives no information about the contribution of particular species, although this is very interesting. General results on this subject are variously presented in Figures 3 and 4. Figure 3 has six curves corresponding to six groups of communities. These curves are formed by the cumulation of production of seven species in each group.

For purely technical reasons only seven successive species are given, although for a full illustration the values of other species should be taken into consideration.

On y-axis the production percentage of successive species are given beginning with those having the highest production (I–VII). Cumulation of these values allows to analyse the contribution to production of a particular species (the height of the triangle) and the contribution to total production of 2nd, 3rd and other species altogether.

The production of few only species, especially the production rate of species I (the height of triangle I) and the difference between the next species, decides about the course of curves. Six different curves have been constructed which are an exponent of different distribution of production for species, which show the gradient or dominance structure of species as regards the production.

When examining the height of triangles and the curves it can be easily seen that in pinewoods, and mainly in *Cladonia* pinewoods, 50–56% of total production is per one dominant species. In acidophilous oak-pine forests and alder-ash carr (*PQ* and *AP*) this is above 30%, whereas in wet alderwoods (*Al*) and oak-hornbeam forests (*CF*) it is above 20%. The difference in the dominance gradient between *Cladonia* pinewoods (*ClP*) and oak-hornbeam forests (*CF*) is very distinct.

The production rate of species I – dominant in coniferous forests (50–65%) is distributed into five-seven species in oak-hornbeam forests. Acidophilous oak-pine forests and alder-ash carr have a similar type of dominance. In wet alderwoods (*Al*) the production is almost evenly distributed into four species and thus the curve runs almost at an angle of 45°. But in all groups only few species decide about the production rate. The contribution of other species is very small and the difference in their production is decreasing.

Dominance structure can be also presented in the form of funnels (glasses) or downward curves as shown in Figure 4. In both cases – similarly as in Figure 3 – Roman numerals (I, II, etc.) indicate the successive species. In the figures of funnel type the top horizontal line (starting from 0) the percentage contributions of species to production are indicated in the 10% scale. Therefore, figures looking like funnels show the type of dominance. Their varying shapes indicate the differences of dominance structure. The narrow funnel of a small diameter and a mildly decreasing volume characterizes the oak-hornbeam forests (Fig. 4 – *TC*). The dominance of species is not great. An extremely different type is the *Cladonia* pinewoods with a broad funnel top and rapidly decreasing volume (Fig. 4 – *ClP*).

These regularities are also well illustrated by the downward curves placed beside the "funnels" (Fig. 4). The mild or very steep decline of these curves illustrate very well the dominance. They resemble the force of water in waterfalls which depends on its volume, height and the steepness of water bar.

4.10. Ecological value of dominance structure

When comparing the results concerning the dominance structure, an attempt may be made of a general approach in ecological categories. In social systems with one main dominant, as it has been observed in *Cladonia* pinewoods (over 50% of total production), where the production in relation to that of other species is very big (e.g., rapidly declining curve in Figure 4 – *ClP*) – the effect of this dominant population on other is so high that there is no room for interspecific competition. The dominant species is so overwhelming that other species have no chance of competition. Thus, the population of such a dominant occupying the area and having a very high biomass and density becomes a leading, controlling factor which not only changes the biocenotic relations but also the environmental ones (edaphic and climatic). The large amount of matter, periodically dying and reaching the soil, has a definite, specific chemical composition and thus by means of chemical pressure it modifies in a particular direction the soil environment. The leading significance of dominants is increasing as this biomass may also have various cycles of decomposition, frequently very slow. Therefore, it may be retained for a longer time in the system. Matter cycling in geochemical cycles is then very slow, whereas the space is considerably filled with particular biomass.

In systems with a poorly indicated dominance, where both production and density are distributed among a considerable number of species (e.g., in oak-hornbeam forests), the competition among species may be much higher and more complicated than in case of a dominant population, when intraspecific competition prevails.
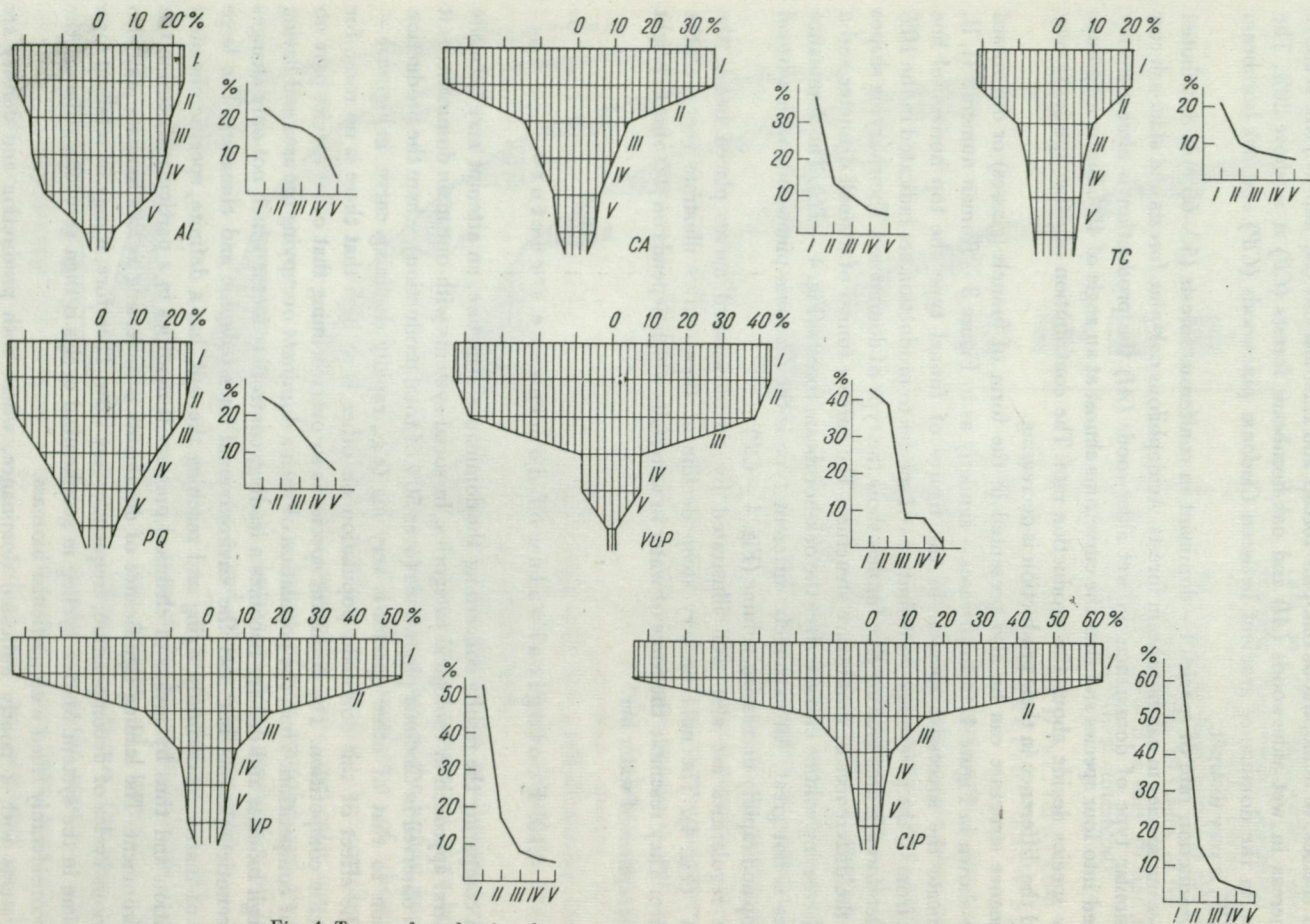
Fig. 4. Types of production dominance in the herb layer of seven forest associations

I–V – successive species according to the decreasing production percentage, Al – Carici elongatae-Alnetum, CA – Circaeo-Alnetum, TC – Tilio-Carpinetum, PQ – Pino-Quercetum, VuP – Vaccinio uliginosi-Pinetum, VP – Vaccinio myrtilli-Pinetum, ClP – Cladonio-Pinetum

It is absolutely necessary to intensify the research on dominance structure in different ecosystems, both in the population aspect (biocenotic) and as regards the cycling of elements. The dominance structure is undoubtedly related to problems of stability and permanence of plant systems (and not only) and it would be worthwhile to follow this direction.

4.11. Dominance structure against the background of the gradient of environments

The distribution of production of species and thus the dominance structure are mainly connected with the forest soil richness. When the soil is sandy and easily permeable, poor and not abundant in nutrients as it is the case of pinewoods and *Cladonia* pinewoods, there is usually a strong domination of one species fully responsible for the biocenotic and edaphic relations of all other species (Figs. 3, 4).

In ecosystems with many species on good sites (alder-ash carr, oak-hornbeam forests) the domination of one or few species is not so intense. Production and density are distributed among a greater number (Figs. 3, 4 − *CF*). Thus, a greater number of populations produce the biomass, accumulate energy and participate in the functioning of the ecosystem.

4.12. Species composition and total production of herb layer in the gradient of environments

The mean number of species decreases from fertile environments to poor, oligotrophic ones. Most abundant in species is the herb layer of alder-ash carr − 41 species, then of oak-hornbeam forests − 38 species. Pinewoods have, on the average, 20 species, *Cladonia* pinewoods − 13 species (Table II). A relatively low number of herb layer species have been also found in flooded sallow scrubs and wet alderwoods. This may be typical of marginal environments as there always exists a possibility of limiting factors. Similar tendencies have been observed as regards density (already discussed) and total production. The production of herb layer of the group of wet alderwoods and alder-ash carr is the highest. Alder-ash carr produces over 10 times more than *Cladonia* pinewoods ($166 \, g/m^2$ and $15 \, g/m^2$). Production of herb layer plants of oak-hornbeam forests, acidophilous oak-pine forests and pinewoods is in between and does not display greater differences.

It is worth indicating that the characteristics analysed only concern the herb layer which is related as a whole to other layers of forest ecosystem. The drastic differences in production and density of herb plants would be certainly smaller if these characteristics were analysed in the whole ground flora, i.e., in the herb layer including moss and lichen layers. This is confirmed by the data from the papers analysed. For example, Wójcik (1970) has found that moss production in the *Cladonia* pinewood examined was about $53 \, g/m^2$. Thus, the difference in production of the whole ground flora between alder-ash carr and dry pine forest would be only 2.5 times higher (166 : 68). There are plenty of such data. These problems are discussed to confirm the general regularity that the production (and not only) of bigger, total systems is less variable and differs less from the values of particular components of the system, which has been already shown by H. Traczyk (1971). This regularity has been very well described by Odum (1959), who wrote that in natural communities different plants, various growth forms "are apparently integrated and adjust, as fully as local limiting factors allow, to the incoming

sun energy...". Therefore, for example, the chlorophyll amount per surface area unit is usually similar in different biocenoses (G e s s n e r 1949).

4.13. The ratio of production to biomass

The problem is worth discussing as it presents some interesting ecological regularities. The ratio of production to biomass $(P : B)$ shows the production turnover and its efficiency (P e t r u s e w i c z 1966, 1967). Forest communities, in which trees prevail, produce largely for "storage", i.e., bind matter and energy in their tissues for a longer period. Such retention may be called "tissue retention". In forests this is mainly done by trees, partly by shrubs and low shrubs, that is by plants with lignifying aboveground shoots. In mesotrophic and eutrophic forests, the trees and shrubs are the main retainers. The majority of plants are the herb plants; their aboveground shoots die almost each year and become quickly mineralized. Several tens of populations forming the herb layer of such forests return in a way a considerable amount of matter to the system of destruents and the soil environment only to take it again in the next season from the efficient and abundant "granary soil". For the majority of herb layer species in eutrophic communities the ratio $P : B$ is close to one, and thus the biomass equals production. The biomass produced during the vegetation season dies and quickly reaches the soil environment (except the reproduction organs, of course). The mineralization rate is fast and the soil sorption capacity high.

In oligotrophic forests (mainly coniferous) growing on loose sandy soils, on endopercolative, podzolic soils with percolates definitely reaching the depths (P u c h a l s k i and P r u s i n-k i e w i c z 1975), this is a different matter. The $P : B$ ratio of herb plants is much lower. Current population production is only a part of the biomass. Low shrubs prevail in the herb layer, they store the majority of biomass and elements in their lignified tissues only contributing leaves to the soil. Therefore, they make up for the loss of nutrients due to soil washing. The marked prevalence of numerous low shrubs in the herb layer of coniferous forests is not accidental but is undoubtedly the result of long-lasting interactions of plant-environment system under oligotrophic conditions.

5. SUMMARY

This has been an attempt to synthetize many years of studies on the herb layer production of main forest communities in Poland conducted chiefly by the Laboratory of Plant Ecology, Institute of Ecology, Polish Academy of Sciences. The aim here, was to show general regularities between the production and structural characteristics of herb layer in different forest communities. This covers six main groups of communities: wet alderwoods, alder-ash carr, oak-hornbeam forests and beechwood, acidophilous oak-pine forests, pinewood and *Cladonia* pinewood. Altogether the material of 19 communities was used; their list including their place in the phytosociological system is given in Chapter 2.

When estimating the herb layer production the method suggested by T. T r a c z y k (1967a, 1967b) was used, thanks to which the material could be compared.

These are the most important results and generalizations:

1. The number of sporadic species of the herb layer (frequency class 1–20%) is the highest regardless of the type of community. On the average, over 80% of all species are rare or very rarely found. Species found several times per 100 samples (class of frequency "+") attain on average 64%. This is the contrary in the case of species with the highest classes of frequency, not numerous and which are, on average, 1–2% of all species. More detailed data are given in Table I and Figure 1.

2. Gradually from fertile communities to poorer ones the total density decreases. These values have been, on the average, as follows: in alder-ash carr 780, in oak-hornbeam forests 487, in acidophilous oak-pine forests 331, in pinewoods 266 and in *Cladonia* pinewoods 132 individuals per 1 m^2 (Table II).

3. In each community a dominance, i.e., numerical prevalence of one or at least few species (usually 2—4), has been observed. Species represented by a small number of individuals are over 80% of all species.

4. The gradient of density dominance is much milder in richer communities from the floristic point of view than in the poor ones (Fig. 2).

5. As regards the density five classes (groups) of species have been distinguished: main dominants, dominants, frequent, rare and sporadic. The greatest number of species is in classes I and II, that is sporadic and rare species which hardly dominate (Table III). This regularity is analogous to frequency.

6. Usually there is a positive correlation between frequency and density. But sometimes this regularity does not occur, i.e., species with low frequency show high densities and vice versa (Fig. 1). The relations between frequency and density explain mainly the distribution of individuals from plant populations in the spatial, horizontal system, i.e., the horizontal structure of the system.

7. Species very frequently found (V, IV classes of frequency) although not many, have, in general, a considerably high production as compared to abundant species forming low classes of frequency. The production rate is not closely related to the classes of frequency (Table I, Fig. 1). Frequency includes neither density nor the size of individuals which mainly decide about the production level.

8. Together with the density of a particular species the production increases. But the production rate is not always positively correlated with the total density of few or several species as, for example, in particular classes of density where several species are frequently considered as one class. This is caused by the highly differentiated biomass produced by individuals. This is why production and density not always correlate in classes of frequency (Fig. 1).

9. An average individual in the herb layer of moist communities (e.g., wet alderwoods) produces 6—7 times more than in other forests (Table II). The production coefficient of an average individual is the quotient of total production and total density of all species $(P : D)$. This may be the index of several environmental factors.

10. Production index per one species $(P : N)$, similarly as above, is an expression of ecological conditions in a given system. Average population in the herb layer of wet alderwood type produces 6.3 g, in alder-ash carr 4 g and in other communities about 1 g/m^2.

11. Quantitative estimates of particular populational characteristics (density, production, number of fruit, etc.), examined in a wide gradient of communities, are used for studying the limits of ecological tolerance and the ecological optima of many species.

12. Dominance structure is connected with the forest soil richness. In pinewoods and *Cladonia* pinewoods, on poor and podzolized soils, there is usually an absolute dominance of one population which forces its own conditions upon other species. In rich ecosystems (alder-ash carr, oak-hornbeam forests) strong dominance has not been observed. Production and density are distributed over a larger number of species (Figs. 3, 4).

13. The influence of the main dominant population is so overwhelming that there is no room for interspecific competition. The fact that it occupies the area, has a high prevalence in numbers and produced biomass of a specific chemical composition and decomposition rate, is why it is a leading factor affecting not only the biocenotic relations but also the soil-microclimatic ones. It seems an absolute necessity to intensify the research on dominance structure in ecosystems as regards biocenosis, energy flow and stability of plant systems.

14. Production of the herb layer is much higher in eutrophic than in oligotrophic environments. Alder-ash carr produces 10 times more than *Cladonia* pinewood. Similar regularities can be also observed in the numbers of species and density.

15. Under oligotrophic conditions, in forests on loose sandy soil, on endopercolative, podzolized soils, the low shrubs prevail in the herb layer and store the majority of biomass and elements in their lignified shoots (tissue retention) only contributing leaves to the soil. Thus, they make up for the loss of nutrients due to soil washing. The marked prevalence of low shrubs in the herb layer of coniferous forests seems to be due to long-lasting interactions of plant-soil system under oligotrophic conditions.

6. POLISH SUMMARY (STRESZCZENIE)

Praca stanowi próbę syntetycznego ujęcia długoletnich badań nad produkcją runa głównych zbiorowisk leśnych Polski, jakie prowadziła przeważnie Pracownia Ekologii Roślin Instytutu Ekologii PAN. Przewodnim celem pracy jest wykazanie ogólniejszych prawidłowości, jakie zachodzą pomiędzy produkcją a cechami

strukturalnymi warstwy zielnej, w szerokim gradiencie zbiorowisk leśnych. Gradient ten obejmuje 6 głównych grup zbiorowisk: grupę olsów, łęgów, grądów i buczyn, borów mieszanych, borów świeżych oraz borów suchych. W sumie wykorzystano materiały z 19 zbiorowisk, których wykaz i miejsce w systemie fitosocjologicznym zamieszczono w rozdziale 2.

Przy ocenie produkcji runa stosowano w każdym przypadku ujednoliconą metodę zaproponowaną przez T. T r a c z y k a (1967a, 1967b), co pozwoliło na uzyskanie porównywalnych materiałów.

Oto ważniejsze wyniki i uogólnienia:

1. Liczba gatunków sporadycznych runa (klasa frekwencji 1—20%) jest zdecydowanie największa, bez względu na typ zbiorowiska. Przeciętnie ponad 80% wszystkich gatunków stanowią gatunki rzadko lub bardzo rzadko spotykane. Gatunki trafiające się kilka razy na 100 prób (klasa frekwencji „+") osiągały przeciętnie 64%. W przeciwieństwie do nich, gatunki o najwyższych klasach frekwencji są bardzo nieliczne i stanowią średnio 1—2% wszystkich gatunków. Szczegółowsze dane przedstawiają tab. I oraz fig. 1.

2. W miarę przechodzenia od zbiorowisk żyznych do stopniowo uboższych następuje równoległe zmiejszanie się wartości zagęszczenia ogólnego. Wartości te – średnio biorąc – wynosiły: w łęgach 780, grądach 487, borach mieszanych 331, borach świeżych 266 oraz w borach suchych 132 osobniki na 1 m^2 (tab. II).

3. W każdym zbiorowisku stwierdzono zdecydowaną przewagę liczbową osobników jednego lub najwyżej kilku gatunków (najczęściej 2—4). Gatunki reprezentowane przez niewielką liczbę osobników stanowią ponad 80% ogółu gatunków.

4. Gradient dominacji zagęszczenia w zbiorowiskach bogatszych florystycznie jest łagodniejszy niż w ubogich (fig. 2).

5. Jeśli chodzi o zagęszczenie, to wydzielono V klas (grup) gatunków: gatunki panujące, dominujące, częste, rzadkie i sporadyczne. Najwięcej gatunków znajduje się w klasach I i II, a więc są to gatunki sporadyczne i rzadkie a bardzo mało dominujących (tab. III). Prawidłowość ta przedstawia się analogicznie jak w zakresie frekwencji.

6. Pomiędzy frekwencją a zagęszczeniem zachodzą najczęściej korelacje dodatnie. Niekiedy jednak reguła ta się nie sprawdza, tzn. gatunki o niskich frekwencjach reprezentowane są przez duże zagęszczenia i na odwrót (fig. 1). Relacje pomiędzy frekwencją i zagęszczeniem rzucają światło głównie na sposób rozmieszczenia osobników populacji roślinnych w przestrzennym układzie poziomym, czyli – na strukturę poziomą układu.

7. Gatunki o wysokiej spotykalności (V, IV klasa frekwencji), mimo że jest ich mało – generalnie rzecz biorąc – produkują stosunkowo dużo, w porównaniu do bardzo licznych gatunków tworzących niskie klasy frekwencji. Wielkość produkcji nie wykazuje ścisłego związku z klasami frekwencji (tab. I, fig. 1). Frekwencja nie uwzględnia przecież ani zagęszczenia, ani wielkości osobników gatunków, co głównie decyduje o poziomie produkcji.

8. Wraz z zagęszczeniem określonego gatunku wzrasta produkcja, co jest sprawą oczywistą. Natomiast wielkość produkcji nie zawsze koreluje dodatnio z łącznym zagęszczeniem kilku lub kilkunastu gatunków, jak np. w określonych klasach zagęszczenia, gdzie do jednej klasy zaliczane jest często kilkanaście gatunków. Przyczyną tego jest bardzo zróżnicowana biomasa wytwarzana przez osobniki. Z tego względu również nie zawsze korelują ze sobą produkcja i zagęszczenie w klasach frekwencji (fig. 1).

9. Przeciętny osobnik warstwy zielnej w zbiorowiskach wilgotnych (np. olsy) produkuje 6—7 razy więcej, niż w innych lasach (tab. II). Wskaźnik produkcji na jednego przeciętnego osobnika jest ilorazem z ogólnej wartości produkcji i ogólnego zagęszczenia wszystkich gatunków ($P : D$). Może on być wykładnikiem wielu czynników środowiska.

10. Wskaźnik produkcji na jeden gatunek ($P : N$) jest – podobnie jak wyżej omówiony wskaźnik – pewną miarą warunków ekologicznych w danym układzie. Przeciętna populacja w runie typu olsowego produkuje 6,3 g, w łęgach – 4 a w pozostałych zbiorowiskach – około 1 g/m^2.

11. Ilościowe mierniki określonych cech populacji (zagęszczenie, produkcja, liczba owoców itd.), rozpatrywane w szerokim gradiencie środowisk, stanowią podstawę do poznawania amplitud i optimów ekologicznych wielu gatunków.

12. Struktura dominacji wiąże się z zasobnością siedlisk. W borach świeżych i suchych, zasiedlających gleby ubogie i przemywne, stwierdzamy najczęściej absolutną dominację jednej populacji, która wywiera wpływ na wszystkie pozostałe gatunki. W ekosystemach bogatych (łęgi, grądy) nie stwierdzono ostrej dominacji. Produkcja i zagęszczenie rozkłada się na większą liczbę gatunków (fig. 3, 4).

13. Siła oddziaływania populacji panującej jest tak przytłaczająca, że nie może być mowy o współzawodnictwie międzygatunkowym. Wypełnienie przestrzeni, ogromna przewaga liczebności i produkowanej biomasy o swoistym chemizmie i tempie rozkładu powoduje, że jest ona przewodnim czynnikiem wpły-

wającym nie tylko na stosunki biocenotyczne, lecz i glebowo-mikroklimatyczne. Wydaje się, że nasilenie badań nad strukturą dominacji w ekosystemach w aspekcie biocenotycznym, przepływu materii i energii oraz stabilności układów roślinnych staje się pilną potrzebą i perspektywicznym kierunkiem badań.

14. Produkcja warstwy zielnej jest zdecydowanie większa w środowiskach eutroficznych niż oligotroficznych. Łęgi produkują ponad 10-krotnie więcej, niż bory suche. Podobne prawidłowości dotyczą również liczby gatunków oraz zagęszczenia.

15. W warunkach oligotroficznych, w borach rozwijających się na luźnych piaskach, na glebach endoperkolatywnych przemywnych, przeważają w runie krzewinki, które przetrzymują większość biomasy i pierwiastków w swych zdrewniałych pędach (retencja tkankowa), zrzucając do gleby tylko niewielkie ich ilości w postaci liści. Dzięki temu przeciwstawiają się wydatnie utracie biogenów przez wymywanie. Zdecydowana przewaga w runie borów krzewinek jest – jak się wydaje – wynikiem długotrwałego procesu współoddziaływania układu roślinno-glebowego w warunkach oligotrofii.

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