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RELATION BETWEEN PRODUCTIVITY AND STRUCTURE OF THE HERB LAYER IN ASSOCIATIONS ON "THE WILD APPLE-TREE ISLAND" (MASURIAN LAKE DISTRICT)

(Ekol. Pol. 19: 333–363). The author presents results of studies on herb layer production and organic fall in four associations on "The Wild Apple-Tree Island" (Masurian Lake District). A large number of comparative analyses are made and the commoner regularities determined. These refer to relations between frequency and density, production and density, division of production among species etc.

The paper forms one of the series of studies on herb layer productivity in the more important lowland associations of Poland carried out by the Institute of Ecology, Polish Academy of Sciences, under the International Biological Programme.

Contents

I. INTRODUCTION

The present paper is one of a series of studies aimed as assessing the amount of herb layer production and plant fall in the more important forest associations of Poland. It simultaneously forms an indispensable basis for studies on the productivity of small rodents which have been continued for many years by the Natural Population Laboratory of the Institute of Ecology, Polish Academy of Sciences, in the woods on "The Wild Apple-Tree Island". In addition to estimation of the amount of herb layer production and organic fall in four forest associations, the purpose of the paper is also to make a comparative analysis of productivity parameters and to establish what regularities occur between them.

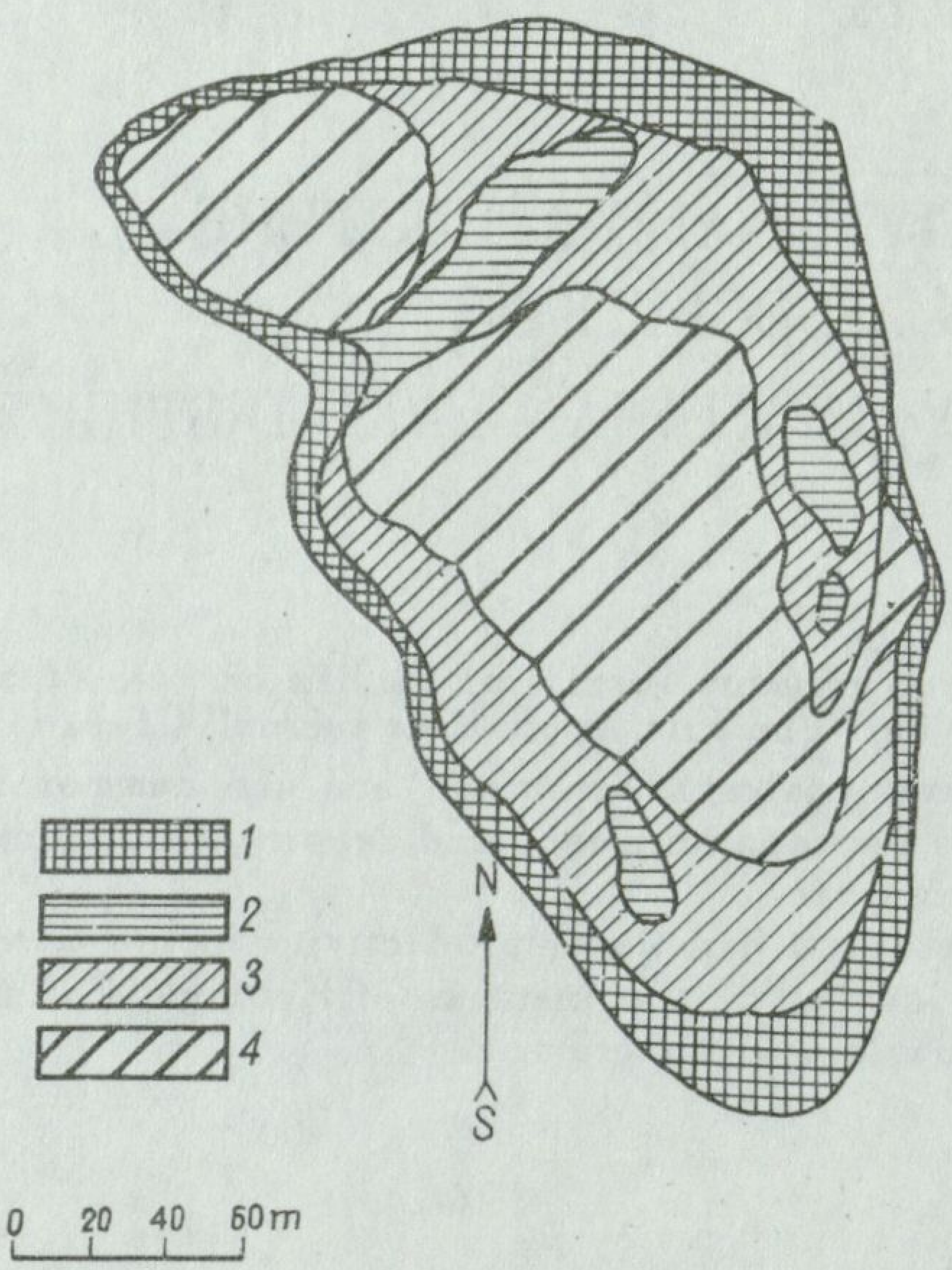

Fig. 1. Distribution of forest associations on "The Wild Apple-Tree Island"
1 – Frangulo-Salicetum, 2 – Circaeo-Alnetum, 3 – Tilio-Carpinetum stachyetosum, 4 – Tilio-Carpinetum typicum

II. DESCRIPTION OF ASSOCIATIONS

"The Wild Apple-Tree Island", on which these studies were carried out, is situated in the north-east part of Poland in Lake Bałdańskie (Masurian Lake District), a few kilometres to the north of the town of Ruciane. It is a small island about 4.5 ha in area, covered by four forest associations which have been identified as: *Frangulo-Salicetum* Malc. 1929, *Circaeo-Alnetum* Oberdorfer 1953 and *Tilio-Carpinetum* Traczyk 1962 in two sub-associations – *T.-C. stachyetosum silvaticae* and *T.-C. typicum*. More detailed data on the phytosociological relations of this island are to be found in a short note (H. Traczyk 1965). The distri-

Frequency (F), density (D), average growth (G_i) and nett production of species in herb layer of *Frangulo-Salicetum*

Tab. I

Species	F	Density per 10 m²	Density %	No.	Individual average growth in g	Net Production-P g/10 m²	Net Production-P %	Net Production-P Cumul.
1. *Dryopteris thelypteris*	30	280	11	30	2.1810	610.680	29	29
2. *Carex acutiformis*	63	607	24	500	0.7295	442.806	21	50
3. *Calamagrostis canescens*	50	1147	46	1000	0.3588	411.544	20	70
4. *Phragmites communis*	40	90	4	90	4.5067	405.603	19	89
5. *Urtica dioica*	10	20	<1	60	2.1825	43.650	2	91
6. *Lysimachia thyrsiflora*	30	60	2	60	0.7115	42.690	2	93
7. *Phalaris arundinacea*	3	40	1	60	0.9700	38.800	1	94
8. *Rubus idaeus*	3	17	<.1	30	2.2100	37.570	1	95
9. *Lythrum salicaria*	23	37	1	60	0.8745	31.246	1	96
10. *Calystegia sepium*	10	20	<1	30	0.5650	11.300	<1	
11. *Stachys palustris*	3	7	<1	10	1.4250	9.975	<1	
12. *Scutellaria galericulata*	13	23	<1	30	0.3380	7.774	<1	
13. *Galium palustre*	20	63	2	60	0.0975	6.142	<1	
14. *Pulmonaria obscura*	3	3	<1	10	0.6750	2.025	<1	
15. *Salix cinerea*	3	3	<1	10	0.3900	1.300	<1	
16. *Solanum dulcamara*	7	7	<1	10	0.1530	1.071	<1	
17. *Alnus glutinosa*	10	23	<1	10	0.0120	0.276	<1	
18. *Epilobium palustre*	3	3	<1	10	0.0520	0.156	<1	
Total		2490				2104.608		
Avg herbage cover – 33%		249/m² 2.490 mill./ha				210.461 g/m² c. 2105 kg/ha		

Number of individuals used for the calculation of individual average growth of species.

Frequency (F), density (D), average growth (G_i) and nett production (P) of species in herb layer of *Circaeo-Alnetum*

Tab. II

Species		F	Density per 10 m²	Density %	No	Individual average growth in g	Net production-P g/10 m²	Net production-P Total g/10 m²	Net production-P %	Net production-P Cumul.
1. *Urtica dioica*		63	263	3	200	3.0204	794.365	794.365	35	35
2. *Eupatorium cannabinum*		6	25	<1	30	11.4000	285.000	285.000	13	48
3. *Geranium Robertianum*		81	575	6	400	0.1765	101.487	209.974	9	57
,, "	f		55	<1	60	1.9725	108.487			
4. *Cirsium oleraceum*		19	63	<1	70	3.0600	192.780	192.780	9	66
5. *Galeobdolon luteum*		48	1063	11	1100	0.1570	166.891	171.983	8	74
" "	f		21	<1	60	0.2425	5.092			
6. *Rubus idaeus*		28	71	<1	70	1.4500	102.950	111.596	5	79
" "	f		3	<1	10	0.2882	8.646			
7. *Chrysosplenium alternifolium*		36	3015	32	1000	0.0234	70.551	87.278	4	83
" "	f		232	2	80	0.0721	16.727			
8. *Geum urbanum*		19	215	2	400	0.2171	46.676	66.596	3	86
" "	f		32	<1	70	0.6225	19.920			
9. *Alliaria officinalis*		60	236	2	200	0.0600	14.160	60.240	3	89
" "	f		24	<1	60	1.9200	46.080			
10. *Galium aparine*		25	154	2	150	0.3755	57.827	57.827	2	91
11. *Dentaria bulbifera*		19	252	3	200	0.1229	30.971	40.571	2	93
" "	f		16	<1	20	0.6000	9.600			
12. *Circaea alpina*		41	967	10	800	0.0354	34.232	34.232	1	94
13. *Aegopodium podagraria*		9	44	<1	50	0.5680	24.992	24.992	1	95
14. *Moechringia trinervia*		54	1265	13	1000	0.0104	13.156	20.086	<1	
" "	f		105	1	150	0.0660	6.930			
15. *Calamagrostis canescens*		9	40	<1	60	0.4550	18.200	18.200	<1	
16. *Pulmonaria obscura*		13	33	<1	30	0.3300	10.890	14.150	<1	
" "	f		6	<1	30	0.5433	3.260			
17. *Convallaria maialis*		19	32	<1	40	0.3175	10.160	10.160	<1	

18. *Lysimachia thyrsiflora*		13	35	<1	40	0.2853	9.985	9.985	<1
19. *Viola mirabilis*		6	8	<1	10	0.4100	3.280	4.720	<1
" "	f		2	<1	10	0.7200	1.440		
20. *Stachys palustris*		2	3	<1	10	1.5650	4.695	4.695	<1
21. *Galeopsis tetrahit*		16	27	<1	30	0.1655	4.198	4.198	<1
22. *Ficaria verna*		16	201	2	200	0.0162	3.256	3.256	<1
23. *Dryopteris thelypteris*		9	27	<1	30	0.1200	3.240	3.240	<1
24. *Ajuga reptans*		2	13	<1	20	0.2300	2.990	2.990	<1
25. *Mycelis muralis*		2	2	<1	10	1.4370	2.874	2.874	<1
26. *Poa trivialis*		14	200	2	150	0.0115	2.300	2.300	<1
27. *Anemone nemorosa*		14	29	<1	50	0.0567	1.644	2.244	<1
" "	f		6	<1	1	0.1000	0.600		
28. *Evonymus europaea*		5	9	<1	10	0.2200	1.980	1.980	<1
29. *Paris quadrifolia*		3	2	<1	10	0.2190	0.438	1.838	<1
" "	f		2	<1	10	0.7000	1.400		
30. *Carex acutiformis*		2	2	<1	20	0.8255	1.651	1.651	<1
31. *Scutellaria galericulata*		2	3	<1	10	0.4350	1.305	1.305	<1
32. *Filipendula ulmaria*		2	3	<1	15	0.2490	0.747	0.747	<1
33. *Corylus avellana*		2	3	<1	10	0.2010	0.603	0.603	<1
34. *Alnus glutinosa*		3	3	<1	10	0.1420	0.426	0.426	<1
35. *Corydalis solida*		2	2	<1	10	0.0180	0.360	0.360	<1
36. *Hepatica nobilis*		3	5	<1	10	0.0700	0.350	0.350	<1
37. *Cardamine impatiens*		13	25	<1	30	0.0130	0.325	0.325	<1
38. *Carpinus betulus*		6	6	<1	10	0.0420	0.252	0.252	<1
39. *Epilobium palustre*		2	2	<1	10	0.1000	0.200	0.200	<1
40. *Adoxa moschatellina*		5	9	<1	20	0.0200	0.180	0.180	<1
41. *Tilia cordata*		3	3	<1	10	0.0467	0.140	0.140	<1
Total			9439					2250.889	
Avg herbage cover – 83%			944/m^2 9.439 mill./ha					225.089 g/m^2 c. 2251 kg/ha	

Number of individuals used for the calculation of individual average growth of species f – fructifying.

Frequency (F), density (D), average growth (G_i) and nett production (P) of species in herb layer of *Tilio-Carpinetum stachyetosum*

Tab. III

Species		F	Density per 10 m²	Density %	No.	Individual average growth in g	Net production-P g/10 m²	Net production-P Total g/10 m²	%	Cumul.
1. *Galeobdolon luteum*		92	1015	15	15	0.1594	161.791	164.491	23	23
" "	f		8	<1	10	0.3375	2.700			
2. *Dentaria bulbifera*		85	800	12	1000	0.1063	85.040	105.060	14	37
" "	f		28	<1	50	0.7150	20.020			
3. *Aegopodium podagraria*		65	190	3	200	0.2902	55.138	55.138	8	45
4. *Hepatica nobilis*		48	142	2	150	0.2770	39.334	46.134	6	51
" "	f		17	<1	20	0.4000	6.800			
5. *Stachys silvatica*		13	32	<1	40	0.9300	29.760	29.760	4	55
6. *Paris quadrifolia*		67	155	2	200	0.1770	27.435	28.995	4	59
" "	f		3	<1	10	0.5200	1.560			
7. *Anemone nemorosa*		53	440	7	500	0.0465	20.460	27.670	4	63
" "	f		70	1	200	0.1030	7.210			
8. *Ajuga reptans*		23	92	1	100	0.2900	26.680	26.680	4	67
9. *Geum urbanum*		22	30	<1	60	0.6900	20.700	24.690	3	70
" "	f		3	<1	15	1.3300	3.990			
10. *Polygonatum multiflorum*		13	27	<1	50	0.7450	23.715	23.715	3	73
11. *Pulmonaria obscura*		23	23	<1	40	0.9700	22.310	22.310	3	76
12. *Oxalis acetosella*		17	1872	28	1800	0.0112	20.966	21.886	3	79
" "	f		23	<1	40	0.0400	0.920			
13. *Urtica dioica*		5	25	<1	40	0.7825	19.562	19.562	3	82
14. *Actaea spicata*		5	8	<1	20	1.3200	10.560	15.300	2	84
" "	f		2	<1	20	2.3700	4.740			
15. *Mycelis muralis*		5	22	<1	40	0.6150	13.530	13.530	2	86
16. *Rubus idaeus*		5	13	<1	20	0.9550	12.415	12.415	2	88
17. *Circaea alpina*		23	400	7	300	0.0288	11.520	11.520	2	90
18. *Adoxa moschatellina*		70	628	9	700	0.0173	10.864	10.864	1	91
19. *Viola mirabilis*		10	13	<1	20	0.5700	7.410	10.150	1	92
" "	f		2	<1	10	1.3700	2.740			

20. *Cirsium oleraceum*	2	2	<1	10	4.1900	8.380	8.380	1	93
21. *Athyrium filix-femina*	7	17	<1	20	0.4260	7.242	7.242	1	94
22. *Lysimachia thyrsiflora*	12	20	<1	40	0.3300	6.600	6.600	<1	95
23. *Geranium Robertianum*	37	87	1	100	0.0517	4.498	4.498	<1	
24. *Stellaria nemorum*	2	10	<1	20	0.3700	3.700	3.700	<1	
25. *Evonymus europaea*	8	25	<1	20	0.1400	3.500	3.500	<1	
26. *Alliaria officinalis*	27	92	1	200	0.0380	3.496	3.496	<1	
27. *Majanthemum bifolium*	10	50	<1	60	0.0617	3.085	3.085	<1	
28. *Tilia cordata*	10	12	<1	20	0.1900	2.280	2.280	<1	
29. *Campanula trachelium*	2	2	<1	15	1.0187	2.037	2.037	<1	
30. *Filipendula ulmaria*	5	5	<1	10	0.3400	1.700	1.700	<1	
31. *Carpinus betulus*	3	3	<1	10	0.5100	1.530	1.530	<1	
32. *Moechringia trinervia*	37	158	2	200	0.0080	1.264	1.264	<1	
33. *Scrophularia nodosa*	2	2	<1	10	0.6150	1.230	1.230	<1	
34. *Viburnum opulus*	2	8	<1	10	0.1150	0.920	0.920	<1	
35. *Corylus avellana*	5	5	<1	10	0.1800	0.900	0.900	<1	
36. *Veronica chamaedrys*	2	7	<1	10	0.1020	0.714	0.714	<1	
37. *Dryopteris thelypteris*	2	2	<1	10	0.1300	0.260	0.260	<1	
38. *Ulmus scabra*	8	8	<1	10	0.0300	0.240	0.240	<1	
39. *Convolvulus sepium*	2	5	<1	10	0.0360	0.180	0.180	<1	
40. *Cardamine impatiens*	2	5	<1	10	0.0190	0.095	0.095	<1	
41. *Corydalis solida*	2	2	<1	10	0.0220	0.044	0.044	<1	
42. *Stellaria media*	2	2	<1	10	0.0190	0.038	0.038	<1	
Total		6616					723.803		
Avg herbage cover – 71%		662/m² 6.616 mill./ha					72.380 g/m² c. 724 kg/ha		

Frequency (F), density (D), average growth (G_i) and nett production of species in herb layer of *Tilio-Carpinetum typicum*

Tab. IV

Species	F	Density per 10m²	Density %	No.	Individual average growth in g	Net production-P g/10 m²	Net production-P %	Net production-P Cumul.
1. *Dentaria bulbifera*	98	1795	28	800	0.0832	149.344	26	26
2. *Galeobdolon luteum*	72	820	13	820	0.0754	61.828	11	37
3. *Asperula odorata*	20	240	4	520	0.1969	47.256	8	45
4. *Hepatica nobilis*	56	125	2	150	0.3660	45.750	8	53
5. *Urtica dioica*	8	14	<1	20	3.0395	42.553	7	60
6. *Adoxa moschatellina*	45	830	13	220	0.0483	40.089	7	67
7. *Anemone nemorosa*	61	697	11	785	0.0572	39.868	7	74
8. *Aegopodium podagraria*	39	129	2	555	0.2408	31.063	5	79
9. *Pulmonaria obscura*	21	52	<1	100	0.4372	22.734	4	83
10. *Corydalis solida*	71	316	5	240	0.0529	16.716	3	86
11. *Oxalis acetosella*	22	984	16	760	0.0149	14.662	3	89
12. *Lathyrus vernus*	6	10	<1	20	1.0700	10.700	2	91
13. *Geranium Robertianum*	5	11	<1	20	0.8780	9.658	2	93
14. *Geum urbanum*	3	9	<1	10	0.6750	6.075	1	94
15. *Athyrium filix-femina*	1	5	<1	10	1.1460	5.730	<1	
16. *Anthriscus silvestris*	2	2	<1	10	2.3400	4.680	<1	
17. *Alliaria officinalis*	26	85	1	100	0.0540	4.590	<1	
18. *Polygonatum multiflorum*	8	8	<1	10	0.5500	4.400	<1	
19. *Paris quadrifolia*	16	20	<1	25	0.2080	4.160	<1	
20. *Viola mirabilis*	7	8	<1	15	0.4733	3.786	<1	
21. *Actaea spicata*	1	1	<1	30	1.9367	1.937	<1	
22. *Stachys silvatica*	1	1	<1	10	1.8000	1.800	<1	
23. *Campanula trachelium*	1	1	<1	15	1.7760	1.776	<1	
24. *Ficaria verna*	7	99	1	200	0.0135	1.336	<1	
25. *Ajuga reptans*	6	8	<1	10	0.1100	0.880	<1	
26. *Mycelis muralis*	1	1	<1	10	0.8120	0.812	<1	
27. *Milium effusum*	1	1	<1	30	0.2873	0.287	<1	
28. *Evonymus europaea*	2	2	<1	10	0.1150	0.230	<1	
29. *Majanthemum bifolium*	3	6	<1	20	0.0100	0.060	<1	
Total		6280				574.760		
Avg herbage cover – 56%		628/m² 6.280 mill./ha				57.476 g/m² c. 575 kg/ha		

Number of individuals used for the calculation of individual average growth of species.

bution of the associations on the island is shown in Fig. 1. The associations reveal a close connection with the land formation and the action of lake water. They are distributed concentrically – the coastal, lowest parts of the island, often submerged, are occupied by the *Frangulo-Salicetum* association, the highest middle parts by patches of *Tilio-Carpinetum typicum*, and the intermediate parts – by *T.-C. stachyetosum* and *Circaeo-Alnetum:* This in consequence leads to formation of different types of soil connected with the different associations.

The floristic composition of the herb layer is given in tables I–IV which, in addition to a list of species, also include different quantitative parameters from those given in phytosociological descriptions. They nevertheless given a better idea of the quantitative relations prevailing in the herb layer than the scales of abundance given in phytosociological studies. On this account the species composition and quantitative relations of the tree and shrub layers in these four associations are given as supplementary to the tables.

1. *Frangulo-Salicetum*: Crown cover 20–40%, shrub cover – 80%. Only *Alnus glutinosa** (3.3) occurred in the tree stand. *Salix cinerea* (5.5) decidedly dominates in the undergrowth, and sporadically *Salix pentandra* (1.1) and *Salix alba* (+).

2. *Circaeo-Alnetum:* Crown cover 60%, shrub cover 10%. *Alnus glutinosa* (4.4), with a slight admixture of *Ulmus scabra* (+), forms the tree stand of this association. *Evonymus europaea* (+) and *Salix cinerea* (+) are encountered singly in the shrub layer.

3. *Tilio-Carpinetum stachyetosum silvaticae:* Crown cover 80%, shrub cover – 90%. *Alnus glutinosa* (4.5) predominates in the upper layer of the tree stand (a_1), with single individuals of *Pinus silvestris* (+). *Ulmus scabra* (2.3) and *Tilia cordata* (2.3) occur in layer a_2 in varying degrees of compactness (30%). The very dense shrub layer is formed by *Coryllus avellana* (5.5) and a few individuals of *Ulmus scabra* (1.2).

4. *Tilio-Carpinetum typicum* – Crown cover 90%, shrub cover – 80%. *Pinus silvestris* (3.3) and *Populus tremula* (1.1) grow in the highest layer of the tree stand; in the lower – a_2: *Carpinus betulus* (3.2) and *Tilia cordata* (2.3). *Coryllus avellana* (4.4), predominates among the shrubs with an admixture of *Tilia cordata* (2.2), *Carpinus betulus* (1.1) and *Evonymus europaea* (+).

The tree-stands are about 120 years old.

III. METHODS

1. General principles

The method described by Traczyk (1967a, 1967b) was used for field work. This consists in principle of carrying out two field analyses independently

* The names of plants are given after Szafer, Kulczyński, Pawłowski (1967).

of each other. The first of them is intended to establish the density of individuals (or shoots) of populations of species occurring in the given association, the second – the average individual growth of a given population during the maximum period of its development and growth. Net primary production (P) of a given species will equal the product of density (D) and average individual growth (G_i)

$$P = D \times G_i$$

In the associations examined only a few sporadic species retain their upper parts throughout the winter. In the case of these species the biomass in the following growing season will consist of the older previous year's shoots and the current year's shoots. In such cases the average individual growth was calculated only on the basis of the current year's biomass after separating it from that of previous years. In the great majority of the species examined the upper parts die during winter and with these species the maximum state of biomass in a given year will simultaneously be maximum growth.

2. Analysis of density of herb layer plants

In each of the four associations examined 100 hoops 0.1 m² in area were distributed at regular intervals. Density analysis was made twice, on May 4th and June 3rd. The first of these analyses was aimed at determining the density of early spring geophytes (*Corydalis*, *Adoxa*, *Dentaria*, *Anemone* etc.) which from a distinct but shortlived spring aspect in associations of the Carpinion alliance. A careful count was made for each sample, depending on the morphology of the species, either of the number of individuals or of shoots above ground, and assessment made in percentages of herb layer cover. There was no ground cover of mosses and lichens.

3. Determination of average individual growth

In accordance with the principles of the method collection was made during the maximum periods of population development (fruitnig phenophase) of a suitable number of individuals or shoots of a given species depending on the results of density analysis. It must be emphasised that it is necessary here to adhere to identical units within the same population both in the density analysis and when analysing the determined average individual growth values. If, for instance, in the density analysis of a population of *Dentaria bulbifera* the basal leaf and shoot from the gemmules formed two units and density was determined for each of them, it is essential to cut off the same elements, i.e. leaves and shoots from gemmules, as separate units when collecting plants.

Plants were cut in three periods – at the beginning of May (e.g. *Corydalis solida, Adoxa moschatellina*), beginning of June (*Dentaria, Anemone, Pulmonaria, Viola, Hepatica, Lathyrus* and others) and about July 20th (*Mycelis muralis, Urtica dioica, Aegopodium podagraria, Geum urbanum, Stachys silvatica, Stellaria nemorum etc.*) Collection dates were adapted to the time when the given populations attained maximum development and growth.

The fourth columns in tables I–IV give the number of individuals (shoots) cut in order to obtain data on growth. The biomass of this number of individuals divided by the number of individuals gives the average individual growth at the time of full development of the population (G_i).

4. Measurements of plant fall

Practical work has shown that it is pointless to use bags for plant fall in regions where tourist traffic is heavy. On this account hoops 0.1 m² in area were placed on ground devoid of herb layer and litter. Thirty of such hoops were permanently arranged in each association and as was the case when analysing density, they were arranged systematically at regular intervals. The hoops were placed in position on April 28th and fall collected from them at the following times: June 5th, July 27th, October 11th and November 17th, that is, over a period of 208 days of the growing season. The material collected was separated into: 1) leaves of deciduous trees, 2) leaves of coniferous trees, 3) fruits and 4) branches, twigs, bark, outer covering of buds etc. Each of the four categories was dried to a constant weight and weighed with accuracy to 0.01 g, like herb layer plants.

IV. RESULTS AND DISCUSSION

1. Frequency

Frequency is a measure of the likelihood of encountering a species in a patch of the given association, regardless of its density. It is usual to express this value in percentages and t divide it into what is known as classes of frequency for each 20%. In order to obtain a more exact estimate of the number of sporadic species, in class I (1–20%). I additionally differentiated a so-called "+" class (plus) containing very rare species encountered only a few times in every 100 samples (class 1–10%). Analysis of data from tables I–IV and tables V–VIII (3 successive columns from left) permits of drawing more general conclusions, namely:

1. Regardless of the type of forest association, or type of site, the number of rare, sporadic species (frequency class I) is decidedly the greatest. This value in the associations examined varied, depending on the association, from 66–78%; taken on an average over 70% of the total number of herb layer species

Distribution of number of species, density and production in frequency classes in *Frangulo-Salicetum*

Tab. V

Frequency classes		Number of species		Density		Net production	
		real	%	1 m²	%	g/m²	%
81–100	V	–	–	–	–	–	–
51–80	IV	1	6	61	25	44.281	21
41–60	III	1	6	115	47	41.154	19
21–40	II	4	22	47	19	109.022	52
11–20	I	2	11	9	4	1.392	1
1–10	+	10	55	17	5	14.612	7
Total		18		249		210.461	

Distribution of number of species, density and production in frequency classes in *Circaeo-Alnetum*

Tab. VI

Frequency classes		Number of species		Density		Net production	
		real	%	1 m²	%	g/m²	%
81–100	V	1	2	63	7	20.997	9
61–80	IV	1	2	26	3	79.436	35
41–60	III	4	10	368	39	28.654	13
21–40	II	3	8	347	37	25.649	11
11–20	I	11	26	114	11	34.656	16
1–10	+	21	52	26	3	35.697	16
Total		41		944		225.089	

Distribution of number of species, density and production in frequency classes in *Tilio-Carpinetum stachyetosum*

Tab. VII

Frequency classes		Number of species		Density		Net production	
		real	%	1 m²	%	g/m²	%
81–100	V	2	5	185	28	26.955	37
61–80	IV	3	7	98	15	9.500	13
41–60	III	2	5	67	10	7.380	10
21–40	II	7	17	88	13	9.405	12
11–20	I	4	10	197	30	8.196	11
1–10	+	24	56	27	4	10.944	17
Total		42		622		72.380	

Distribution of number of species, density and production in frequency classes in *Tilio-Carpinetum typicum*

Tab. VIII

Frequency classes		Number of species		Density		Net production	
		real	%	1 m²	%	g/m²	%
81–100	V	1	3	179	28	14.934	26
61–80	IV	3	10	183	29	11.841	21
41–60	III	2	7	96	16	8.584	15
21–40	II	4	14	125	20	6.362	12
11–20	I	2	7	26	4	5.142	8
1–10	+	17	59	19	3	10.613	18
Total		29		628		57.476	

are species rarely or very rarely encountered (class I). Very rare species (class +) formed over 50% of the number of species.

2. Unlike sporadic species, species with maximum frequency (most often encountered) are few in number (2–5%). This means that from a number varying from 50–80 herb layer species, only 1 or at most 2 species are encountered in more than 80 out of 100 samples. More detailed data on this are given in tables V–VIII.

2. Density

The average general density of individuals or shoots, without regard to species appurtenance, varies fairly considerably in the associations examined (Tab. I–IV), as follows: in *Frangulo-Salicetum* there are, on an average, 249 shoots per 1 m², with average herb layer cover of 33%. This is relatively the lowest value. Maximum density of individuals, exceeding the previous value by almost four times, was found in the herb layer of *Circaeo-Alnetum*; where it was as high as 944 units per 1 m², with herb layer cover of 83%. In the two associations of the Carpinion alliance density was similar: in *Tilio-Carpinetum* stachyetosum silvaticae, with herb layer cover of 71% the density of individuals was 662/m², and in *T.–C. typicum* – 628/m², with herb layer cover of 56%.

It is obvious that the density value of plants depends on many factors. In a forest factors limiting density often include lack of a sufficient amount of light, when the upper layers of the forest are very dense, then humidity relations in the soil, the size of the plants themselves and even the way in which they reproduce. Mention must also be made of an important group of biocenotic factors, particularly the interactions of plants. Such interactions must be very important, since so large a number of individuals occur per unit of area equal to 1 m². These questions still require more detailed investigation.

Frequency, density and production of

Species	*Frangulo-Salicetum* F	Density per 10 m²	Production g/10 m²	*Circaeo-* F	Density per 10 m²
1. *Calamagrostis canescens*	50	1147	411.544	9	40
2. *Carex acutiformis*	63	607	442.806	2	2
3. *Dryopteris thelypteris*	30	280	610.680	9	27
4. *Phragmites communis*	40	90	405.603		
5. *Chrysosplenium alternifolium*				36	3247
6. *Moehringia trinervia*				54	1370
7. *Circaea alpina*				41	967
8. *Geranium Robertianum*				81	630
9. *Urtica dioica*	10	20	43.650	63	263
10. *Alliaria officinalis*				60	260
11. *Ficaria verna*				16	201
12. *Galeobdolon luteum*				48	1084
13. *Oxalis acetosella*					
14. *Paris quadrifolia*				3	4
15. *Aegopodium podagraria*				9	44
16. *Hepatica nobilis*				3	5
17. *Dentaria bulbifera*				19	268
18. *Adoxa moschatellina*				5	9
19. *Anemone nemorosa*				14	35
20. *Corydalis solida*				2	2
21. *Asperula odorata*					

Density within the different populations (species) of the herb layer exhibits a similar regularity to that found for frequency. Species with low density value are the most numerous. In every association, however, we find distinct domination in the herb layer of one, or at most a few, species. Taking the different degrees of density into consideration these two categories of species could respectively be termed sporadic and dominants, and with accepted classes of value a scale of density with several degrees can be drawn up. The range of density values for the different populations in a given herb layer varies from 1 to several thousand individuals per 10 m².

The density of a given species (population) differs greatly, depending on the type of plant association. As an example of this in table IX I have compared frequency value, density value and production value of a large number of species in the associations examined. The pattern of these values in different associations explains many problems in the field of specific ecology and is also of assistance in determining their optimum ecological amplitudes.

In extensive comparative studies it was not infrequently possible to see that the given species under given ecological conditions (in the given type of some species in four associations

Tab. IX

Alnetum	*Tilio-Carpinetum stachyetosum*			*Tilio-Carpinetum typicum*		
Production g/10 m²	*F*	Density per 10 m²	Production g/10 m²	*F*	Density per 10 m²	Production g/10 m²
18.200						
1.651						
3.240						
87.278						
20.086	37	158	1.264			
34.232	23	400	11.520			
209.974	37	87	4.498	5	11	9.658
794.365	5	25	19.562	8	14	42.553
60.240	27	92	3.496	26	85	4.590
3.256				7	99	1.336
171.986	92	1023	164.491	72	820	61.828
	17	1895	21.886	22	984	14.662
1.838	67	158	28.995	16	20	3.786
24.992	65	190	55.138	39	129	31.063
0.350	48	159	46.134	36	125	45.256
40.571	85	828	105.060	98	1795	149.344
0.180	70	628	10.864	45	830	40.089
2.244	53	510	27.670	61	697	39.868
0.360	2	2	0.044	71	316	16.716
				20	240	47.256

association) exhibits very high density with low current biomass per individual, and in others – lesser density but great biomass (considerable growth). The analysis made in this connection is aimed at establishing the biocenotic optimum and habitat-ecological optimum of species. A classic illustration of these two types of ecological relations is the behaviour of *Picea excelsa* in the Białowieża Primeval Forest. The spruce attains optimum habitat conditions there (its ecological-habitat optimum) in *Tilio-Carpinetum* associations. It grows there to a height of over 40 m, and attains vast individual biomass. Its density, however, is very low, as it cannot withstand competition with deciduous trees. The reverse situation was found in coniferous forest habitats: its density decidedly exceeds the numbers of all other species of trees, despite the fact that single individual biomasses are never as great there as in tree stands of the Carpinion alliance. In this second case it is possible to speak of the spruce's biocenotic optimum. Attention was drawn to those questions by Paczoski (1925a, 1925b).

The population of a given species finds relatively the best living conditions if both the size of the individual and density of individuals, and consequently its productivity, reach maximum values. Numerous tabulated data supply examples of the above discussion (Tab. I–IX).

3. Frequency and density

It is worth while devoting slightly more space to the relations between frequency (chance of encountering a species in a given patch of vegetation) and density (number of individuals of a species in a given area). Comparative analysis of data in this connection permits of establishing the two most frequently encountered relations, namely:

1. It is usually found that species rarely encountered in samples are also represented by a small number of individuals (numerous data in Tab. I–VIII). For example: *Corydalis solida* was found only twice out of 100 samples and then only two individuals in number (Tab. II position 35), or *Adoxa moschatellina*, 9 individuals in number, in 5 samples out of 100.

2. Species with a high degree of frequency occur simultaneously with a large number of individuals (e.g. *Dentaria bulbifera*, *Galeobdolon luteum*, *Anemone nemorosa* etc. in Tab. IV).

These two most often encountered rules do not of course exhaust all possibilities. It may happen that species with low frequency are characterized by considerable density and vice versa. The relations between frequency and density permit of drawing conclusion as to the way in which the population is distributed in a horizontal space, that is, of the distribution and gregariousness of species. We have found four basic possibilities here:

When the species exhibits high frequency and density it may be considered that it is distributed in the given stretch of vegetation in the form of a field, or else in more or less evenly dispersed large clusters.

Species with minimum frequencies and low densities occur rarely and at random, in the form of single individuals.

Species with high frequencies (classes IV, V) and relatively low density occur frequently and more or less evenly, but singly.

Species with low frequency but far greater density exhibit random-clumped distribution – i.e. occur in larger groups but unevenly distributed over the area of the patch of vegetation. The last type of spatial distribution can be explained by the example of a mosaic-like habitat, vegetative reproduction e.g. from rhizomes or stolons, as in *Oxalis acetosella* (in *Tilio-Carpinetum*) or the situation when the study area includes several facies or subassociations etc. These are of course somewhat general and approximate assumptions. The question of the spatial distribution of populations requires more detailed study methods, taking into consideration the ratio of sample size to number of samples and size of patch (Odum 1963).

4. Production and density

Production of a species and its density

The net production of a given species is the function of density of individuals and of average individual growth. Four basic possibilities may occur in this connection:

1) great individual growth (G_i) with simultaneously great density,
2) low values G_i and – low population density,
3) great individual growth – low density,
4) low values G_i – high density.

In the first case the species is responsible for decidedly the most production. Among such species are, for example: *Carex acutiformis* in *Frangulo-Salicetum*, *Urtica dioica* in the alluvial tree stand, *Dentaria bulbifera* in *Tilio-Carpinetum typicum*. In the second case, where we have low density and low average individual growth, the species' production is negligibly small. The largest number of such species occur in the herb layer. In the third and fourth case production exhibits intermediate values. Obviously the terms "large" "small" "intermediate" are relative values covering a large range of variations. For instance *Oxalis acetosella* in *T.–C. stachyetosum* attains a density of 1895/m², that is, very great density, but individual growth is very small, and production value in consequence forms only about 3% of the whole. A similar production value is found for *Urtica dioica*, despite the fact that the ratio of density to individual growth is the exact reverse (Tab. III).

Total production and density

It is possible to draw conclusions as to the size of the average individual in the herb layer of a given association from the ratio of total production to density. If, for instance, we take the average individual in the herb layer of *T.–C. typicum* as 1, then in *T.–C. stachyetosum* this index would be 1, 2, in *Circaeo-Alnetum* – 2.6, and in *Frangulo-Salicetum* as high as 9, 4. This index can provide reliable information on ecological and habitat relations.

Similarly by dividing total herb layer production by the number of species we obtain the index of production value per species. Again in *Frangulo-Salicetum* this index is decidedly the highest, i.e. 11.1, whereas in *Circaeo-Alnetum* it is 5.5, in *T.–C. typicum* 2.0 and in *T.–C. stachyetosum* 1.7.

The production of a given population also rises with increase in density, but this relation does not always apply to total values. It often happens that the given group of species or the whole herb layer, despite the fact that it exhibits considerable density, may have low production. This of course depends on the size of individuals. A striking example of this are species in frequency classes II and III in the alluvial tree stand, such as: *Chrysosplenium alternifolium*, *Circaea alpina*, *Moehringia trinervia* and others, which jointly reach as much as 76% of total density, although their production is only 24%. On the other hand two species in frequency classes IV and V – *Urtica dioica* and *Geranium robertianum* – despite the fact that they constitute only 10% of the density value, produce as much as 44% of total production. Tables V–VIII and Fig. 2 present the relations between production value and the number of species and their density.

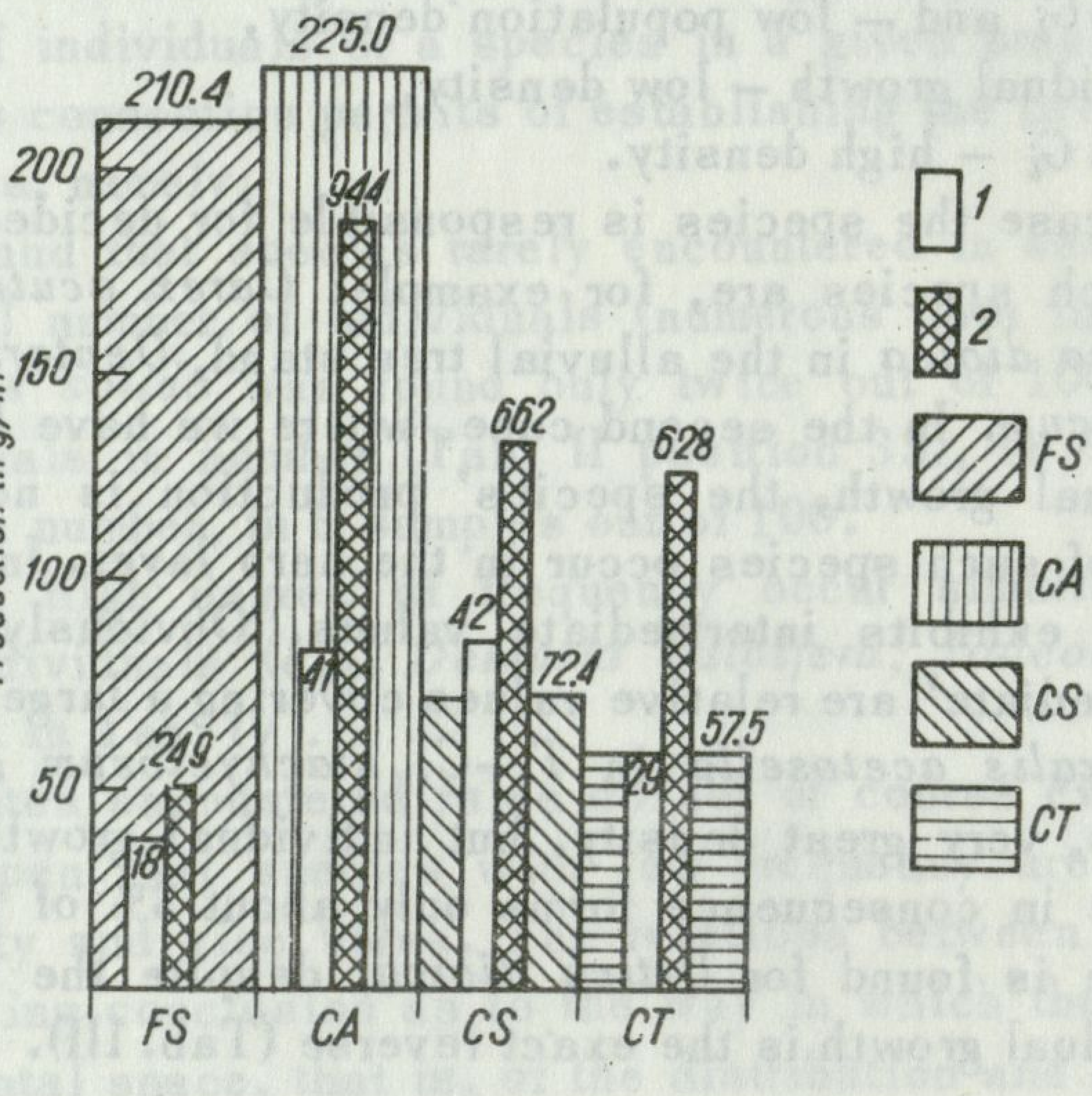

Fig. 2. Relation between production value and number of species and their density in the herb layer of the four associations examined

1 – number of species: *2* – density per 1 m², *FS* – *Frangulo-Salicetum; CA* – *Circaeo-Alnetum; CS* – *Tilio-Carpinetum stachyetosum silvaticae; CT* – *Tilio-Carpinetum typicum*

5. Distribution of production among species

It was found that in each association there is one, or at most a few, species, the production of which distinctly exceeds that of other species. In the associations examined on an average approximately 30% of total production is produced by a dominant of this kind. Data in Fig. 3 illustrate the relations between the number of species and production value expressed in percentages. Except for the herb layer in *Frangulo-Salicetum*, the course taken by the lines is in general similar. As from the greatest dominant, differences in production between subsequent species become increasingly smaller (gentle rise in curve). In *Frangulo-Salicetum* there is a distinct break in the curve of production value which coincides with the number of 4 species. In this case as much as 89% of total production is accounted for by the four dominating species, which are: *Dryopteris thelypteris*, *Carex acutiformis*, *Calamagrostis canescens* and *Phragmite communis*. If we enquired how many species in the remaining

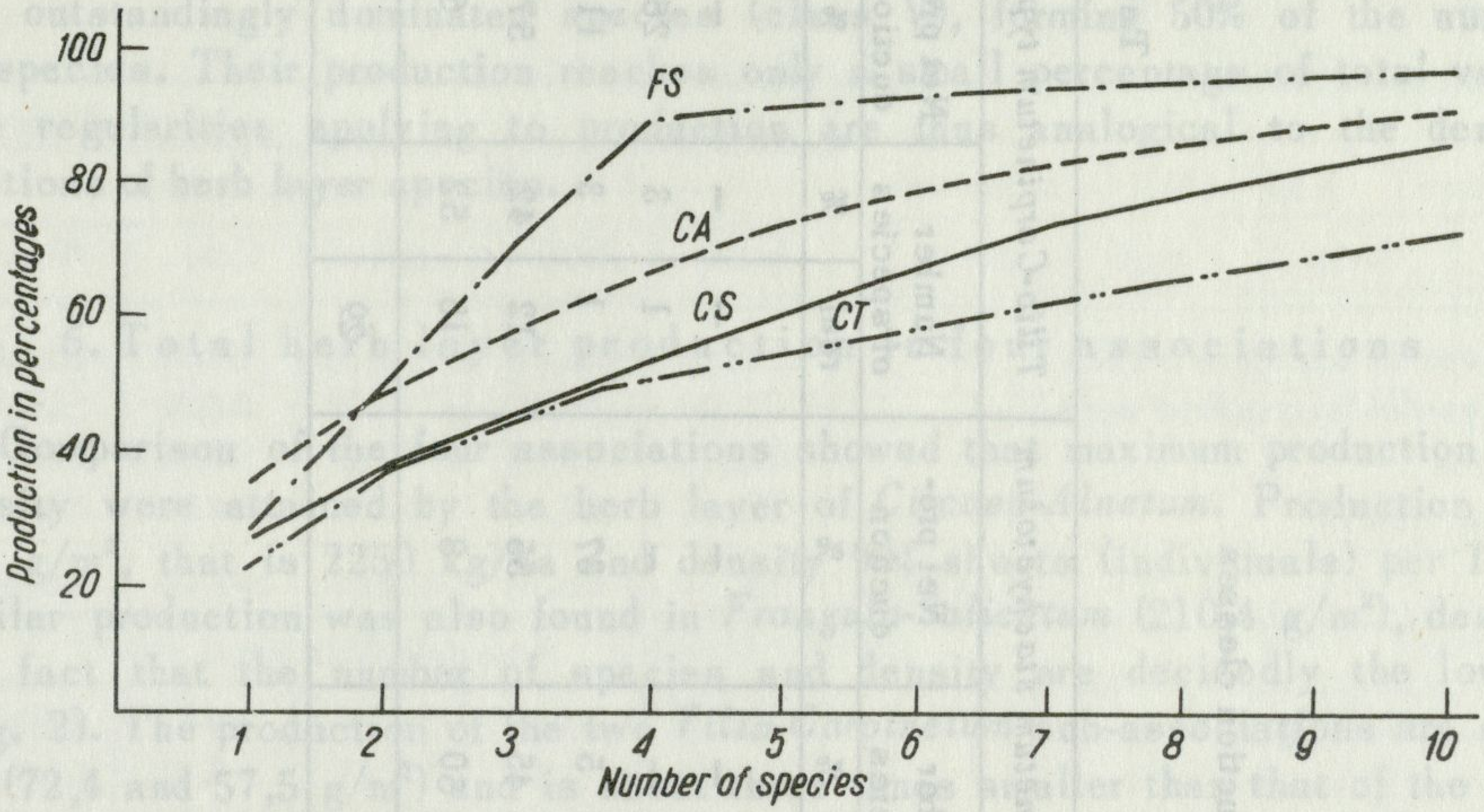

Fig. 3. Relation between production value and number of species
FS – *Frangulo-Salicetum, CA* – *Circaeo-Alnetum; CS* – *Tilio-Carpinetum stachyetosum; CT* – *Tilio-Carpinetum typicum*

associations from such production value it would appear that there are 9 – in the herb layer of *Tilio-Carpinetum stachyetosum*, 11 in *T.–C. typicum* and as many as 16 species in *Circaeo-Alnetum*. Generally speaking the shape taken by curves of percentage of production (Fig. 3) is a good measure of the weight structure of the herb layer or distribution of production among species.

Depending on the amount of biomass produced by species it is possible to suggest a conventional division of species into several classes (groups). I have given below division of species into five classes according to the amount of biomass produced, expressed in percentages:

Class I: absolutely dominating species (order I absolute dominant) producing over 50% of total production,

Class II: dominating species (order II dominant) – amount of production within limits of 25,1 – 50%,

Class III: co-dominating species (order III dominant) – amount of production 10,1 – 25%,

Class IV: dominated species – value 1,1 – 10%,

Class V: species outstandingly dominated – production below 1%.

Division into such classes of production corresponds most closely to the actual data supplied by analysis of the herb layer in different associations.

Table X presents the percentage of number of species and their production value in the above classes. Order I dominant was not recorded in these associations. A species of this kind usually occurs under extreme ecological conditions. There are few dominating species in any of the associations examined. They from a very small percentage of the total number of species, but produce

Distribution of number of species and production in production classes

Tab. X

Production classes		*Frangulo-Salicetum*			*Circaeo-Alnetum*			*Tilio-Carpinetum stachyetosum*			*Tilio-Carpinetum typicum*		
		Number of species		Net production	Number of species		Net production	Number of species		Net production	Number of species		Net production
		real	%	%	real	%	%	real	%	%	real	%	%
I	50.1–100%	–	–	–	–	–	–	–	–	–	–	–	–
II	25.1– 50	1	5	29	1	2	35	–	–	–	1	3	26
III	10.1– 25	3	17	60	1	2	13	2	5	37	1	3	11
IV	1.1– 10	5	28	7	11	26	47	19	45	55	12	42	57
V	<1– 1	9	50	4	28	70	5	21	50	8	15	52	6
Total		18			41			42			29		

nearly half the total production value. The most numerous, on the other hand, are outstandingly dominated species (class V), forming 50% of the number of species. Their production reaches only a small percentage of total value. The regularities applying to production are thus analogical to the density relations of herb layer species.

6. Total herb layer production in four associations

Comparison of the four associations showed that maximum production and density were attained by the herb layer of *Circaeo-Alnetum*. Production was 225 g/m², that is 2250 kg/ha and density 994 shoots (individuals) per 1 m². Similar production was also found in *Frangulo-Salicetum* (210,4 g/m²), despite the fact that the number of species and density are decidedly the lowest (Fig. 2). The production of the two *Tilio-Carpinetum* sub-associations are similar (72,4 and 57,5 g/m²) and is about three times smaller than that of the herb layer in the two other associations.

The results obtained refer to defined stretches of forest examined on "The Wild Apple-Tree Island". It is difficult to say to what extent they are representative of units of a more general character, such as associations. It would be necessary to carry out field studies by means of appropriate methods, and also statistical calculations in order to determine this question. In the present case I was chiefly concerned with obtaining – using a uniform method – the order of relative values for given associations, without taking into consideration the significance of differences and other statistical calculations.

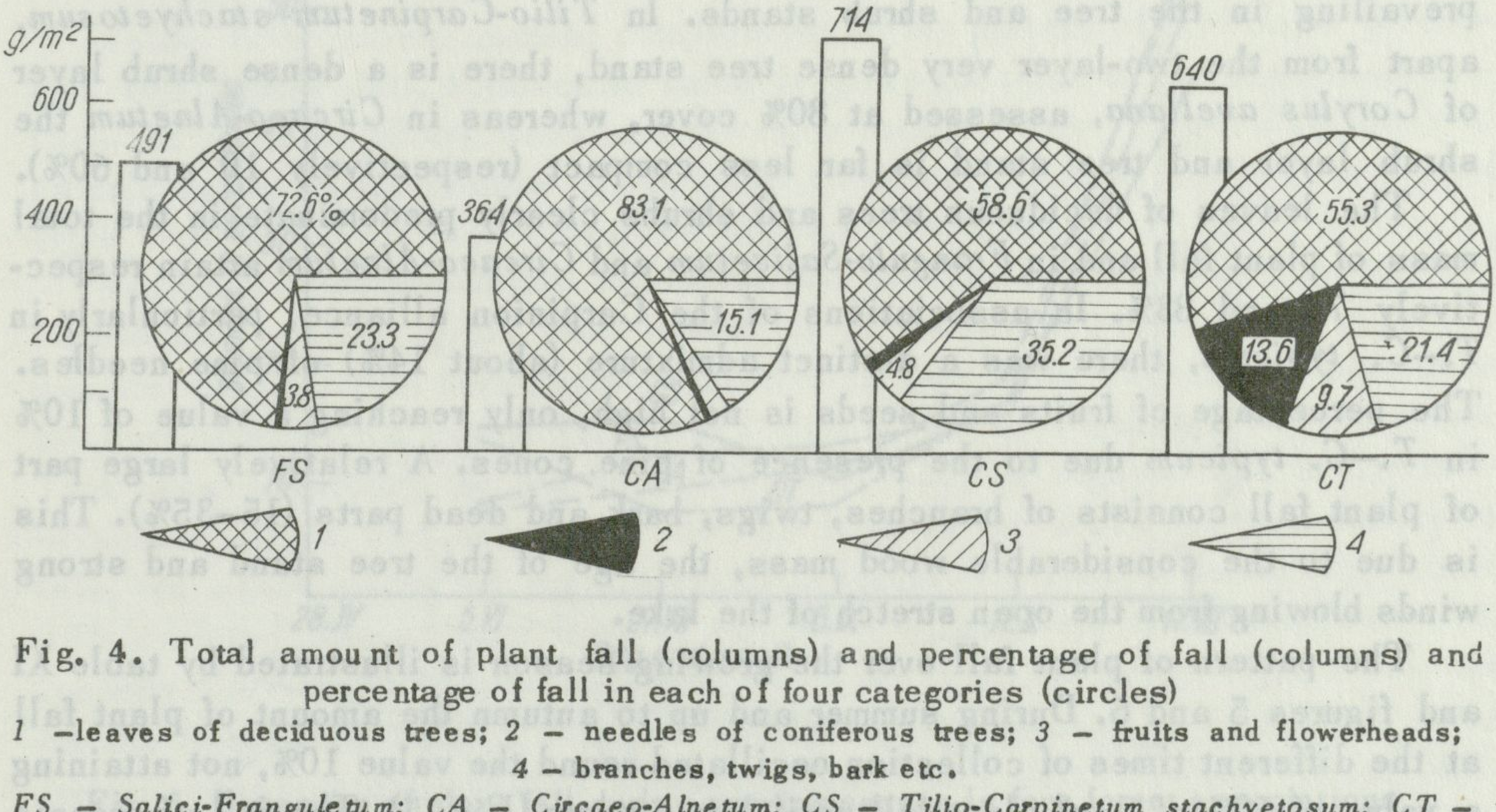

Fig. 4. Total amount of plant fall (columns) and percentage of fall (columns) and percentage of fall in each of four categories (circles)
1 –leaves of deciduous trees; *2* – needles of coniferous trees; *3* – fruits and flowerheads; *4* – branches, twigs, bark etc.
FS – *Salici-Frangul etum; CA* – *Circaeo-Alnetum; CS* – *Tilio-Carpinetum stachyetosum; CT* – *Tilio-Carpinetum typicum*

Tree and shrub fall in four associations during vegetation

Kind of fall	Associations				
	Tilio-Carpinetum typicum				
	June	Juli	Sept.	Oct.	Nov.
Leaves of deciduous trees	5.26	6.16	22.16	55.36	264.85
Leaves of coniferous trees	12.90	4.49	8.18	36.98	24.76
Fruits	30.91	6.39	7.58	0.83	16.55
Plant debris	33.07	25.34	16.13	14.06	48.26
Total	82.14	42.38	54.05	107.23	354.42
	Frangulo-Salicetum				
Leaves of deciduous trees	15.19	20.99	42.04	68.83	209.14
Leaves of coniferous trees	0.08	0.18	0.11	0.98	0.18
Fruits	2.18	3.37	0.69	0.84	11.84
Plant debris	19.60	36.11	22.24	8.54	27.51
Total	37.05	60.65	65.08	79.19	248.67

7. Plant fall

The amount of plant fall in the associations and percentages of fractions are illustrated by Fig. 4. Maximum organic fall was found in *Tilio-Carpinetum stachyetosum* (714 g/m^2), which is almost twice higher than fall in *Circaeo-Alnetum* (364 g/m^2). The causes of this must be sought for in the relations prevailing in the tree and shrub stands. In *Tilio-Carpinetum stachyetosum*, apart from the two-layer very dense tree stand, there is a dense shrub layer of *Corylus avellana*, assessed at 80% cover, whereas in *Circaeo-Alnetum* the shrub layer and tree stand is far less compact (respectively 10 and 60%).

The leaves of deciduous trees and shrubs clearly predominate in the total mass of plant fall and in *Frangulo-Salicetum* and *Circaeo-Alnetum* attain respectively 73 and 83%. In associations of the Carpinion alliance, particularly in *T.–C. typicum*, there was a distinct admixture (about 14%) of pine needles. The percentage of fruits and seeds is not high, only reaching a value of 10% in *T.–C. typicum* due to the presence of pine cones. A relatively large part of plant fall consists of branches, twigs, bark and dead parts (15–35%). This is due to the considerable wood mass, the age of the tree stand and strong winds blowing from the open stretch of the lake.

The pattern of plant fall over the growing season is illustrated by table XI and figures 5 and 6. During summer and up to autumn the amount of plant fall at the different times of collection oscillated round the value 10%, not attaining a value of 50% of total plant fall until late autumn (Fig. 5). The fall of organic matter to the forest floor is thus continuous and gradual throughout the growing season 1967 (data in grams of ovendry weight per square meter)

Tab. XI

and months

Total g/m²	%	June	Juli	Sept.	Oct.	Nov.	Total g/m²	%
		Tilio-Carpinetum stachyetosum						
353.79	55.3	2.62	28.84	31.89	85.20	269.47	418.02	58.6
87.31	13.6	0.35	0.45	0.61	7.40	1.09	9.90	1.4
62.26	9.7	7.05	8.38	11.48	0.55	6.81	34.27	4.8
136.86	21.4	86.55	70.48	27.56	27.86	39.28	251.73	35.2
640.22	100.0	96.57	108.15	71.54	121.01	316.65	713.92	100.0
Total		*Circaeo-Alnetum*					Total	
356.19	72.6	3.31	23.42	33.65	57.76	184.51	302.65	83.1
1.53	0.3	0.12	–	0.09	0.86	0.45	1.52	0.4
18.92	3.8	2.50	0.92	0.08	–	1.40	4.90	1.4
114.05	23.3	19.28	10.50	4.73	10.62	9.83	54.96	15.1
490.69	100.0	25.21	34.84	38.55	69.24	196.19	364.03	100.0

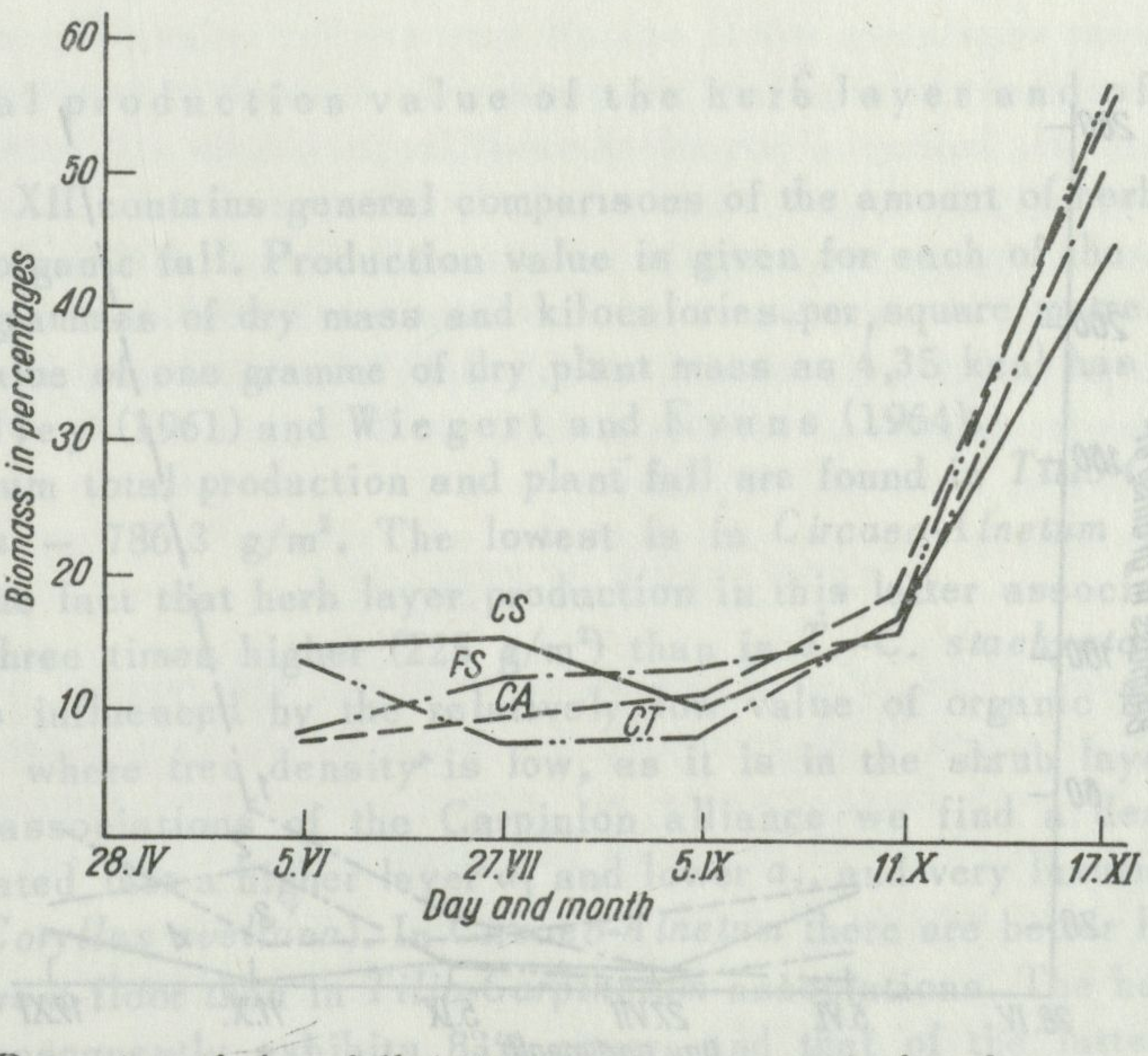

Fig. 5. Dynamics of plant fall during growing season in four forest associations

FS – Frangulo-Salicetum, CA – Circaeo-Alnetum, CS – Tilio-Carpinetum stachyetosum, CT – Tilio-Carpinetum typicum

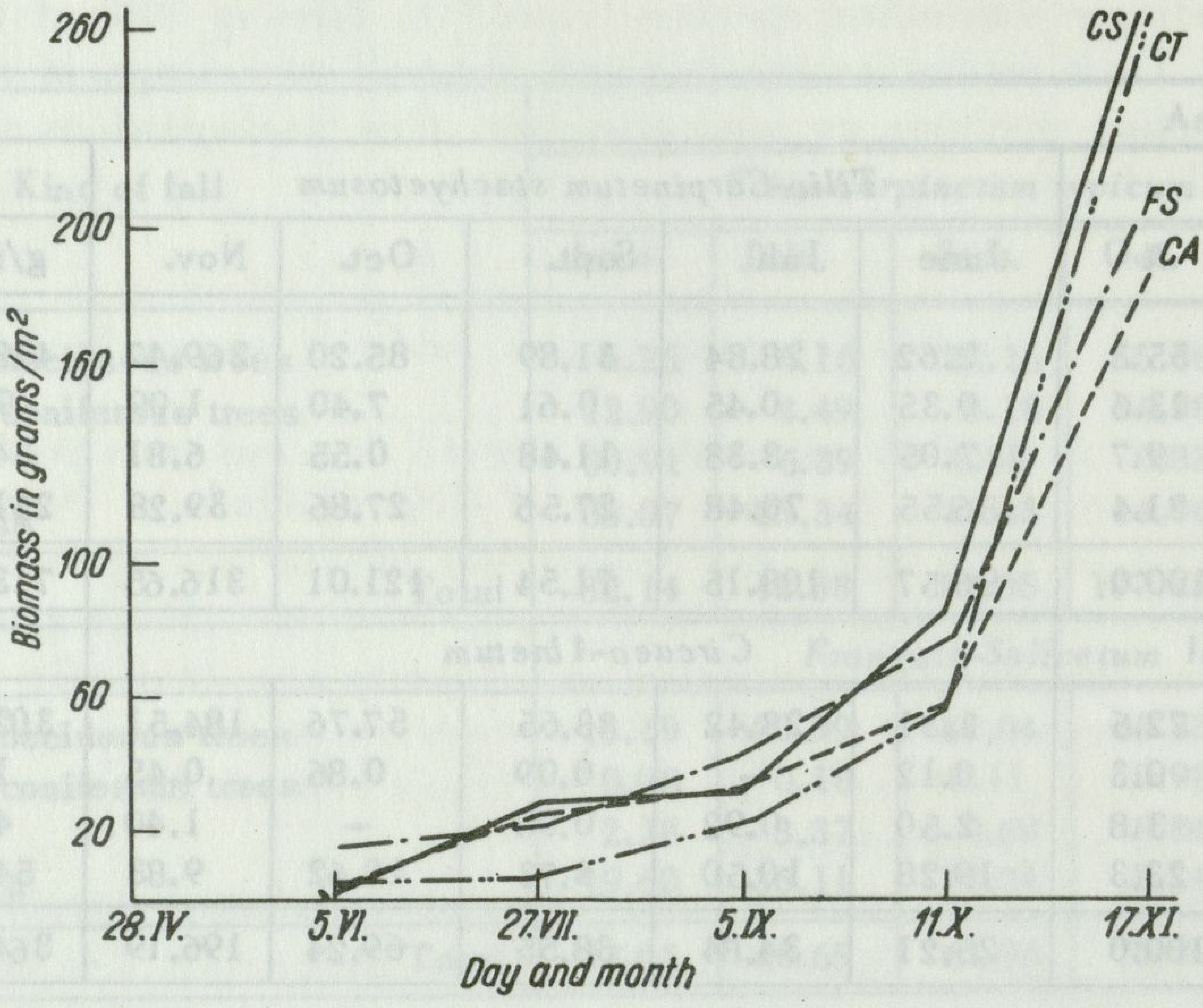

Fig. 6. Fall of leaves of deciduous trees and shrubs in four associations

FS – Frangulo-Salicetum, CA – Circaeo-Alnetum, CS – Tilio-Carpinetum stachyetosum silvaticae, CT – Tilio-Carpinetum typicum

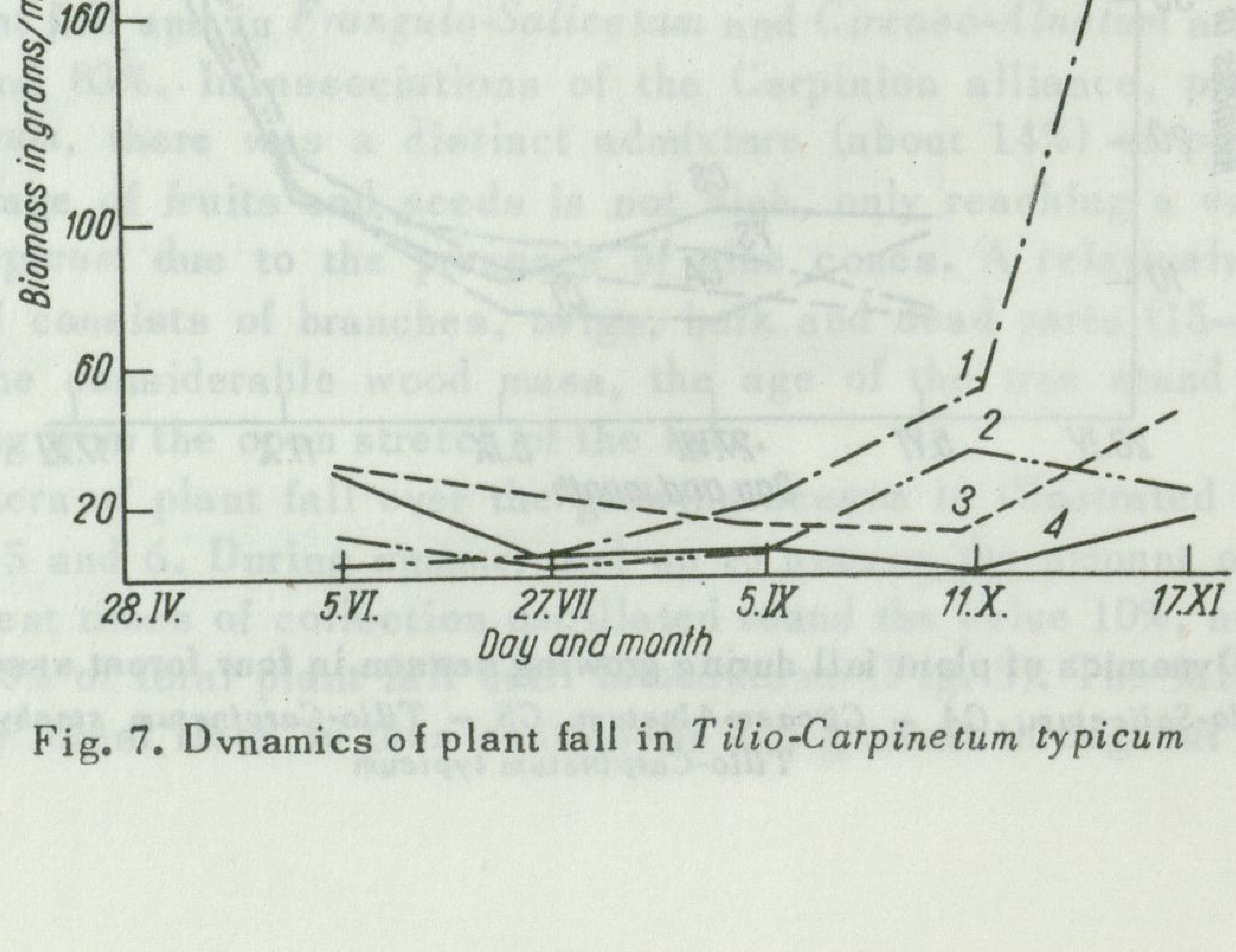

Fig. 7. Dvnamics of plant fall in *Tilio-Carpinetum typicum*

season. From spring and summer until the autumn a great amount of leaf fall, almost half the annual organic fall, finds its way to the forest floor. Intensiveness of fall of the different fractions differs in time. This can be traced, using fall in *Tilio-Carpinetum typicum* (Fig. 7) as an example.

The smallest fall of leaves of deciduous trees and shrubs occurs during the formation and development of young leaves (up to the end of May). Throughout the summer months this value exhibits a very slight but constant tendency to increase. It is not until autumn that leaf fall abruptly increases (Fig. 6).

In the case of coniferous trees there are two distinct periods of needle fall: the first in spring is far smaller (about 13 g/m²) and a second in October, almost three times greater than the spring fall (Fig. 5).

Leaf fall from deciduous trees and shrubs, as mentioned above, attains its decidedly maximum value in autumn from mid-October to mid-November, but maximum fall from coniferous trees takes place a month earlier, i.e. from approximately mid-September to mid-October. This regularity is repeated in all four associations, regardless of differences in the species composition of the treestand (Tab. XI).

The amount of biomass of dead branches, bark etc. is greater in spring than in summer. Frozen twigs and branches and bark peeling after winter are easily knocked off by the strong winds blowing from the lake. The tree crowns, at that time leafless, provide no shelter from the wind. The second peak of fall of this fraction takes place in autumn; the fall of fruits and seeds follows a similar pattern.

8. Total production value of the herb layer and of plant fall

Table XII contains general comparisons of the amount of herb layer production and organic fall. Production value is given for each of the study associations in grammes of dry mass and kilocalories per square metre. The index of caloric value of one gramme of dry plant mass as 4,35 kcal has been accepted after Golley (1961) and Wiegert and Evans (1964).

Maximum total production and plant fall are found in *Tilio-Carpinetum stachyetosum* – 786,3 g/m². The lowest is in *Circaeo-Alnetum* – 589,1 g/m², despite the fact that herb layer production in this latter association proved to be over three times higher (225 g/m²) than in *T.–C. stachyetosum* (72 g/m²). This was influenced by the relatively low value of organic fall in *Circaeo-Alnetum*, where tree density is low, as it is in the shrub layer. Contrary to this, in associations of the Carpinion alliance we find a dense tree stand differentiated into a higher layer a_1 and lower a_2, and very luxuriant shrub layer (chiefly *Coryllus avellana*). In *Circaeo-Alnetum* there are better light conditions on the forest floor than in *Tilio-Carpinetum* associations. The herb layer in the former consequently exhibits 83% cover, and that of the latter 71 and 56%.

Summary of net production in four association

Tab. XII

Production	*Frangulo-Salicetum*		*Circaeo-Alnetum*		*Tilio-Carpinetum stachyetosum*		*Tilio-Carpinetum typicum*	
	g/m²	kcal/m²	g/m²	kcal/m²	g/m²	kcal/m²	g/m²	kcal/m²
Plant fall	490.69	2130	364.03	1580	713.92	3100	640.22	2780
Herbs	210.46	910	225.09	980	72.38	310	57.48	250
Total	701.15	3040	589.12	2560	786.30	3410	697.80	3030

The more general regularities merit attention in this connection, namely total production values of four associations (in this case of the herb layer and plant fall) exhibit far less variability than the values of different component elements of such production.

In the herb layer the production values of different populations exhibit wide variations (Tab. I–IV)., these differences attaining the order of several thousand times more or less than other given values.

The range of variations in herb layer production between associations is slight (in *T.–C. typicum* 574.8 – in *Circaeo-Alnetum* 2250,9 g/10 m²) and is about 4 times greater. When the herb layer and fall values are compared we find that they are very similar (Tab. XII). The extreme values between *Circaeo-Alnetum* and *Tilio-Carpinetum stachyetosum* are from 589 to 786 g/m². Perhaps if production of trunk and branches were measured, the total production of all elements of forest vegetation would exhibit very similar values per unit of area and time. Even without taking this last possibility into consideration it can be said that in natural, balanced associations different plants, different forms of growth "quite clearly form one whole adapted, wherever local limiting factors permit, to the solar energy reaching the ecosystem" (Odum 1963). We find here an analogy with the observations made by Gessner 1949 (cited after Odum 1963), who proved that the amount of chlorophyll incident at a given moment per unit of surface is in general similar in different biocenoses.

V. COMPARISON OF RESULTS

1. Regardless of the type of forest association, the number of sporadic species (frequency class I) id decidedly the greatest. On an average over 70% of the number of herb layer species are rarely encountered species. Unlike sporadic species, species with maximum frequency (class V) are few in number and from 2–5% of the number of species (cf. Tab. V–VIII).

2. The average total density of individuals (or shoots) in herb layer of four associations per 1 m² is as follows:

Frangulo-Salicetum	249 (with herb layer cover of 33%),
Circaeo-Alnetum	944 (" " " " 83%),

Tilio-Carpinetum stachyetosum 662 (with herb layer cover of 71%),
Tilio-Carpinetum typicum 628 (" " " " 56%).

3. Species with low density value (sporadic species) are in the majority. In each association, however, we find one, or at most a few, dominating species (Tab. I–IV).

4. There are most often positive correlations between frequency and density: species rarely encountered in samples are also represented by a small number of individuals and vice versa (Tab. I–VIII). It does, however, happen that species with relatively low frequency are distinguished by considerable density. The relations between frequency and density provide a basis for drawing conclusions as to the way individuals of a population are distributed in horizontal space, that is, as to the distribution and gregariousness of species.

5. Conclusions can be reached as to the size of the average individual in the herb layer from the ratio of total production to density. Fairly considerable differences occur here. If an average individual in *Tilio-Carpinetum typicum* is taken as 1, then in *T.–C. stachyetosum* this index would be 1,2, in *Circaeo-Alnetum* – 2,6 and in *Frangulo-Salicetum* as much as 9,4. An index of this kind can provide reliable information on certain habitat properties, e.g. water relations in the soil.

6. By dividing total herb layer production by the number of species responsible for this production we obtain the index of production value per species. In *Frangulo-Salicetum* this index is decidedly the greatest, 11.1, whereas ir *Circaeo-Alnetum* it is 5.5, in *Tilio-Carpinetum typicum* 2.0 and in *T.–C. stachyetosum* – 1.7.

7. As a rule, production of a given population also increases as density increases, but this relation does not always apply to total values. Frequently species with very great density have relatively low production (e.g. *Oxalis acetosella*, *Chrysosplenium alternifolium*), this of course depending on the amount of individual biomass produced in a given year.

8. In each association we find one or at most a few species which markedly exceed others in respect of their production. On an average about 30% of total production is accounted for by a dominant of this kind in the associations examined. Figure 3 illustrates the relations between the number of species and amount of production in the various associations.

9. The species were divided into five classes depending on the amount of biomass produced. The percentage of number of species and their production value in the classes are given in table X. The most numerous are species producing less than 1% of total production. They from over 50% of the number of species, and their joint production forms only a small percentage (about 5%).

There are very few species producing a large amount of biomass (about 9%), but their participation in production is as much as approximately 50% of the total value. The regularities applying to production are thus analogical with the density relations of the species.

10. Density and production values provide considerable information on the ecology of the species. A species finds relatively the optimum habitat conditions in a place where its density and production attain maximum values (Tab. IX).

11. Herb layer production values are as follows:

Circaeo-Alnetum	225.0 g/m²,
Frangulo-Salicetum	210.4 g/m²,
Tilio-Carpinetum stachyetosum	72.4 g/m²,
Tilio-Carpinetum typicum	57.5 g/m².

12. The amount and qualitative composition of plant fall depends on the quantitative relations and species composition of the tree and shrub layers. Leaves of deciduous trees and shrubs distinctly predominate in the total mass of plant-fall (from 55–83%). The percentage of pine needles does not exceed 1% of total fall, and it is only in *Tilio-Carpinetum* typicum that this percentage is as much as about 14. Similarly fruits and seeds from a relatively small percentage (9,7–1,4%, Fig. 4 and Tab. XI).

13. The flow of organic matter to the forest floor is continuous during the growing season, although differentiated as to quality and guantity. Taken jointly about 50% of total fall takes place from spring to autumn, the remaining 50% during a few weeks in autumn (Fig. 5 and Tab. XI). Maximum autumn needle fall occurs a month earlier than that of the leaves of deciduous trees. The value of the biomass of dead branches, twigs, bark etc. and fruits and seeds exhibits two peaks – in spring and autumn.

14. Total production values (of herb layer and plant fall) exhibit decidedly less variation than the value of different component elements of this production. Within the herb layer production values of different species exhibit variations several thousand times lesser or greater (Tab. IV). Variation within the herb layer production of the associations examined is slight and is about four times greater, while the values of herb layer production and plant fall taken jointly are very similar in all the associations (Tab. XII).

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ZALEŻNOŚCI POMIĘDZY PRODUKTYWNOŚCIĄ RUNA A JEGO STRUKTURĄ W ZBIOROWISKACH „WYSPY DZIKIEJ JABŁONI"

Streszczenie

W pracy przedstawiono wyniki badań nad produktywnością runa oraz opadu drzew i krzewów w czterech zespołach leśnych „Wyspy Dzikiej Jabłoni". Jest to jedno z opracowań większej serii prac poświęconych produktywności runa i opadu roślinnego ważniejszych zbiorowisk niżowych Polski. W zbiorowiskach tych Instytut Ekologii PAN prowadzi od lat równoczesne badania nad produktywnością drobnych gryzoni.

Celem pracy jest przede wszystkim ocena wielkości produkcji runa i opadu roślinnego, przeprowadzenie porównawczej analizy wybranych parametrów produktywności oraz ustalenie prawidłowości jakie między nimi zachodzą.

Badano runo i opad roślinny w czterech następujących zbiorowiskach: *Frangulo-Salicetum* Malc. 1929, *Circaeo-Alnetum* Oberdorfer 1953 oraz *Tilio-Carpinetum* Traczyk 1962 w dwu podzespołach *T.–C. stachyetosum silvaticae*, oraz *T.–C. typicum*. Rozmieszczenie zespołów na wyspie ilustruje figura 1.

Przy ocenie produktywności runa zastosowano metodę Traczyka (1967a, 1967b), polegającą na ustaleniu zagęszczenia poszczególnych populacji oraz przeciętnego przyrostu osobniczego w maksymalnym okresie wzrostu populacji. Produkcja pierwotna (P) równa się iloczynowi zagęszczenia (D) oraz przeciętnego przyrostu osobniczego (G_i): $P = D \times G_i$.

W każdym z czterech badanych zbiorowisk rozmieszczono w regularnych odstępach po 100 prób kolistych o powierzchni 0,1 m^2. Analizę zagęszczenia przeprowadzono w dwu terminach: 4 maja (dla wczesnowiosennych geofitów) oraz 3 czerwca (dla pozostałych roślin).

W okresach maksymalnego rozwoju populacji (fenofaza owocowania) zbierano odpowiednią do wyników analizy zagęszczenia liczbę gatunków (pędów). Rośliny ścinano trzykrotnie – w maju, czerwcu i lipcu.

Opad roślinny zbierano z obręczy drucianych (0,1 m^2) położonych na ziemi pozbawionej runa i ścioły. Prób takich rozmieszczono po 30 w każdym zbiorowisku. Materiał roślinny zbierano czterokrotnie w okresie od końca kwietnia do 17 listopada. Następnie segregowano go na cztery kategorie: 1) liście drzew liściastych, 2) liście drzew szpilkowych, 3) owoce oraz 4) gałązki, korowinę itp. Materiał roślinny suszony był do stałej wagi oraz ważony z dokładnością do 0,01 g.

W pracy uzyskano następujące wyniki:

1. Bez względu na typ zbiorowiska leśnego, liczba gatunków sporadycznych (I kl. frekwencji) jest zdecydowanie największa. Średnio biorąc, ponad 70% ogólnej liczby gatunków runa – to gatunki rzadko spotykane. W przeciwieństwie do gatunków sporadycznych, gatunki o najwyższej frekwencji (V kl.) są bardzo nieliczne i stanowią 2–5% liczby gatunków (por. Tab. V–VIII).

2. Przeciętne, ogólne zagęszczenie osobników (lub pędów) w runie czterech zbiorowisk kształtuje się na 1 m^2 następująco:

w *Frangulo-Salicetum*	249	(przy pokryciu runa 33%)
" *Circaeo-Alnetum*	944	(" " " 83%)
" *Tilio-Carpinetum stachyetosum*	662	(" " " 71%)
" *Tilio-Carpinetum typicum*	628	(" " " 56%)

3. Najwięcej jest gatunków o niskiej wartości zagęszczenia (gatunki sporadyczne). W każdym jednak zbiorowisku stwierdzamy w runie dominację jednego lub co najwyżej kilku gatunków (Tab. I–IV).

4. Pomiędzy frekwencją a zagęszczeniem zachodzą najczęściej korelacje dodatnie: gatunki rzadko napotykane w próbach są również reprezentowane przez małą liczbę osobników i odwrotnie (Tab. I–VIII). Zdarza się jednak, że gatunki o stosunkowo małej frekwencji odznaczają się dużym zagęszczeniem. Relacje pomiędzy frekwencją a zagęszczeniem pozwalają wnioskować o sposobie rozmieszczenia osobników populacji w przestrzeni poziomej, czyli o rozkładzie i towarzyskości gatunków.

5. Ze stosunku globalnej produkcji do zagęszczenia można wnosić o wielkości przeciętnego osobnika w runie. W tym zakresie zachodzą dosyć duże różnice. Gdyby przyjąć przeciętnego osobnika w *Tilio-Carpinetum typicum* za 1, to w *T.–C. stachyetosum* wskaźnik ten byłby równy 1,2, w *Circaeo-Alnetum* – 2,6, a w *Frangulo-Salicetum* aż 9,4. Wskaźnik taki może dobrze informować o niektórych właściwościach siedliska, np. stosunkach wodnych w glebie.

6. Dzieląc globalną produkcję runa przez liczbę gatunków wytwarzających tę produkcję uzyskujemy wskaźnik wielkości produkcji przypadającej na jeden gatunek. I znów w *Frangulo-Salicetum* wskaźnik ten jest zdecydowanie największy i wynosi 11,1 podczas gdy w *Circaeo-Alnetum* – 5,5, w *Tilio-Carpinetum typicum* – 2,0 a w *T.–C. stachyetosum* – 1,7.

7. Z reguły, ze wzrostem zagęszczenia określonej populacji wzrasta również jej produkcja. Nie zawsze jednak taka zależność dotyczy globalnych wartości. Często gatunki o bardzo dużym zagęszczeniu mają stosunkowo małą produkcję (np. *Oxalis acetosella*, *Chrysosplenium alternifolium*). Zależy to oczywiście od wielkości biomasy osobniczej wyprodukowanej w danym roku.

8. W każdym zbiorowisku stwierdzamy jeden lub co najmniej kilka gatunków, które wyraźnie przewyższają swoją produkcją inne. Średnio biorąc, na takiego dominanta przypada w omawianych zbiorowiskach ok. 30% ogólnej produkcji. Figura 3 ilustruje zależności pomiędzy liczbą gatunków a wielkością produkcji w poszczególnych zbiorowiskach.

9. W zależności od wielkości wyprodukowanej biomasy podzielono gatunki na pięć klas. Udział liczby gatunków i ich wielkości produkcji w klasach przedstawia tabela X. Najliczniejsze są gatunki produkujące poniżej 1% ogólnej produkcji. Stanowią one powyżej 50% liczby gatunków, a ich produkcja łączna osiąga zaledwie kilka procent (ok. 5%). Gatunków produkujących dużą masę jest bardzo niewiele (ok. 9%). Natomiast

udział ich w produkcji sięga ok. 50% wartości ogólnej. Prawidłowości dotyczące produkcji są więc analogiczne do stosunków zagęszczenia gatunków.

10. Wielkości zagęszczenia oraz produkcji wyjaśniają wiele zagadnień z zakresu ekologii gatunków. Gatunek znajduje względnie najlepsze warunki środowiskowe tam, gdzie jego zagęszczenie i produkcja osiągają najwyższe wartości (Tab. IX).

11. Wielkość produkcji runa przedstawia się następująco:

Circaeo-Alnetum	225.0 g/m²
Frangulo-Salicetum	210.4 g/m²
Tilio-Carpinetum stachyetosum	72.4 g/m²
Tilio-Carpinetum typicum	57.5 g/m²

12. Wielkość i skład jakościowy opadu roślinnego zależy od stosunków ilościowych i składu gatunkowego warstwy drzew i krzewów. W globalnej masie opadu przeważają wyraźnie liście drzew i krzewów liściastych (od 55—83%). Udział szpilek sosny nie przekracza 1% ogólnego opadu, jedynie w *Tilio-Carpinetum typicum* dochodzi do ok. 14%. Podobnie stosunkowo nieduży udział w opadzie mają owoce i nasiona (1,4—9,7% — Fig. 4 i Tab. XI).

13. W sezonie wegetacyjnym dopływ materii organicznej do dna lasu jest ciągły, choć zróżnicowany ilościowo i jakościowo. Od wiosny aż do jesieni opada w sumie ok. 50% ogólnego opadu, pozostałe 50% przypada na kilka tygodni jesieni (Fig. 5 i Tab. XI). Maksimum jesiennego opadu szpilek przypada o miesiąc wcześniej niż liści drzew liściastych. Wielkość biomasy martwych gałązek, korowiny itp. oraz owoców i nasion wykazuje dwa szczyty — wiosenny i jesienny.

14. Wielkość produkcji ogólnej (runa i opadu) wykazuje zdecydowanie mniejszą zmienność niż wielkości poszczególnych elementów składowych tej produkcji. W obrębie runa wielkości produkcji poszczególnych gatunków wykazują zmienność rzędu kilku tysięcy razy (Tab. I—IV). Zmienność w obrębie produkcji runa badanych zbiorowisk jest niewielka i wynosi tylko około czterech razy. Natomiast wartości runa i opadu roślinnego łącznie są już bardzo zbliżone pomiędzy zespołami (Tab. XII).

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