

EKOLOGIA POLSKA

Vol. XX

Warszawa 1972

No. 22

Instytut Ekologii, Pracownia Ekologii Roślin, Warszawa

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PRIMARY PRODUCTION OF THE HERB LAYER AND PLANT FALL IN THE *VACCINIO MYRTILLI-PINETUM* FOREST ASSOCIATION IN THE PISZ FOREST (NORTH-EAST POLAND)

(Ekol. Pol. 20: 253-285). Assessment was made of the herb layer production, moss biomass and plant fall from trees and shrubs in two plant communities belonging to the association of *Vaccinio myrtilli-Pinetum* (Kobendza 1930, Tüxen, Vlieger 1959) and in a young pine tree plantation adjoining them.

These studies form part of an extensive research programme on the biological production of forest ecosystems carried out in several forest associations in the north of Poland by the Institute of Ecology, Polish Academy of Sciences.

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I. INTRODUCTION

The purpose of the studies was to assess the annual production of the forest herb layer and plant fall from trees and shrubs in several stands of *Vaccinio myrtilli-Pinetum* (Kobendza 1930, Tüxen et Vlieger 1959) association of different ages. This assessment forms part of an extensive research programme on the biological production carried out under the IBP in recent years, particularly in 1967, by the Institute of Ecology, Polish Academy of Sciences, in a large number of forest associations. These researches include not only the study of primary production but also the investigations of small vertebrates populations.

The studies presented in this paper were carried out during the growing season of 1967, with the exception of samples for plant fall which were taken throughout the year, that is, from April 1967 to April 1968. The study area is situated in the Mazurian Lake District, in the northern part of the Pisz Forest, in the forests of the Krutyń Forest Administration District. The one-hectare areas chosen for the studies were located in three different forest sectors: a coniferous forest 140 years old in sector 290, one 40 years old in sector 233, and a young pine plantation in sector 281.

II. DESCRIPTION OF STUDY AREAS

The study stand of 140-year old *Vaccinio myrtilli-Pinetum* is situated on flat ground. The tree stand consists of spruce and pine with the addition of planted beech. There are occasional open places in the dense tree stand made by felling groups of pines. The average age of the pines was estimated as 140 years, and height about 25 m. Spruce attains heights from 15 to 18 m and varies from 40–60 years in age. These trees sprout again and grow back afresh better than the pine, which produces single seedlings only. On account of certain differences in the composition and structure of the vegetation in the study area, two phytosociological records illustrating the floristic composition of the association were made and two soil pits characterizing the prevailing habitat conditions (Tab. I and II, Fig. 1).

Vaccinio myrtilli-Pinetum (Kobendza 1930) Br.-Bl. et Vlieg. 1939 forest association
in the Pisz Forest

Tab. I

Successive number of the record	1	2	3	4
The age of the tree stand	140	140	40	5
Cover of the tree layer %	90	60	70	—
" " " shrubs " "	—	40	—	40
" " " herb " "	40	80	30	50
" " " moss " "	90	100	100	40
Total number of the species	37	36	49	76
Number of the herb layer species	29	31	43	67
Trees:				
<i>Picea excelsa</i> a ₁	3.4	1.1		
a ₂		+		
b		2.3	+	
c	1.2	+	+	+
<i>Pinus silvestris</i> a ₁	1.1	3.4	4.4	
a ₂		+		
b		+		
c	+			3.1
<i>Betula verrucosa</i> a	+			
b		+		
c				+
<i>Fagus silvatica</i> a		+		
b		+		
c				+
<i>Quercus robur</i> c	+		+	+
<i>Populus tremula</i> c	+		+	+
<i>Sorbus aucuparia</i> c	+	+	+	+
Characteristic of <i>Vaccinio-Piceetea</i>				
<i>Vaccinium myrtillus</i>	3.3	4.4	+2	1.2
<i>V. vitis idaea</i>	+	2.2	1.2	1.2
<i>Melampyrum pratense</i>	2.2	+	1.1	+
<i>Calamagrostis arundinacea</i>	1.2	2.2	2.2	2.2
<i>Rubus saxatilis</i>	+	+	+	+2
<i>Scorsonera humilis</i>	+	+	+	+
<i>Veronica officinalis</i>	+		1.2	2.3
<i>Trientalis europaea</i>	+	+		+
<i>Dicranum undulatum</i>	1.2	2.3	1.2	
<i>Ptilium crista castrensis</i>	+2	2.3	1.2	
<i>Chimaphila umbellata</i>	+	+	+	
<i>Pirola secunda</i>	+		+	
<i>P. chlorantha</i>	+		+	
<i>Lycopodium annotinum</i>		+		

Tab. I (con.)

<i>Monotropa hypopitys</i> var. <i>hirsuta</i>				+2
Characteristic of <i>Quercus-Fagetea</i>				
<i>Convallaria maialis</i>	+	+	+	+
<i>Viola silvestris</i>	+	+	+	+
<i>Carex digitata</i>	+2			
<i>Corylus avellana</i> b			+	+
<i>Lilium martagon</i>				+
<i>Melica nutans</i>				+
Characteristics of <i>Qercetalia-pubescentis</i> and <i>Trifolio-Geranietea</i>				
<i>Geranium sanguineum</i>		+	+	+
<i>Trifolium alpestre</i>		+	+	
<i>Vincetoxicum officinale</i>			+2	
<i>Anthericum ramosum</i>			+	+
<i>Campanula persicifolia</i>			+	+
<i>Polygonatum odoratum</i>			+	+
<i>Astragalus glycyphyllos</i>				+2
<i>Pulmonaria angustifolia</i>				+
<i>Salix caprea</i> b	+			+
Characteristic of <i>Epilobietea angustifolii</i>				
<i>Fragaria vesca</i>	+	+	+	+
<i>Chamaenerion angustifolium</i>				+
Characteristic of <i>Sedo-Scleranthea</i>				
<i>Festuca ovina</i>	+2	+2	+2	+2
<i>Thymus serpyllum</i>			+2	3.2
<i>Ceratodon purpureus</i>				3.3
<i>Polytrichum piliferum</i>				2.2
<i>Astragalus arenarius</i>				+
<i>Helichrysum arenarium</i>				+
<i>Jasione montana</i>				+
<i>Rumex acetosella</i>				+
Characteristic of <i>Festuco-Brometea</i>				
<i>Pimpinella saxifraga</i>			+	
<i>Helianthemum ovatum</i>				+
<i>Polygala comosa</i>				+
Characteristic of <i>Nardo-Callunetea</i>				
<i>Calluna vulgaris</i>	+	+	+	+2
<i>Hieracium pilosella</i>	+	+	+2	+2
<i>Luzula multiflora</i>	+2			+2
<i>Potentilla erecta</i>		+		+
<i>Sieglingia decumbens</i>			+	+2
<i>Antenaria dioica</i>			+	

Tab. I (con.)

Characteristic of *Molinio-Arrhenatheretea*

<i>Vicia cracca</i>	+	+	+	+
<i>Succisa pratensis</i>		+	+	+ .2
<i>Galium boreale</i>	+			+
<i>Lathyrus pratensis</i>	+			+ .2
<i>Poa pratensis</i>	+			
<i>Lotus corniculatus</i>			+	+
<i>Achillea millefolium</i>			+	+
<i>Cerastium vulgatum</i>				+
<i>Juncus effusus</i>				+
<i>Lychnis flos-cuculi</i>				+
<i>Trifolium repens</i>				+
Accompanying species				
<i>Hylocomium splendens</i>	1.2	1.2		
<i>Entodon schreberi</i>	5.5	4.5	5.5	
<i>Juniperus communis b i c</i>	+	1.3	2.2	
<i>Luzula pilosa</i>	1.1	1.2	+ .2	+ .2
<i>Senecio vernalis</i>	+			1.2
<i>Peucedanum oreoselinum</i>		+	+	+
<i>Solidago virga-aurea</i>		+	+	+
<i>Anthoxanthum odoratum</i>		+	+ .2	+
<i>Gensista tinctoria</i>		+	+	+
<i>Polytrichum commune</i>		+		
<i>Hypericum perforatum</i>			+	+
<i>Potentilla reptans</i>			+	+
<i>Pulsatilla patens</i>			+	+
<i>Erigeron canadensis</i>				1.2
<i>Erigeron acer</i>				+
<i>Agrostis vulgaris</i>				+
<i>Carex ericetorum</i>				+
<i>C. pairaei</i>				+
<i>Cirsium arvense</i>				+
<i>C. lanceolatum var. silvaticum</i>				+
<i>Gnaphalium silvaticum</i>				+
<i>Leontodon autumnalis</i>				+
<i>Polygonum dumetorum</i>				+
<i>Polytrichum juniperinum</i>				+
<i>Salix pentandra b</i>				+
<i>Spergula arvensis</i>				+
<i>Trifolium montanum</i>				+

Spruce predominates in the high tree layer (a_1) in the place in which record No 1 (Tab. I) was made. This part of the forest is dark, completely devoid of a lower tree layer without a shrub layer, and almost devoid of undergrowth of young trees.

Some chemical properties of the soils

Tab. II

No. prof.	Forest community	Depth in cm	pH		Content of*		Content of			C: N
			H ₂ O	Kcl	K ₂ O	P ₂ O ₅	C in %	humus	N in %	
1	140 years old	0-5	4.0	3.3	3.6	1.0	2.85	4.91	0.162	17.6
		15-25	4.7	4.0	1.6	2.0	0.38	0.65	0.025	15.2
		40-50	6.8	6.3	1.7	2.0	0.14	0.24	0.017	8.2
		90-100	7.7	7.2	0.4	38.0	0.07	0.12	0.006	11.7
2	140 years old	7-17	4.5	3.8	2.1	3.4	1.57	2.71	0.078	20.1
		17-52	4.8	4.2	1.4	5.8	0.32	0.55	0.024	13.3
		52-87	5.2	4.5	2.1	5.4	0.086	0.15	0.006	14.3
		87-130	6.0	5.6	1.1	7.5	0.038	0.065	0.003	12.7
3	40 years old	5-15	4.5	3.7	2.1	3.0	2.07	3.57	0.071	29.1
		35-45	5.1	4.3	0.2	3.0	0.12	0.21	0.010	12.0
		90-100	5.8	5.5	0.5	4.5	0.025	0.043	0.003	8.3
		120-130	7.2	7.0	0.2	10.1	0.037	0.064	0.003	12.3
4	5 years old	3-10	4.4	3.6	1.2	5.0	2.29	3.95	0.097	23.6
		40-50	5.1	4.3	1.1	4.1	0.24	0.41	0.013	18.5
		90-100	6.5	5.7	1.6	7.0	0.15	0.26	0.007	21.4

*mg/100 g of soil (Enger's method).

Conditions for the development of tree seedlings are good in the place in which pine predominates in the tree stand (record No. 2), Spruce occurs fairly abundantly in layer a₂, and is still numerous in layer b; 3 other species of trees are encountered in this layer. A number of species from the *Quercion pubescentis* alliance is characteristic of this floristic composition.

The 40 year old stand of *Vaccinio myrtilli-Pinetum* chosen for the studies also grows on flat ground. The tree stand is entirely composed of pine, the height of the trees being about 15 m. Pine had been planted in rows along furrows between straight ridges. The floor of the wood is covered by a dense moss carpet in which one species - *Entodon schreberi* - clearly dominates. The floristic composition of the community under study is given in phytosociological record No. 3 (Tab. I).

The young pine plantation was established in the place previously occupied by an old *Vaccinio myrtilli-Pinetum* forest. Two different parts can be distinguished in the plantation. One of these is covered by 7-8 year old pines up to 2 m in height, the other by far younger trees, 5 years old at most and smaller, only about 60 cm high. The furrows and ridges at intervals of 1.5 m are still clearly shaped in this part, and consequently the spatial distribution of the vegetation still reveals a belt structure. The furrows are occupied by rows of

young pines planted out, with the addition of other species of trees which had sown themselves there. The furrows soles are covered by a moss carpet. Species which had occurred in previous association had remained on the sides of the ridges, and photophilous species typical of clearings grew on the crests (Tab. I, record 4).

The soils under all the forest communities examined are podsolized, formed of clayey sands gradually changing to coarse-grain sands or gravel in the subsoil. pH value in the soil profile increases from 4.5 to 5 near the surface to 6.3-7 in the deeper parts. The soil is covered by a thin layer of raw humus and by a more or less compact moss carpet.

III. RESEARCH METHODS

The primary production of the herb layer in three patches, differing in age, of *Vaccinio myrtilli-Pinetum* was assessed by Traczyk's method (1967) a, 1967b) of analyzing average individual increment and density. This method consist in defining the average annual increase of individuals of each species occurring in the herb layer and also their density. By multiplying these values we obtain the growth of different herb layer populations. The total sum of production of different populations is the production of the association or a given selected component part of it, in this case the herb layer. Although Traczyk's method was adhered to in principle on account of the structure of the association examined, certain small alterations and additions were made to it.

Studies by this method were made on vascular plants only, that is, the true herb layer. Only frequency, degree of cover and standing crop biomass on the sampling day were defined in relation to the moss layer.

Density of plants was defined on June 10, 15 and 17th 1967. We made a total of 100 random casts of a hoop 0.1 m² in area; we evaluated the number of individuals within the hoop, or of the aerial shoots or tufts of different vascular plants, depending on their life form.

Only those species which occurred in the study areas with frequency of at least 1% (which occurred at least once out of 100 random casts) were used for estimating the production of the herb layer. No use was made of species only found in the phytosociological record or at another time of searching the study area.

The average growth of individuals in each of the 3 study areas was defined from samples taken in quantities proportionate to the density of the species, samples being taken separately for vegetative individuals (shoots) and for fruiting individuals. Sampling was carried out in mid-June, towards the end of August and at the beginning of September, as the various species attained

their full development. The plant material taken was dried (at 85°C for 46 hours) and weighed with accuracy to 0.01 g.

Two different methods were applied for assessing production in the five-year old pine plantation, which was composed of two parts differing considerably in respect of the age of the pines and structure of the herb layer. In the younger part of the plantation the same method was adopted as in the older parts of the coniferous forest, i.e. the method based on analysis of density and growth of individuals. In the older part herb layer production was assessed by the harvest method, 20 samples being taken on the ridges, but only 10 in the furrows, in accordance with the percentage of the area in the total area of the forest floor they occupy. This method was used because it was extremely difficult to separate the various individuals of shoots from each other in the compact turf, and such separation is fundamentally essential in Traczyk's method. Only the results of samples taken at random in the five-year old pine plantation were used for comparing with the relations prevailing in two other forest associations.

Phytosociological records and soil studies were made in the 140-year old coniferous forest on July 13th, in the 40-year old forest on July 14th and in the pine plantation on July 26th 1967.

Samples for plant fall were taken through the growing season approximately once a month, beginning June 15th and ending November 16th 1967, and after the winter period on May 15th 1968, in the two older forest associations, omitting the pine plantation.

IV. RESULTS

1. Frequency

The data obtained from random samples permit of drawing conclusions as to frequency, that is, the chances of encountering species (ratio of number of samples with the given species to the number of samples taken, expressed in percentages) in the given forest association.

Combined tables (III, IV and V) containing data for calculating herb layer production and the comparative diagram (Fig. 2) make it obvious that in all three communities the great majority, about 80%, of vascular plant species of the herb layer occur with very low frequency of 1 to 20%. These species occurring sporadically of course play only a negligible part in total herb layer production.

The second significant fact is that in none of these three forest communities there was a single species which belonged to the highest class of frequency

Species	Frequency %	Average density		No.	Individual average increase	Net production <i>P</i> in g/10 m ²			
		per m ²	%			<i>v + f</i>	common	%	% cum.
1. <i>Vaccinium myrtilus</i>	73	511	28	520	0.1698	86.768			
" " <i>f</i>		60		80	0.1104	66.624	153.392	33	33
2. <i>Calamagrostis arundinacea</i>	43	688	34	200	0.2202	151.498	151.498	32	65
3. <i>Melampyrum pratense</i> <i>f</i>	39	131	7	130	0.4138	54.208	54.208	12	77
4. <i>Festuca ovina</i>	14	30	2	40	0.5412	16.236	16.769	4	81
" " <i>f</i>		13		20	0.0410	0.533			
5. <i>Potentilla erecta</i>	8	20	1	20	0.6500	13.000	14.100	3	84
" " <i>f</i>		4		20	0.2750	1.100			
6. <i>Vaccinium vitis-idea</i>	42	162	8	120	0.0792	12.830	12.830	3	87
7. <i>Convallaria maialis</i>	13	21	1	20	0.4350	9.135	9.135	2	89
8. <i>Lycopodium annotinum</i>	2	13	1	20	0.6990*	9.087*	9.087*	2	91
9. <i>Luzula pilosa</i>	26	51	4	50	0.1498	7.640	8.938	2	93
" " <i>f</i>		22		30	0.0590	1.298			
10. <i>Carex ericetorum</i>	7	40	6	40	0.1850	7.400	8.545	2	95
" " <i>f</i>		72		80	0.0159	1.145			
11. <i>Calluna vulgaris</i>	1	10	1	20	0.4625	4.625	4.625	1	96
12. <i>Veronica officinalis</i>	1	34	2	21	0.1314	4.468	4.468	1	97
13. <i>Solidago virga-aurea</i>	6	13	1	20	0.3375	4.387	4.387	1	98
14. <i>Fragaria vesca</i>	8	18	1	20	0.1375	2.475	2.475	1	99
15. <i>Picea excelsa</i> - seedling	13	18	1	10	0.1250	2.250	2.250	1	
16. <i>Poa pratensis</i>	3	12	1	20	0.1865	2.238	2.238	1	
17. <i>Galium boreale</i>	3	13	1	10	0.0900	1.170	1.170	1	

18. <i>Pirola chlorantha</i>		2	4	1	10	0,1300	0,520	1,146	1	
19. " "	f		2	1	10	0,3130	0,626			
19. <i>Melica nutans</i>	f	2	7	1	10	0,1550	1,085	1,085	1	
20. <i>Trientalis europaea</i>		3	12	1	20	0,0260	0,312	0,760	1	
" "	f		8	1	10	0,0560	0,448			
21. <i>Vicia sativa</i>		2	3	1	10	0,2010	0,603	0,603	1	
22. <i>Peucedanum oreoselinum</i>		1	1	1	10	0,4670	0,467	0,467	1	
23. <i>Sorbus aucuparia</i>		1	2	1	4	0,2125	0,425	0,425	1	
24. <i>Viola silvestris</i>		1	1	1	10	0,0900	0,090	0,375	1	
" "	f		1	1	10	0,2850	0,285			
25. <i>Betula pubescens</i>		1	2	1	10	0,1800	0,360	0,360	1	
26. <i>Anthericum ramosum</i>		1	1	1	6	0,3400	0,340	0,340	1	
27. <i>Polygonatum odoratum</i>		1	1	1	10	0,3010	0,301	0,301	1	
28. <i>Chimaphila umbellata</i>		1	1	1	10	0,1600	0,160	0,160	1	
29. <i>Scorzonera humilis</i>		1	1	1	15	0,1500	0,150	0,150	1	
30. <i>Hieracium pilosella</i>		1	1	1	15	0,0933	0,093	0,093	1	100
			2004				466,380	466,380		

f — fruiting individual plants (non-fruiting individuals without any mark).

* — biomass (not production).

Tab. IV

Species	Frequency %	Average density <i>P</i>		No.	Individual average increase	Net production <i>P</i> in g/10 m ²		%	% cum
		par 10 m ²	%			<i>v + f</i>	Common		
1. <i>Calamagrostis arundinacea</i>	25	467	39	140	0,2500	116,750	116,750	52	52
2. <i>Vaccinium myrtillus</i>	9	37	3	40	0,6380	23,606	26,336	12	64
" " <i>f</i>		2		10	1,3650	2,730			
3. <i>Festuca ovina</i>	38	89	8	200	0,1558	13,866	16,116	7	71
" " <i>f</i>		10		10	0,2250	2,250			
4. <i>Fragaria vesca</i>	17	40	4	70	0,1651	6,604	15,084	7	78
" "		8		20	1,0600	8,480			
5. <i>Solidago virga-aurea</i>	19	26	2	20	0,3475	9,035	9,035	4	82
6. <i>Peucedanum oreoselinum</i>	21	28	2	100	0,2430	6,804	6,804	3	85
7. <i>Anthericum ramosum</i>	9	13	1	10	0,4650	6,045	6,045	3	88
8. <i>Juniperus communis</i> — seedling	7	11	1	10	0,4050	4,455	4,455	2	90
9. <i>Hieracium pilosella</i>	6	38	3	20	0,1000	3,800	4,089	2	92
" " <i>f</i>		1		10	0,2890	0,289			
10. <i>Vaccinium vitis-idea</i>	74	322	27	197	0,0126	4,057	4,057	2	94
11. <i>Poa pratensis</i>	3	37	3	40	0,1000	3,700	3,700	2	96
12. <i>Pirola secunda</i>	4	22	2	10	0,1550	3,410	3,410	1	97
13. <i>Genista tinctoria</i>	1	5	1	10	0,3350	1,675	1,675	1	98
14. <i>Carex ericetorum</i>	1	3	1	10	0,4700	1,410	1,510	1	99
" " <i>f</i>		2		10	0,0500	0,100			
15. <i>Veronica officinalis</i> <i>f</i>	2	3	1	20	0,3375	1,012	1,012	1	
16. <i>Calluna vulgaris</i>	2	3	1	10	0,3230	0,969	0,969	1	

17. <i>Luzula pilosa</i>		2	3	1	10	0.1900	0.570	0.800	1	
" "	f		2		10	0.1150	0.230			
18. <i>Pirola chlorantha</i>		2	2	1	10	0.1650	0.330	0.766	1	
" "	f		1		10	0.4360	0.436			
19. <i>Luzula multiflora</i>		4	5	1	20	0.1045	0.522	0.522	1	
20. <i>Potentilla erecta</i>		2	3	1	10	0.0650	0.195	0.427	1	
" "	fj		1		20	0.2325	0.232			
21. <i>Viola silvestris</i>		1	1	1	10	0.1500	0.150	0.421	1	
" "	f		1		10	0.2710	0.271			
22. <i>Agrostis vulgaris</i>		1	6	1	10	0.0500	0.300	0.300	1	
23. <i>Polygonatum odoratum</i>		1	1	1	10	0.2700	0.270	0.270	1	
24. <i>Potentilla reptans</i>		1	2	1	10	0.1020	0.204	0.204	1	
25. <i>Achillea millefolium</i>		1	1	1	10	0.1340	0.134	0.134	1	
26. <i>Veronica chamaedrys</i>		1	1	1	10	0.0320	0.032	0.032	1	
27. <i>Anthoxanthum odoratum</i>		1	1	1	20	0.0100	0.010	0.010	1	100
			1198				224.933	224.933		

f — fruiting individual plants (non fruiting without any mark).

Frequency density and biomass production of herb layer *Vaccinio myrtilli-Pinetum* 5 years old

Tab. V

Species	Frequency %	Average density		No.	Individual average increase	Net production <i>P</i> in g/10 m ²			% %
		per m ²	%			<i>v</i> + <i>f</i>	common	%	
1. <i>Veronica officinalis</i>	54	1117	28	360	0.0425	47.472	255.931	16	16
" " <i>f</i>		649		100	0.3212	208.459			
2. <i>Carex ericetorum</i>	9	83	1	100	3.0104	249.863	250.470	16	32
" " <i>f</i>		9		10	0.0674	0.607			
3. <i>Vaccinium myrtilus</i>	37	353	6	100	0.5426	191.538	191.538	12	44
4. <i>Calamagrostis arundinacea</i>	40	1211	20	1130	0.0997	120.737	158.786	10	54
" " <i>f</i>		55		60	0.6918	38.049			
5. <i>Rubus saxatilis</i>	11	38	2	40	0.4412	16.766	94.235	6	60
" " <i>f</i>		119		10	0.6510	77.468			
6. <i>Senecia vernalis</i>	30	337	5	680	0.2371	79.903	79.903	5	65
7. <i>Erigeron canadensis</i>	14	160	3	320	0.3792	60.672	60.672	4	69
8. <i>Poa pratensis</i>	16	472	8	460	0.0868	40.970	52.254	3	72
" " <i>f</i>		26		40	0.4340	11.284			
9. <i>Molinia coerulea</i>	2	99	2	100	0.4765	47.173	47.173	3	75
10. <i>Calluna vulgaris</i>	6	22	1	30	1.8866	41.505	41.505	2	78
11. <i>Luzula pilosa</i>	14	25	1	40	1.5475	38.687	41.297	2	80
" " <i>f</i>		30		50	0.0870	2.610			
12. <i>Chamaenerion angustifolium</i>	9	30	1	30	1.3500	40.500	40.500	2	82
13. <i>Potentilla erecta</i>	12	95	2	50	0.1900	18.050	32.585	2	84
" " <i>f</i>		38		20	0.3825	14.535			
14. <i>Galium mollugo</i>	3	67	1	10	0.4020	26.934	28.448	2	86
" " <i>f</i>		4		70	0.3784	1.514			
15. <i>Luzula multiflora</i>	26	150	3	160	0.1503	22.545	23.806	1	88
" " <i>f</i>		13		50	0.0970	1.261			

16. <i>Galium boreale</i>		4	72	1	40	0.2767	19.922	22.305	1	89
" "	if		4		30	0.5957	2.383			
17. <i>Ajuga reptans</i>	f	2	46	1	40	0.3880	17.848	17.848	1	90
18. <i>Lotus corniculatus</i>	f	1	13	1	10	1.2500	16.250	16.250	1	91
19. <i>Sieglingia decumbens</i>		1	132	2	70	0.1193	15.748	15.748	1	92
20. <i>Achillea millefolium</i>		2	15	1	20	1.0200	15.300	15.300	1	93
21. <i>Convallaria maialis</i>		7	14	1	20	1.0775	15.085	15.085	1	94
22. <i>Cerastium vulgatum</i>		4	22	1	20	0.1300	2.860	8.987	1	
" "	f		19		20	0.3225	6.127			
23. <i>Vicia cracca</i>		10	17	1	10	0.2500	4.250	8.430	1	95
" "	f		4		10	1.0450	4.180			
24. <i>Anthericum ramosum</i>	f	1	3	1	10	2.7290	8.187	8.187	1	
25. <i>Fragaria vesca</i>		25	139	3	150	0.0484	6.728	8.078	1	96
" "	f		27		40	0.0500	1.350			
26. <i>Vaccinium vitis-idaea</i>		20	142	2	100	0.0564	8.009	8.009	1	
27. <i>Trientalis europaea</i>		14	57	1	80	0.1294	7.376	7.884	1	97
" "	f		8		20	0.0635	0.508			
28. <i>Viola odorata</i>		16	85	2	90	0.0442	3.757	6.464	1	
" "	f		25		30	0.1083	2.707			
29. <i>Lathyrus pratensis</i>	f	3	6	1	10	0.9860	5.916	5.916	1	
30. <i>Sergula arvensis</i>	f	3	17	1	40	0.2920	4.964	4.964	1	98
31. <i>Betula verrucosa</i> - seedling		8	22	1	30	0.2183	4.803	4.803	1	
32. <i>Rumex acetosa</i>		4	23	1	30	0.1540	3.542	4.322	1	
" "	f		8		20	0.0975	0.780			
33. <i>Hieracium pilosella</i>		4	37	1	40	0.0962	3.559	3.968	1	
" "	f		13		20	0.0315	0.409			
34. <i>Pinus silvestris</i> - seedling		1	2	1	10	0.1740	3.480	3.480	1	99
35. <i>Polygonatum odoratum</i>		1	9	1	20	0.2800	2.520	2.520	1	
36. <i>Trifolium repens</i>		2	25	1	30	0.0966	2.415	2.415	11	
37. <i>Rumex acetosa</i>		4	6	1	7	0.3286	1.972	1.972	1	
38. <i>Melampyrum pratense</i>	f	1	1	1	10	0.8650	1.730	1.730	1	
39. <i>Picea excelsa</i> - seedling		2	7	1	10	0.2400	1.680	1.680	1	

Tab. V (con.)

Species	Frequency %	Average density		No.	Individual average increase	Net production <i>P</i> in g/10 m ²			%
		per m ²	%			<i>v + f</i>	common	%	
40. <i>Anthoxanthum odoratum</i>	3	20	1	20	0.0575	1.150	1.520	1	100
" " <i>f</i>		2		10	0.1850	0.370			
41. <i>Taraxacum officinale</i>	2	2	1	10	0.7250	1.450	1.450	1	
42. <i>Scorzonera humilis</i>	1	1	1	10	1.0530	1.053	1.053	1	
43. <i>Agrostis vulgaris</i>	1	6	1	20	0.1390	0.834	0.834	1	
44. <i>Campanula persicifolia</i>	1	1	1	10	0.3860	0.386	0.386	1	
45. <i>Thymus serpyllum</i>	1	19	1	20	0.0200	0.380	0.380	1	
46. <i>Melica nutans</i>	1	2	1	10	0.0840	0.168	0.168	1	
47. <i>Plantago maior</i>	1	1	1	30	0.1600	0.160	0.160	1	
		6280				1603.528	1603.528		

f — fruiting individual plants.

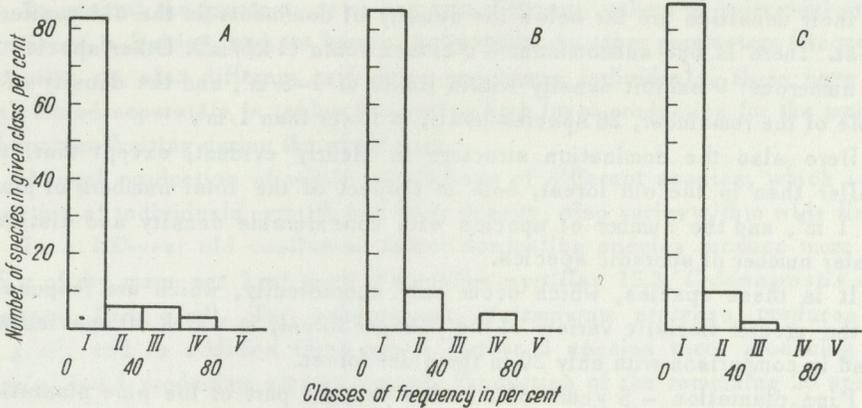


Fig. 2. Frequency diagrams of species in *Vaccinio myrtilli-Pinetum* forest communities
A — 140 years old, B — 40 years old, C — 5 years old

($F > 80\%$). In the two older forest communities the most frequently encountered species (*Vaccinium myrtillus* in one, and *V. vitis idaea* in the second) can be allocated to frequency class IV ($F = 61-80\%$), and in the pine plantation the most frequently encountered species, *Veronica officinalis*, only to frequency class III ($F = 41-60\%$).

2. Density

As the basis for assessment of herb layer production by Traczyk's method is the most accurate possible definition of density of individuals or of the upper shoots of plants on a described area, I shall discuss in turn the results obtained in this connection for each of the study areas (Tab. III, IV and V).

Vaccinio myrtilli-Pinetum — 140 years old. In the old coniferous forest density of plants on the forest floor proved to be fairly great, over 200 individuals per 1 m^2 . The two species occurring there most frequently: *Calamagrostis arundinacea* ($69/\text{m}^2$) and *Vaccinium myrtillus* ($57/\text{m}^2$) clearly dominate in numbers over the other species. In addition there are 3 subdominants there with far lower density, namely: *V. vitis idaea* ($16/\text{m}^2$), *Melampyrum pratense* $13/\text{m}^2$ and *Carex ericetorum* ($11/\text{m}^2$); *Luzula pilosa* ($7/\text{m}^2$) can also be added to this. Further species exhibit far lesser density: in 11 species this value comes between 1 and $5/\text{m}^2$, and in 13 falls below $1/\text{m}^2$. This distribution of densities points to distinct domination structure.

Vaccinio myrtilli-Pinetum — 40 years old. In the younger stand of the coniferous forest the total density of plant individuals on the forest floor is almost half the previous value, i.e. $120/\text{m}^2$. There are also two clearly dominating species: *Calamagrostis arundinacea* ($47,5/\text{m}^2$) and *Vaccinium vitis idaea* ($36/\text{m}^2$),

but their densities are far below the density of dominants in the old coniferous forest. There is one subdominant - *Festuca ovina* ($14.5/m^2$). Other species are not numerous: 9 exhibit density within limits of $1-5/m^2$, and the density of the whole of the remainder, 28 species in all, is lower than $1/m^2$.

Here also the domination structure is clearly evident, except that it is smaller than in the old forest, both in respect of the total numbers of plants per $1 m^2$, and the number of species with considerable density and distinctly greater number of sporadic species.

It is these species, which occur only sporadically, which are responsible for the greater floristic variety of the younger forest, in which 40 species were found in comparison with only 30 in the older forest.

Pine plantation - 5 years old. In the younger part of the pine plantation, where assessment was made by the same method as in the preceding areas, the combined density of species attained a value far higher than in the coniferous areas discussed above, since it was $628/m^2$. The two dominating species attained very considerable density: *Calamagrostis arundinacea* $121/m^2$, and *Veronica officinalis* - $112/m^2$. There are 3 species with density of over fifty individuals per $1 m^2$ and a further 8 with numbers over $10/m^2$. On the other hand, of the 34 species occurring in small numbers, 13 exhibit a density value lower than $1/m^2$.

3. Annual production of herb layer species

Annual biomass production of each population is composed of the annual growth of all individuals (shoots, tufts) forming the given population. The average maximum increases of herb layer species which we use for calculating the population's production are, as can be seen from the enclosed tables (Tab. III, IV and V), extremely varied.

The average yearly increase of individuals of the different species in the herb layer of a 140-year old *Vaccinio-myrtilli-Pinetum* community comes within limits of 0.0260 g (barren shoots of *Trientalis europaea*) to 1.1104 g (fruiting shoots of *Vaccinium myrtillus*).

In the 40-year old forest the range of average values of annual individual increase is even greater; these values vary from 0.0100 g (barren shoots of *Anthoxanthum odoratum*) to 1.3650 g (fruiting shoots of *Vaccinium myrtillus*).

In the 5-year old pine plantation the minimum value of average individual growth is similar to those found in older coniferous forests (0.0200 g in *Thymus serpyllum*), and maximum value is far greater (3.0104 g in *Carex ericetorum*).

In general the greatest, or at any rate different, values of individual growth are found in fruiting, and not barren, individuals. As other parameters (frequency, density) are also different in fruiting and barren individuals, these have been calculated separately in tables presenting herb layer production for the majority of species fruiting during the study year.

Annual production of whole populations of different species, which is the function of individuals' growth and their density, also varies within wide limits.

In a 140-year old coniferous forest dominating species produce more than 15 g of dry mass per 1 m² each (*Vaccinium myrtillus* 15.3, *Calamagrostis arundinacea* 15.1 g/m²). The subdominant, *Melampyrum pratense*, produces over 5 g/m², and in addition there are a further 3 species there producing over 1 g/m² and 4 producing almost 1 g/m². Production of the remaining 20 species did not attain a value of 1 g/m². The lowest production value (0.0093 g/m²) was found for *Hieracium pilosella*.

In the 40-year old coniferous forest the production of the dominating species, *Calamagrostis arundinacea*, was 11.7 g/m². The three subdominants produce little more than 1 g/m² (*Vaccinium myrtillus* - 2.6 g, *Festuca ovina* 1.6 g and *Fragaria vesca* 1.5 g/m²). The remaining 36 species are responsible for production below 1 g/m², the lowest value for annual production of species being only 0.001 g/m² (in *Anthoxanthum odoratum*).

In the 5-year old pine plantation values of annual production for dominating species are higher than in the older forests: *Veronica officinalis* produces 25.6 g/m², *Carex ericetorum* - 25 g/m², *Vaccinium myrtillus* - 19.2 and *Calamagrostis arundinacea* - 15.9 g/m². In addition there are a further 4 species producing from 5 to 10 g, 13 species producing 1-5 g/m², and 26 remaining species producing less than 1 g/m². Lowest production value is found in *Plantago maior* (0.016 g/m²).

4. Fruiting of herb layer species

Fruiting of a species in a given plant community is one of the manifestations of its vitality. A simple percentage index, expressing the ratio of number of fruiting plants to the total number of individuals in a given population, was used for comparing the vitality of species in the three study areas of coniferous forest vegetation.

It can be seen from the comparative list of fruiting indices for species in 3 communities (Tab. VI) that these indices are different for different species in a given community.

Participation of fruiting individuals in the total number of individuals of herb layer species in fresh coniferous forests

Tab. VI

Age of forest community Plant species	140 years old		40 years old		5 years old	
	total No of indiv.	% fruct. indiv.	total No of indiv.	% fruct. indiv.	total No of indiv.	% fruct. indiv.
<i>Melica nutans</i>	7	100				
<i>Viola silvestris</i>	2	50	2	50		
<i>Pirola chlorantha</i>	6	33	3	33		
<i>Festuca ovina</i>	43	30	99	10		
<i>Vaccinium myrtillus</i>	571	10	39	5		
<i>Melampyrum pratense</i>	131	100			2	100
<i>Trientalis europaea</i>	20	40			65	12
<i>Carex ericetorum</i>	112	64	5	40	92	10
<i>Luzula pilosa</i>	73	30	5	40	55	54
<i>Potentilla erecta</i>	24	17	4	25	133	28
<i>Veronica officinalis</i>			3	100	1766	4
<i>Fragaria vesca</i>			48	17	166	16
<i>Hieracium pilosella</i>			39	3	50	26
<i>Senecio vernalis</i>					337	100
<i>Erigeron canadensis</i>					160	100
<i>Molinia coerulea</i>					99	100
<i>Ajuga reptans</i>					46	100
<i>Chamaenerion angustifolium</i>					30	100
<i>Calluna vulgaris</i>					22	100
<i>Spergula arvensis</i>					17	100
<i>Lotus corniculatus</i>					13	100
<i>Lathyrus pratensis</i>					6	100
<i>Anthericum ramosum</i>					3	100
<i>Rubus saxatilis</i>					157	76
<i>Cerastium vulgatum</i>					41	46
<i>Rumex acetosa</i>					31	26
<i>Viola odorata</i>					110	23
<i>Vicia cracca</i>					21	19
<i>Anthoxanthum odoratum</i>					22	9
<i>Luzula multiflora</i>					163	8
<i>Galium mollugo</i>					71	6
<i>Poa pratensis</i>					498	5
<i>Galium boreale</i>					76	5
<i>Calamagrostis arundinacea</i>					1266	4

In the young pine plantation in which the tree crown layer has not yet formed, as many as 11 species, i.e. 23.4%, attain a fruiting index of 100%, and a total number of 29 species, i.e. over 60% produce fruits.

In the 40-year-old forest a 100% fruiting index was found in one species only, while in 10 species, i.e. 37% of the whole, a lower index of fruiting was observed.

In the 140-year-old forest a fruiting index = 100% is attained by two species. 10 other species fruit there, and they attain slightly higher fruiting indices than in the younger forest. They form 33% of the whole.

In effect the percentage of fruiting individuals in the total number of individuals of all herb layer species is different in these three communities. In the young pine plantation it is expressed by the high index of 28.5%, in the 40-year old *Vaccinio myrtilli-Pinetum* community it is more than ten times smaller – 2.6%, and in the 140-year old forest again reaches a fairly high value – 16%.

Only 3 species fruit in all 3 forest stands (*Carex ericetorum*, *Luzula pilosa*, *Potentilla erecta*). The last two markedly prefer the young pine plantation, and the first the old pine forest.

The biomass percentage of fruits and seeds in aggregated production for 1967 is small. In the oldest forest stand it is expressed by a mere fraction of a percentage, in the forest of medium age little more, than 1%, and in the young pine plantation about 5% (Tab. VII).

Ratio of fruit production to total production in herb layer of *Vaccinio-myrtilli-Pinetum*

Tab. VII

Age of forest community	Total primary production on 1 m ²	Fruit production on 1 m ²	Fruit production to total in %
140 years old	46.6	0,094	0.20
40 " "	22.5	0,288	1.26
5 " "	160.4	8,439	5.26

5. Annual production of species and their density and frequency

There is no complete agreement between the annual production of species and its numerousness and frequency in the given plant community (Tab. III-V).

Although species producing maximum biomass in all three communities are simultaneously most numerous ones, this applies only to the first producer, or at most to the first two, which belong to the most numerous species (*Vaccinium myrtillus* and *Calamagrostis arundinacea* in the 140-year old forest, *C. arun-*

dinacea in the 40-year old pine forest and *Veronica officinalis* in the young pine plantation). In the case of species lower down in order of the value of their production, numerousness of frequency, the differences are sometimes even very great.

For instance *Vaccinium vitis idaea* in the 140-year old forest is the third in order of numerousness, but in respect of production it only comes sixth. In the 40-year old forest this species is the second in order of numerousness, but is only tenth in order of production value. In the young pine plantation the most numerous species, *Calamagrostis arundinacea*, occupies only the fourth place in order of production. The second species in order of production in the young pine plantation – *Carex ericetorum*, comes only fifteenth in order of numerousness. *Vaccinium vitis idaea* in the young pine plantation is ninth in order of numerousness, but only twentysixth in order of production. *Vaccinium myrtillus* is the second greatest producer in the herb layer of the 40-year old forest, but in respect of density occupies a fifth place together with *Hieracium pilosella*, which as a producer comes only ninth.

Production value diverges even more widely from frequency value. For instance *Convallaria maialis* and pine seedlings in the 140-year old pine forest occupy fifth place in respect of frequency, and in respect of production the first of these species occupies seventh place, and the second only comes fifteenth on account of its very different individual weight. *Potentilla erecta* and *Fragaria vesca* occupy sixth place in order of frequency in this association, and in respect of production the first of them comes fifth and the second only fourteenth.

In the 40-year old forest the most commonly encountered species, *Vaccinium vitis idaea*, comes only tenth in order of production, while two species occupying sixth place in order of frequency occupy the following places in order of production – *Vaccinium myrtillus* second, and *Anthoxanthum odoratum* seventh.

In the young pine plantation, although the production dominant – *Veronica officinalis* – is the most frequently encountered species, the second in order of production value, *Carex ericetorum*, comes only seventeenth in order of frequency, like *Chamaenerion angustifolium*, which occupies only the twelfth place in order of production. *Vaccinium vitis idaea* in respect of frequency comes sixth, but only twentysixth as producer of organic matter.

6. Annual production of the herb layer

Annual production of the herb layer in the three study forest communities differs considerably, amounting to twice as much in the 140-year old forest as in the 40-year old forest, and 7 times as much in the 5-year young pine plantation. The figures are as follows:

in the 140-year old forest	46.6 g/m ²	with density of individuals of	200/m ²
" " 40-year " "	22.5 "	" "	120/m ²
" " 5-year old pine plantation	160.4 "	" "	628/m ²

The production in these communities is approximately 2 : 1 : 7, and density 1.7 : 1 : 5.

The value of herb layer production of the young pine plantation depends not only on the considerably greater density of species than in the other two communities, but in the case of some species also on a far higher individual growth than in the older forest stands.

Total annual production of the herb layer was also assessed in the older part of the young pine plantation. Since the harvesting method was used in this association on account of the structure of the herb layer, the results obtained are not fully comparable with those obtained in the three communities discussed. They do, however, supplement them, and are by no means at variance with the general picture of relations obtained by the method of analysing density and average individual increase. This production, assessed in July 1967 at the assumed peak moment, was 101.1 g/m². The result obtained in June was lower and was 96.0 g/m². Herb layer production in the 8-year old pine plantation is thus lower than production in this layer in the 5-year old plantation, but higher than in the 40 year old forest, and even than in the 140-year old forest. It can thus be seen that herb layer production decreases with the age of the treestand and its progressive intensification of density up to a certain time. In far older tree stands it again increases.

7. Weight structure of herb layer production

Annual production of the herb layer in the three forest communities examined was distributed in 1967 over a large number of species:

in the 140-year old forest	— 30 species
40-year	— 27 "
5-year old pine plantation	— 47 "

As can be seen from tables of annual increases (Tab. III-V) in all three associations the main mass of organic matter is produced by a small number of dominating species (1-4).

In the 140-year old forest the two outstanding dominants produce 65% of the whole herb layer production; 10 species produce 95% of total production, 14 species — 99%, while the remaining 16 species contribute only 1% of this production.

In the 40-year old forest 1 dominating species supplies 52% of the herb layer production, 2 species, the most productive, yield, as in the previous community 64%, 10 species – 95%, 13 species – 99%, and 14 species contribute to the remaining 1%.

It can be seen that in both these forests the domination structure is very clearly marked in herb layer production and is fairly similar.

The situation is slightly different in the young pine plantation, since production is distributed over a larger number of species and there are more dominants. Four dominating species together form 58% of herb layer biomass and 64% of this biomass is formed by 5 species, 93% of the whole production is formed by 18 species, that is, almost half; the remainder, that is 7% of production is distributed over the remaining 19.

The domination structure in this community, although distinguishable, is not so clearly marked as in the two preceding community.

8. Standing crop biomass of herb layer and percentage formed in it by biomass of previous years

The biomass of vascular plants forming the herb layer consists of two elements: increase from the current year and old biomass retained from previous years. Its amount thus depends not only on the amount of annual increase but also on the percentage formed in the herb layer by plants, the upper parts of which do not die completely in winter.

In the *Vaccinio myrtilli-Pinetum* forest stands which we examined there is a high percentage of *Vaccinium myrtillus*, *V. vitis idaea* and *Calluna vulgaris*.

The enclosed table (Tab. VIII) shows differences both in the total biomass and in its two component elements. There is considerable similarity between the 140-year old and 40-year old forest association and complete difference in the 5-year old pine plantation, which differs from the forest areas by its greater herb layer biomass (3–6 times greater), which is understandable, since the young pines had not yet reached the tree crown layer, had not altered the microclimate and the plant community was still of a semigrass character. The percentage of the shrub-like plants typical of coniferous forests is small in the grassy vegetation, and the young pine plantation therefore differs from the old forests in respect of the low percentage of biomass retained from year to year in the herb layer (12% as compared with 31 and 29% in the old forests), with a ratio of biomass from previous years to the biomass formed in the current year of respectively 14, 40 and 45, thus increasing with the age of the tree stand.

Ratio of previous years biomass to current biomass production and to total standing crop biomass in herb layer of fresh pine forest

Tab. VIII

Forest community	140 years old	40 years old	5 years old
Total standing crop biomass in g/m^2	674	316	1803
Current biomass production in g/m^2	466	225	1604
Previous years biomass in g/m^2	208	91	230
Ratio of old to current biomass in %	46	40,5	14
Ratio of old biomass to total standing crop in %	31	29	12

9. Moss layer – biomass and production

The ground layer of mosses in the two older forest communities plays an important role. Mosses reach a high value of frequency and surface cover. They produce and permanently maintain considerable biomass. It can be seen from the enclosed table (Tab. IX), in which only data from the 140-year old and 40-year old forest have been taken into consideration, that the moss layer is far richer in the younger forest. It attains biomass of $257 g/m^2$, that is, over 3 times greater than biomass in the older forest ($71,8 g/m^2$).

The moss layer in the fresh pine forest

Tab. IX

Forest community	140 years old	40 years old
Frequency of mosses %	86	100
Cover of mosses %	68	90
Standing crop biomass g/m^2	72	257
Estimative year production g/m^2	24	86

Annual production was not estimated for mosses, as it was impossible to make an analysis of annual increases in them. If, however, it is assumed that the annual increase of mosses is about 1/3 of their biomass (T. Traczyk – 1967b), then their production would be $85,53 g/m^2$ in the 40-year old forest and $23,93 g/m^2$ in the 140-year old forest.

The biomass and production of the herb layer and of mosses to some extent complement each other. In the 140-year old forest, where biomass and annual production of herb layer vascular plants is greater, there are fewer mosses. Conversely, in the 40 year old forest, where conditions are poorer for vascular plants, there are far more mosses (Tab. X).

The total primary production on forest floor of fresh pine forest

Tab. X

Forest community	140 years old		40 years old	
	biomass	current production	biomass	current production
Herb layer	674	474	316	225
Moss layer	72	24	257	86
Total	746	498	573	311
Ratio of mosses in total biomass and production (%)	10	5	45	28

In the 40-year old forest the biomass of the herb layer formed only 47% of the biomass of mosses, whereas the reverse is the case in the 140-year old forest, where the biomass of mosses formed 19% of the herb layer biomass.

10. Plant fall

Plant fall from trees and shrubs was assessed only in the two older forest associations, omitting the pine plantation.

The amount of plant fall per 1 m² of the study area (Tab. XI and Fig. 3) exhibits distinct seasonal variation. The general mass of fall, and also the mass of needles and leaves, increases as from September, but is particularly marked in October and November.

The greatest percentage of the plant fall of a coniferous forest consists of pine and spruce needles, forming almost 40% of the whole fall in the 140-year old forest and almost 50% in the 40-year old forest. On this account the course taken by annual needle fall has an important effect on the course of the whole fall.

Leaves form the smallest percentage in the joint mass of fall, since the admixture of deciduous trees and shrubs is negligible. This fraction is only

Plant fall from trees and shrubs in *Vaccinio myrtilli-Pinetum* forest association since June 1967 till April 1968
 where: A = 40 years old, B = 140 years old forest community

Tab. XI

Kind of fall	16. VI				19. VII				7. IX				11. X				16. XI				20. IV				Total			
	A		B		A		B		A		B		A		B		A		B		A		B		A		B	
	g/m ²	%																										
Deciduous trees leaves	0.06	1	1.18	2	0.25	1	0.60	1	0.37	1	1.25	2	2.43	2	0.88	1	0.27	1	5.01	4	0.15	1	0.10	1	3.53	1	9.02	2
Coniferous trees leaves	15.60	21	13.32	27	14.81	31	15.81	28	16.50	31	11.18	17	79.14	75	42.14	50	102.23	65	60.06	53	35.58	37	42.98	46	263.86	49	185.49	40
Fruits	9.07	12	19.27	39	4.99	10	23.86	42	13.27	25	26.41	39	1.93	2	20.27	24	1.05	1	19.24	17	1.65	2	6.59	7	31.96	6	115.64	25
Plant debris	50.62	67	15.74	32	27.72	58	16.70	29	23.28	43	28.03	42	21.89	21	21.39	25	53.61	34	29.01	26	59.40	61	43.51	47	236.52	44	154.38	33
Total fall	75.35	100	49.51	100	47.77	100	56.97	100	53.42	100	66.87	100	105.39	100	84.68	100	157.16	100	113.32	100	96.78	100	93.18	100	535.87	100	464.53	100

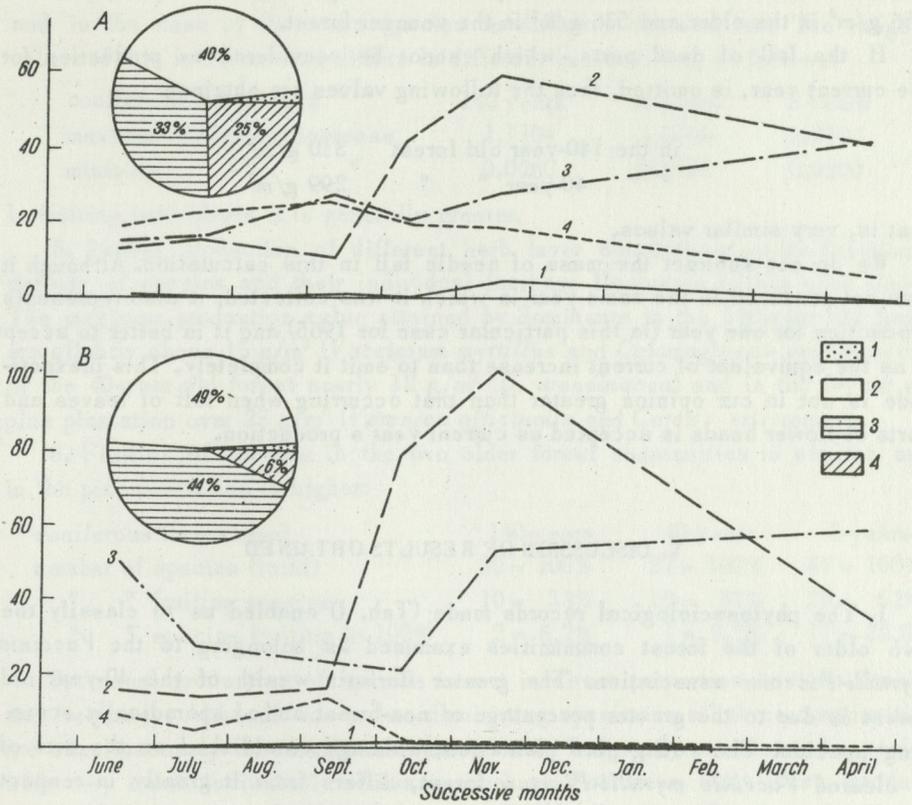


Fig. 3. Tree and shrub fall in *Vaccinio myrtilli-Pinetum* forest communities
 A - 140 years old, B - 40 years old, 1 - deciduous trees leaves, 2 - coniferous trees leaves,
 3 - plant debris, 4 - fruits

2.14% in the 140-year old forest, and only 0.7% of the whole mass of fall in the 40-year old forest. Its seasonal variation therefore in no way affects variation of the whole fall.

Flowers, fruits, seeds and parts of inflorescences in the older forest occurred in large amounts in the fall in summer and early autumn, exerting considerable influence on the amount of fall in this period. During the whole year this fraction was 25% in the 140-year old forest, and only 6% in the 40-year old forest.

The participation of branches, bark and other dead parts is considerable throughout the whole season, and they form the second fraction in order of size after needles, being almost 40% in the older forest and 44% in the 40-year old forest.

The whole of the fall for the period from April 1967 to April 1968 was 466 g/m² in the older and 536 g/m² in the younger forest.

If the fall of dead parts, which cannot be considered as production for the current year, is omitted, then the following values are obtained:

in the 140-year old forest	310 g/m ²
" " 40-year " "	299 g/m ²

that is, very similar values.

We do not subtract the mass of needle fall in this calculation. Although it was not produced in the same year in which it was collected, it also represents production for one year (in this particular case for 1965) and it is better to accept it as the equivalent of current increase than to omit it completely. This inexactitude is not in our opinion greater than that occurring when fall of leaves and parts of flower heads is accepted as current year's production.

V. DISCUSSION OF RESULTS OBTAINED

1. The phytosociological records made (Tab. I) enabled us to classify the two older of the forest communities examined as belonging to the *Vaccinio myrtilli-Pinetum* association. The greater floristic wealth of the 40-year old forest is due to the greater percentage of non-forest and of sporadically occurring species. The young pine plantation, although established on the site of a cleared *Vaccinio myrtilli-Pinetum* forest, differs from it greatly in respect of its floristic composition, in which species typical of open spaces dominate, and of its floristic wealth.

2. The frequency of species in all three forest communities is low. The majority of the species ($\pm 80\%$) occur with frequency of 1–20%. This points to the uneven distribution of species on the forest floor. The most frequently encountered species attain a frequency of only 73 and 74% in the older communities and only 54% in the pine plantation.

3. The density of herb layer species in the 140- and 40-year old forests point to a distinct domination structure, it being half as great in the latter as in the former. Density is several times greater in the pine plantation, and the domination structure slightly less distinctly marked than in the older communities. The form it takes is as follows:

coniferous forest aged	140 years	40 years	5 years
density, combined	2004/m ²	1198/m ²	6277/m ²
number of species	30	27	47
density of 2 dominating species	62%	66%	48%

4. The average individual increase estimated at the time of maximum development of the species differs in different species in the same community and in the case of the same species in different communities. The range of values of this increase also differs in different communities, as follows:

coniferous forest aged	140 years	40 years	5 years
maximum individual increase	1,1104	1,3650	3,0104
minimum " "	0,0260	0,0100	0,0200

In fruiting individuals it is generally greater.

5. Annual production of different herb layer populations as the function of density of species and their individual increase fluctuates within wide limits. The maximum production value attained by dominants in the 140-year old forest are slightly above 15 g/m² (*Vaccinium myrtillus* and *Calamagrostis arundinacea*), in the 40-year old forest nearly 12 g/m² (*C. arundinacea*) and in the 5-year old pine plantation over 25 g/m² (*Veronica officinalis* and *Carex ericetorum*).

6. Fruiting of species in the two older forest communities is similar, and in the pine plantation is higher:

coniferous forest aged	140-years	40-years	5-years
number of species (total)	30 = 100%	27 = 100%	47 = 100%
" " fruiting species	10 = 33%	10 = 37%	29 = 62%
" " species fruiting in 100%	2 = 6.7%	1 = 3.7%	11 = 23.5%

7. Annual production of species is not in direct proportion to their density and frequency. Although one or two dominating species in all three communities are simultaneously the most numerous and most frequently encountered, species with very small individual increases, such as *Vaccinium vitis idaea*, produce only small biomass despite their considerable density. On the other hand, species distinguished by considerable individual increase come high in the range of population production, although their numbers are small, e.g. *Fragaria vesca*, *V. myrtillus*, *Potentilla erecta*, *Convallaria maialis*.

8. The weight structure of herb layer production is clearly determined by dominants in all three study communities.

In the two older communities two species give over 60% of the whole herb layer production, and only 50% of the total number of species occurring there make up 99% of production. In the pine plantation dominating species produce only 33% of total biomass, as many as 6 species are responsible for 65% of production and 27 species 99% of production.

9. Annual production of the herb layer is greatest in the young pine plantation, which is not yet a true forest. It decreases greatly in the dense 40-year old forest and increase again in the oldest community (140 years old). Its value is in turn: 628, 120 and 200 g/m² of the areas.

10. The standing crop biomass of the herb layer is several hundred g/m² in the old forest and nearly 2 kg/m² in the young pine plantation. The percentage in it of biomass from previous years is high in the older forests, approximately 30%, but only 14% in the pine plantation. Thus the ratio of old biomass to that produced by the herb layer during the current year increases with the age of the tree stand, being 12% in the young pine plantation, 40% in the 40-year old forest and 46% in the 140-year old forest.

11. The moss layer was evaluated in the two older communities only, since it plays an important part in them, mosses occurring with considerable frequency and area of surface cover, and forming a large amount of biomass (Tab. X). The latter is 72 g/m² in the 140-year old forest and 257 g/m² in the 40-year old forest. Greater biomass of mosses was therefore found in the 40-year old forest, where biomass and vascular plant production of the herb layer is smaller.

12. Plant fall from trees and shrubs was investigated only in the two older communities. The greatest percentage in annual fall was formed by needles (40% in the 140-year old and 50% in the 40-year old forest), maximum fall of needles occurring in autumn. Their seasonal variation gives a seasonal rhythm to the whole of plant fall. The percentage formed in fall by leaves is negligible. Fall of flowers and fructifications is very marked in the summer months being far greater in the 140-year old forest (25% of annual fall) than in the 40-year old forest (6%). The percentage of branches and bark is considerable throughout the whole year, forming about 40% of total annual fall in both associations. The total fall in the 140-year old forest is 465 g/m² and 536 g/m² in the 40-year old forest.

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PRODUKCJA PIERWOTNA WARSTWY ZIÓŁ I OPAD ROŚLINNY W BORZE ŚWIEŻYM (*VACCINIO MYRTILLI-PINETUM*) W PUSZCZY PISKIEJ NA POJEZIERZU MAZURSKIM

Streszczenie

W borze świeżym (*Vaccinio myrtilli-Pinetum*) porastającym gliniaste piaski w północnej części Puszczy Piskiej (Nadleśnictwo Krutyń) zbadano produkcję pierwotną warstwy ziół, stan biomasy w warstwie mchów i opad roślinny z drzew i krzewów.

Przedstawiona praca obejmuje część wyników rozległych kompleksowych badań przeprowadzonych przez Zakład Ekologii PAN w ramach Międzynarodowego Programu Biologicznego w kilkunastu zbiorowiskach leśnych. Oprócz oceny produkcji pierwotnej runa i opadu leśnego obejmują one ocenę produkcji wtórnej populacji gryzoni.

Badania przeprowadzono w dwu różnowiekowych zbiorowiskach boru świeżego (140- i 40-letniego) oraz w sąsiednim 5-letnim młodniku sosnowym, w sezonie wegetacyjnym 1967 r. z przeciągnięciem pobierania prób na opad na wiosnę 1968 r.

Produkcję pierwotną runa oceniono metodą analizy zagęszczenia gatunków i średniego przyrostu osobniczego zaproponowaną przez Traczyka (1967a, 1967b).

Uzyskano następujące wyniki:

1. Na podstawie wykonanych zdjęć fitosocjologicznych (Tab. I) zaliczono dwa starsze ze zbadanych zbiorowisk leśnych do zespołu *Vaccinio myrtilli-Pinetum*. O większym bogactwie florystycznym 40-letniego boru decyduje wyższy udział w nim gatunków nie leśnych i gatunków występujących sporadycznie. Młodnik sosnowy choć założony na miejscu wyciętego boru świeżego odbija silnie składem florystycznym, w którym dominują gatunki miejsc otwartych, oraz bogactwem florystycznym.

2. Frekwencja gatunków we wszystkich trzech zbiorowiskach borowych jest niska. Większość gatunków ($\pm 80\%$) występuje z częstotliwością zaledwie 1–20%. Gatunki spotykane najczęściej osiągają zaledwie frekwencję 73 i 74% w starszych zbiorowiskach, a w młodniku tylko 54%. Dowodzi to nierównomiernego rozmieszczenia gatunków na dnie lasu.

3. Zagęszczenie gatunków runa w 140-letnim i 40-letnim borze wskazuje na wyraźną strukturę dominacyjną z tym, że w borze 40-letnim jest ono o połowę mniejsze niż w 140-letnim. W młodniku sosnowym zagęszczenie jest kilkakrotnie większe, a struktura dominacyjna nieco słabiej zaznaczona niż w starszych zbiorowiskach. Kształtuje się ono w sposób następujący:

w zbiorowisku borowym	140-letnim	40-letnim	5-letnim
zagęszczenie łączne	2004/m ²	1198/m ²	6277/m ²
liczba gatunków	30	27	47
zagęszczenie 2 gatunków dominujących	62%	66%	48%

4. Średni przyrost osobniczy oceniany w momencie maksymalnego rozwoju gatunku jest różny u różnych gatunków w tym samym zbiorowisku i u tych samych gatunków w różnych zbiorowiskach. Różna jest też rozpiętość wartości tego przyrostu w poszczególnych zbiorowiskach, a mianowicie:

w zbiorowisku borowym:	140-letnim	40-letnim	5-letnim
maksymalny przyrost osobniczy	1,1104	1,3650	3,0104
minimalny przyrost osobniczy	0,0260	0,0100	0,0200

U osobników owocujących jest na ogół większy.

5. Produkcja roczna poszczególnych populacji warstwy ziół jako funkcja zagęszczenia gatunków i ich przyrostów osobniczych waha się w dużych granicach. Maksymalne wartości produkcji osiągnięte przez dominanty w 140-letnim borze wynoszą nieco powyżej

15 g/m² (*Vaccinium myrtillus* i *Calamagrostis arundinacea*), w borze 40-letnim blisko 12 g/m² (*C. arundinacea*), a w 5-letnim młodniku sosnowym ponad 25 g/m² (*Veronica officinalis* i *Carex ericetorum*).

6. Owocowanie gatunków w dwu starszych zbiorowiskach leśnych przedstawia się podobnie, w młodniku sosnowym natomiast znacznie korzystniej, a mianowicie:

w zbiorowisku borowym	140-letnim	40-letnim	5-letnim
gatunków wszystkich	30 = 100%	27 = 100%	47 = 100%
" owocujących	10 = 33%	10 = 37%	29 = 62%
" " w 100%	2 = 6,7%	1 = 3,7%	11 = 23.5%

7. Produkcja roczna gatunków nie jest ściśle proporcjonalna do ich zagęszczenia i frekwencji. Co prawda we wszystkich trzech zbiorowiskach jeden lub dwa gatunki dominujące są zarazem najliczniejszymi i najczęściej spotykanymi. Gatunki jednak o bardzo małym przyroście osobniczym, jak np. *Vaccinium vitis-idaea*, produkują małą biomasa pomimo dużego zagęszczenia. Natomiast gatunki odznaczające się dużym przyrostem osobniczym uzyskują w zakresie produkcji populacyjnej miejsca wysokie przy małej liczebności, np. *Fragaria vesca*, *V. myrtillus*, *Potentilla erecta*, *Convallaria maialis*.

8. Struktura wagowa produkcji runa jest wyraźnie dominacyjna we wszystkich trzech badanych zbiorowiskach.

W dwu starszych zbiorowiskach dwa gatunki dają ponad 60% całej produkcji warstwy ziół, a na 99% produkcji składa się tylko 50% łącznej liczby gatunków tam występujących. W młodniku sosnowym dominujące gatunki produkują tylko 33% całej biomasy, na wytworzenie 65% produkcji składa się aż sześć gatunków, a na 99% aż 27 gatunków.

9. Produkcja roczna warstwy ziół jest najwyższa w młodniku sosnowym, który jeszcze nie jest prawdziwym lasem. Zmniejsza się bardzo w gęstym 40-letnim borze i znowu wzrasta w najstarszym 40-letnim. Wartości jej wynoszą kolejno: 628, 120 i 200 g/m² powierzchni.

10. Stan biomasy w warstwie ziół wynosi po kilkaset g/m² w starych borach, a blisko 2 kg/m² w młodniku sosnowym. Udział w niej biomasy z lat ubiegłych w starych borach jest duży, wynosi około 30%, gdy tymczasem w młodniku sosnowym tylko 14%. Stosunek zatem biomasy starej do wyprodukowanej przez runo w bieżącym roku rośnie z wiekiem drzewostanu, wynosząc 12% w młodniku, 40% w 40-letnim i 46% w 140-letnim borze.

11. Warstwa mchów podległa ocenie tylko w dwu starszych zbiorowiskach. Odgrywa ona w nich dużą rolę, mchy występują z dużą frekwencją i pokryciem oraz stanowią dużą biomasa (Tab. X). Ta ostatnia wynosi w 140-letnim borze 72 g/m², a w 40-letnim — 257 g/m². Większą biomasa mchów stwierdzono zatem w borze 40-letnim, gdzie biomasa i produkcja roślin naczyniowych runa jest mniejsza.

12. Opad roślinny z drzew i krzewów zbadano tylko w dwu starszych zbiorowiskach. Najwyższy udział w opadzie rocznym mają szpilki (40% w 140-letnim borze i 50% w 40-letnim), których maksimum przypada w jesieni. Ich zmienność sezonowa nadaje rytm sezonowy całości opadu. Udział liści w opadzie jest znikomy. Opad kwiatów i owocostanów zaznacza się wyraźnie w miesiącach letnich z tym, że

w 140-letnim borze jest on znacznie wyższy (25% opadu rocznego) niż w 40-letnim (6%). Udział gałęzi i kory jest znaczny przez cały rok, stanowiąc w obu zbiorowiskach około 40% całorocznego opadu. Łączna suma opadu w 140-letnim borze wynosi 465 g/m², a w 40-letnim -- 536 g/m².

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