

Tadeusz TRACZYK

STUDIES ON HERB LAYER PRODUCTION ESTIMATE
AND THE SIZE OF PLANT FALL*

The present paper presents results of studies on the evaluation of herb layer production and the size of plant fall in four forest associations in the Kampinos National Park. In the estimate of herb layer production there was used a new method based on an analysis of density and the determination of so-called index of average individual increment for different species. In order to estimate the size of plant fall from trees and shrubs the technique of catchers has been used. There are data cited concerning certain quantitative characters of herb layer as: density, size of standing crop, fructification index, ratio of actual increment to plant material from previous years. There has been carried out also the comparison of production estimate obtained with the use of two methods. It has been indicated that the way of selection of sampling places affects seriously the estimate.

Contents

1. Plant associations
2. Method
 - 2.1. General assumptions
 - 2.2. Analysis of the increment of above-ground parts of vascular plants
 - 2.3. Analysis of density
 - 2.4. Analysis of moss layer
 - 2.5. Analysis of plant fall
3. Results
 - 3.1. General
 - 3.2. Frequency
 - 3.3. Density
 - 3.4. Weight structure of population
 - 3.5. Comparison of abundance and standing crop of populations in several associations

*From the Institute of Ecology, Polish Academy of Sciences, Warszawa.

This study was carried out under the Small Mammal Project of the International Biological Programme in Poland.

- 3.6. Fructification index
 - 3.7. Current to old material ratio
 - 3.8. Estimate of the production of above-ground parts of herb layer
 - 3.9. Estimate of moss production
 - 3.10. Estimate of the size of plant fall
 - 3.11. The size of production (compilation)
4. Summary

The beginning of the definite phase of studies on productivity within the International Biological Programme has been preceded by few years long period of preparations. Preliminary works, which have been carried out in selected forest and meadow communities, made it possible to come across some specific problems, what to a serious extent enabled the evaluation of their significance and possibilities of solution with techniques in use.

The first work, carried out by the Laboratory of Plant Ecology, Institute of Ecology, Polish Academy of Sciences, on the estimate of herb layer production (Traczyk and Traczyk 1967) presented a rough attempt and introduction to further works. Although results obtained could not be considered satisfactory, even due to the use of simplified methods, still they suggested many afterthoughts, mainly procedural ones, which forced to search other solutions.

The present paper is just another attempt of the evaluation of herb layer production with the use of another method. It is restricted to the estimate of net primary production of above-ground parts of herb layer and of plant fall in several forest communities. The problem of the estimate of the production of root systems of herbaceous plants, the production of tree-stand and shrub layer have been omitted.

1. PLANT ASSOCIATIONS

The forest studied is situated in the Kampinos National Park near the Field Station of the Institute of Ecology, Polish Academy of Sciences, at Dziekanów Leśny, some 20 km to the north-west of Warsaw. Six hectares of area of this forest has been from long ago used by the Laboratory of Natural Populations for studies on small mammals. The area studied includes mainly four forest associations: *Tilio-Carpinetum*, *Pino-Quercetum*, *Vaccinio myrtilli-Pinetum*, and *Carici elongatae-Alnetum*. The phytosociological characteristics of these associations is given by Traczyk and Traczyk (1965). Here I would like to mention that stands in these associations are rather young and did not passed the age of 30 to 55 years. Numerous stands reveal considerable deformations in structure and decimation in species composition what resulted from wrong silvicultural treatments. Hence, results of production estimates made in these associations not always might be considered as representative ones for definite communities.

In the same area and in the same associations there was undertaken in 1964 an attempt of the estimate of herb layer production with the use of another method (Traczyk and Traczyk 1967).

2. METHOD

2.1. General assumptions

The procedure of field works and the estimate of primary production accepted in the present paper presents a considerably modified procedural proposal which remarkably deviates from broadly used methods in this sphere (Lieth 1962, Ovington 1962, Sočava, Lipatova and Groškova 1962, Wiegert and Evans 1964, Medwecka-Kornaś 1965, Rajchel 1965 and others). Its use, as a rather simple and at the same time accurate method, was suggested for works of the working group studying the production of small mammals. In this connection I shall devote some more place to the discussion of this procedure.

In majority of cases the herb layer of forest associations due to its spatial structure (moderate density of individuals) is suitable for the analysis of individual plant populations. The fundamental principle of the method suggested here is the estimate of maximal current increment separately for each population creating the vegetation of definite association. The sum of maximal, instantaneous increment of all populations reflects at best the primary net production (Petrusewicz 1966). The highest current increment of population one can determine through the direct separation of the current standing crop from that of previous years during the period of its greatest development. It seems that this assumption is undoubtedly right, because, if the net production is based on increments, then the estimate should be based on direct measurements of green crop increments, and not on indirect methods as, for example, on the difference between the maximal and minimal state of total crop both old and the current one, or on the total of maximal standing crop of populations, or, finally, on the rate of the disappearance and standing crop of dead plant material.

It has been accepted that the maximal current standing crop, which is at the same time the highest increment, is reached by a population during the period from the phenological phase of maximal flowering to the phase of ripe fruits. This is supported by observations of the increase in standing crop of single individuals, as also of the whole population of definite species during the vegetation season. It is suggested (if, of course, it is not too late period for some species) to sample during the fructification, because it enables at the same time the determination of the size of fruit production in given population.

In the case of annual plants or perennials, which above-ground shoots die

off entirely in definite year, the maximal state of standing crop at the time of fructification will be at the same time a maximal increment, since populations of these species begin to built their above-ground crop almost from nothing at spring. In evergreen species, in which a part of above-ground shoots is permanent, the standing crop in a new vegetation season will consist of the old material from previous years and the current standing crop. The maximal increment is calculated then exclusively on the basis of the current standing crop after its separation from the material from previous years.

When the peak increment of current standing crop and the number of individuals and above-ground shoots are known, one calculates so-called index of the average individual increment during the period of maximal growth for given population (abbreviation for this concept: average individual increment — G_i). This value is obtained from the division of the total increment of standing crop of given population by the number of individuals. It should be stressed again that this value presents an index of only actual, maximal increment, and not the average of whole standing crop produced also in previous years. The value of this index should be determined on the basis of possibly greatest number of individuals in definite species. The index is used for the calculation of net production for at will numerous population. The knowledge of the another, very important parameter — the number or density of individuals in the population studied (D) is indispensable for this, however. In plant associations, especially those with poor density, the determination of density is a simple matter and has the advantage that in probably best and reliable way illustrates actual quantitative relations prevailing in vegetation. Primary net production of the definite population will be equal to the product of average individual increment (G_i) and density (D):

$$P = G_i \times D \quad (1)$$

2.2. Analysis of the increment of above-ground parts of vascular plants

Two ways of herb layer analysis, partially complementary to each other and yielding comparable material, were used in the present paper.

In phytocoenoses of each of the associations studied there were installed 20 circular samples of the area of 2,000 cm² each (diameter = 50.5 cm). They were installed in stands homogeneous from phytosociological standpoint. These samples, adequately marked, remained untouched during the whole study period (I call them “permanent samples”). For each sample during the full swing of herb layer development the cover by vascular plants and mosses was recorded. Individual species were selectively clipped most often during their fructification period, and individuals were counted. The number

of individuals fructifying, damaged by animals, etc. was also noted. From fructifying specimens fruits were collected in order to determine their biomass in relation to vegetative crop. In the case of evergreen plants, current year parts were separated from previous year ones. Segregated material was dried at the temperature of 85°C during 48 hours, and then weighed with the accuracy to 0.01 g. The material from permanent samples served also for the calculation of mean individual increments (G_i). When, however, the number of individuals from samples was too low for mean calculation, this number has been increased through the collection of individuals from the given population beyond samples. Density analysis decided about the value of this number. When species density amounted to, e.g. 300 individuals, while the species occurred only 50 times within permanent samples, then additional 250 specimens were collected beyond samples. In the calculation of individual increment index we tried to observe the rule that it should be based upon individuals' number not less than that found in density analysis.

2.3. Analysis of density

If we are to conclude about the whole on the basis of part, one should meet the condition that this part is possibly most representative for the whole studied. Unfortunately, the collection of 20–30 samples with an area of 4–6 m² and concluding on their basis about relations prevailing in the whole association occupying several or hundreds of hectares, arises serious reservations. To be sure that samples taken are the representation of actual, average floristic and quantitative relations prevailing in the whole phytocoenosis studied, it is best to take possibly many samples in entire random manner. Analysis of density meets this requirement. The concept of density and techniques of its examination have been described in handbooks by Sławiński (1950), Braun-Blanquet (1964) and others. In our case we made 100 random throws with a circle with diameter of 36.7 cm (0.1 m²) within the whole stand. In the circle there was recorded each time not only the occurrence of species (frequency), but also the number of individuals from each species (number, density). In this connection the density can be determined as “weighed frequency” on the “weighed mean” model. In the case when individuals could not be distinguished, above-ground shoots were counted, and in clumpy species as, for example, some grasses or sedges, the whole tussock comprised an unit-individual. Cover by herbaceous plants and mosses has been recorded also in each sample, while the number of shrubs and tree regeneration within the shrub and herb layer in a radius of 1 m from the centre of sample. In associations with mosaic structure, i.e. in *Carici elongatae-Alnetum*, where the herb layer is differentiated into elevations and depressions, analysis of density should be carried out separately for elevations and for depressions. In the present paper we restricted ourselves to depressions in

Carici elongatae-Alnetum. The determination of density is very simple and quick. For example, the analysis of 100 throws was done by two persons during two days. Hence the increase in sampling intensity up to 200, 300 or more throws does not cause much trouble.

The calculation of production on the basis of density and mean individual increment as well as the direct estimate of production on 20 permanent circular samples enabled to carry a comparative analysis and the evaluation of results with these two methods.

2.4. Analysis of moss layer

From twenty permanent samples there were taken also all mosses, after previous recording their cover. Following to drying and weighing we obtained the average dry biomass from precisely determined area and with determined average cover. The records on moss cover in random samples (100 throws) enabled the calculation of their average cover in these samples (from the area of 10 m²). In turn, the correction was introduced to calculations. This correction allowed for the difference in cover. From the ratio between the general standing crop of mosses in permanent samples (Bc) with average cover (Cc) and the mean cover from random samples (Cf) the standing crop of mosses in random samples (Bf) was calculated according to the formula:

$$Bf = \frac{Bc \times Cf}{Cc} \quad (2)$$

In order to determine what a per cent of the total standing crop of mosses presents the current growth there were taken additionally 20 samples with the area of 250 cm² each. In these samples we tried to separate the current year biomass from that of previous years. From the ratio of these two values the index of instantaneous increment of biomass was calculated. Afterwards the average state of total biomass found in random samples has been reduced by the value of this index.

2.5. Analysis of plant fall

Twenty catchers have been installed in each association during first days of June. The "catcher" presents a wire circle sawn with bag and fixed to a pole. The size of catchers was various: greater ones with the area of 1/10 m² and smaller ones – with the area of 1/15 m². With the beginning of October there were used also 20 circular ground samples with the area of 1/10 m². These circles were put on mineral soil after the removal of litter and vegetation. The differentiation of samples was intended to give even approximate data about the effect of this experiment upon results.

The content of bags (catchers) was taken with the beginning of each month. The plant fall was segregated into leaves of coniferous trees, leaves of deciduous trees, fruits and other parts (bark, twigs, etc.).

3. RESULTS

3.1. General

Tables I–IV contain more important quantitative characters of individual populations (species) in four forest associations. Values obtained with the use of two methods are compared in them: from 20 permanent samples (C) and from 100 random samples (D), converted into 1 m². The use of great number of random samples enabled the analysis of many valuable features of quantitative character in the ground vegetation stratum within associations studied. I shall discuss briefly some of them, as: frequency, density, weight structure of population, fructification index and the ratio of actual and previous year biomass. I shall describe also comparative levels of these values in various associations.

3.2. Frequency

Frequency is a quantitative property illustrating the presence of species in phytocoenosis studied. It is determined in per cents as the ratio of throws (samples), in which the given species occurred (without counting of individuals) to all throws. If by N the number of all samples is denoted, and by n the number of samples, in which the given species was recorded, then the frequency (F) is expressed by following formula:

$$F = \frac{n}{N} \times 100 \quad (3)$$

These values for the studied species and associations are presented in Tables I–IV. These values are frequently grouped into frequency classes (at intervals of 20%) in a form of so-called frequency diagram (Fig. 1). It appears that in all associations studied the most numerous are sporadic species, with a low frequency of occurrence, revealing frequency coefficient from 1 to 20% (I frequency class). Species with high frequency are poorly represented, although they form the main mass of herb layer. Data from random samples (D) proved that there did not occurred a single species, which would form the Vth class (81–100%) or there was no such species, which on 100 throws would occur more than 80 times. Apart of *Vaccinio myrtilli-Pinetum molinietosum*, where only 60% of species belongs to the 1st frequency class, in remaining associations not less than 80% species – are rare, not common

Frequency, density and biomasses of various species in herb layer of *Tilio-Carpinetum*

Tab. I

Species	Frequency in per cent		Average density per 1 m ²		No.***	Individual average growth in g	Net production in g/m ²	
	C*	D**	C	D			C	D
<i>Milium effusum</i>	40	30	45.2	21.8	231	0.13753	3.325	2.998
<i>Majanthemum bifolium</i>	85	66	61.5	52.5	246	0.02980	1.837	1.564
<i>Stellaria holostea</i>	85	45	57.2	26.1	229	0.05713	3.271	1.491
<i>Convallaria maialis</i>	20	10	5.2	4.4	21	0.30476	1.600	1.341
<i>Deschampsia caespitosa</i>	5	8	0.2	0.8	1	1.67000	0.417	1.336
<i>Luzula pilosa</i>	15	7	2.2	2.3	19	0.51736	0.995	1.190
<i>Anemone nemorosa</i>	95	79	301.2	73.2	1,205	0.01420	4.288	1.039
<i>Oxalis acetosella</i>	90	68	283.0	138.3	1,132	0.00566	1.603	0.783
<i>Ajuga reptans</i>	40	22	8.5	5.2	34	0.15000	1.275	0.780
<i>Galeobdolon luteum</i>	45	38	68.2	29.9	273	0.02553	1.742	0.763
<i>Geum urbanum</i>	15	4	9.5	1.0	58	0.55568	2.155	0.556
<i>Crepis paludosa</i>	5	2	0.5	0.9	32	0.51375	0.062	0.462
<i>Athyrium filix-femina</i>	30	8	3.7	2.7	15	0.16466	0.617	0.445
<i>Viola silvestris</i>	25	20	9.0	3.8	86	0.10261	0.867	0.390
<i>Vaccinium myrtillus</i>	40	16	4.7	2.9	19	0.12052	0.572	0.349
<i>Veronica chamaedrys</i>	15	4	1.2	2.9	5	0.07600	0.095	0.220
<i>Rubus saxatilis</i>	15	4	1.5	0.6	6	0.31833	0.477	0.191
<i>Lysimachia vulgaris</i>	40	13	10.7	2.3	43	0.07325	0.787	0.168
<i>Moehringia trinervia</i>	5	5	0.2	1.5	21	0.07023	0.030	0.105
<i>Carex digitata</i>	10	2	9.2	0.2	57	0.50210	1.880	0.100
<i>Aegopodium podagraria</i>	5	3	0.5	0.9	2	0.11000	0.055	0.099
<i>Hepatica nobilis</i>	5	1	0.7	2.0	73	0.04917	0.060	0.098
<i>Paris quadrifolia</i>	10	7	1.5	1.8	57	0.04473	0.032	0.080
<i>Stellaria nemorum</i>	5	7	2.7	2.6	11	0.02909	0.080	0.076
<i>Dryopteris spinulosa</i>	5	1	0.2	0.1	1	0.39000	0.097	0.039
<i>Melica nutans</i>	30	2	17.7	0.8	131	0.04687	0.765	0.037
<i>Polygonatum multiflorum</i>	10	1	2.5	0.1	10	0.18600	0.465	0.019
<i>Calamagrostis arundinacea</i>	5	—	0.2	—	1	0.72000	0.180	—
<i>Melampyrum pratense</i>	5	—	1.0	—	4	0.08500	0.085	—
<i>Trientalis europaea</i>	15	—	1.5	—	56	0.06089	0.027	—
<i>Potentilla erecta</i>	5	—	0.5	—	2	0.02000	0.001	—
Total			911.6	381.6			29,702	16,719

* Values obtained from permanent samples.

** Values obtained from random samples.

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

species distributed among dominant species with high frequencies. This fact indicates that only a small per cent of species builds herb layer.

The frequency does not say much about the actual significance of

Frequency, density and biomasses of various species in herb layer of *Pino-Quercetum*
Tab. II

Species	Frequency in per cent		Average density per 1 m ²		No.***	Individual average growth in g	Net production in g/m ²	
	C*	D**	C	D			C	D
<i>Vaccinium myrtillus</i>	100	77	72.7	29.7	291	0.16690	12.142	4.957
<i>Melampyrum pratense</i>	40	52	25.7	28.4	103	0.13067	3.364	3.711
<i>Pteridium aquilinum</i>	35	10	2.5	1.2	21	2.78476	6.652	3.342
<i>Luzula pilosa</i>	20	10	1.7	1.8	47	0.62723	0.345	1.129
<i>Convallaria maialis</i>	55	12	14.5	3.8	58	0.16362	2.372	0.622
<i>Solidago virga-aurea</i>	20	9	1.0	1.1	20	0.45600	0.255	0.502
<i>Festuca ovina</i>	5	8	0.5	0.9	20	0.51200	0.047	0.461
<i>Calamagrostis arundinacea</i>	30	2	3.5	0.3	21	1.01142	4.635	0.303
<i>Viola silvestris</i>	5	3	2.0	1.0	28	0.27232	0.230	0.272
<i>Majanthemum bifolium</i>	25	18	9.5	6.7	38	0.03578	0.340	0.240
<i>Oxalis acetosella</i>	55	24	259.7	38.8	1,039	0.00577	1.499	0.224
<i>Peucedanum oreoselinum</i>	5	1	0.5	0.2	10	0.87400	0.075	0.175
<i>Equisetum silvaticum</i>	15	7	1.5	1.0	6	0.16000	0.240	0.160
<i>Vaccinium vitis-idaea</i>	25	9	3.0	1.8	20	0.08350	0.242	0.150
<i>Anemone nemorosa</i>	75	18	70.7	11.2	283	0.01300	0.920	0.146
<i>Trientalis europaea</i>	55	25	9.0	3.4	36	0.01819	0.164	0.062
<i>Rubus saxatilis</i>	15	1	1.0	0.2	20	0.28050	0.322	0.056
<i>Molinia coerulea</i>	10	1	2.7	0.4	31	0.09258	0.222	0.037
<i>Fragaria vesca</i>	5	1	4.7	0.2	19	0.12368	0.587	0.025
<i>Scorzonera humilis</i>	5	1	0.2	0.1	51	0.19666	0.100	0.019
<i>Milium effusum</i>	5	—	5.7	—	83	0.18915	0.895	—
<i>Veronica chamaedrys</i>	10	—	1.7	—	7	0.05428	0.095	—
<i>Lysimachia vulgaris</i>	5	—	1.5	—	6	0.04166	0.062	—
<i>Galium boreale</i>	5	—	0.7	—	3	0.04000	0.030	—
Total			496.2	132.2			35.835	16.595

* Values obtained from permanent samples.

** Values obtained from random samples.

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

a species in the herb layer within community, if the number of individuals of given species per definite area, or its density remains unknown.

3.3. Density

This character plays the first role in the method in use. Owing to density analysis one can obtain in an objective way the most accurate picture of number (abundance) within all populations occurring in the herb layer.

Frequency, density and biomasses of various species in herb layer of *Vaccinio myrtilli-Pinetum*

Tab. III

Species	Frequency in per cent		Average density per 1 m ²		No.***	Individual average growth in g	Net production in g/m ²	
	C*	D**	C	D			C	D
<i>Vaccinium myrtillus</i>	100	76	88.2	19.8	353	0.18067	15.940	6.378
<i>Molinia coerulea</i>	45	53	55.2	34.0	221	0.04651	2.570	1.581
<i>Luzula pilosa</i>	15	6	2.2	2.3	49	0.47571	0.422	1.094
<i>Festuca ovina</i>	5	5	0.2	1.3	20	0.72400	0.035	0.941
<i>Rubus saxatilis</i>	5	5	0.5	1.1	20	0.74950	0.072	0.824
<i>Melampyrum pratense</i>	50	20	37.7	6.3	153	0.10490	3.960	0.661
<i>Vaccinium vitis-idaea</i>	60	31	12.2	9.1	49	0.06734	0.825	0.613
<i>Pteridium aquilinum</i>	15	2	0.7	0.2	3	1.79000	1.342	0.358
<i>Majanthemum bifolium</i>	20	53	7.7	6.1	31	0.03387	0.262	0.207
<i>Trientalis europaea</i>	40	37	5.7	7.1	23	0.02195	0.126	0.156
<i>Anemone nemorosa</i>	10	6	4.2	2.0	67	0.03014	0.055	0.060
<i>Solidago virga-aurea</i>	10	2	0.5	0.2	2	0.09000	0.045	0.018
<i>Calamagrostis arundinacea</i>	15	—	1.2	—	5	1.07400	1.342	—
<i>Scorzonera humilis</i>	—	4	—	0.5	51	0.37901	—	0.189
Total			216.2	90.0			26.996	13.080

* Values obtained from permanent samples.

** Values obtained from random samples.

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

Numerical values of this character, as it was mentioned, multiplied by the average individual increment, yield the estimate of the size of production by individual population. Density is rather frequently correlated with frequency, although sometimes the situation is reversed. This depends to a serious extent upon structural features of herb layer, upon the manner of species distribution, upon size of individuals. Sometimes a species with low frequency reveals very high numbers, since it occurs sparsely, but in greater groups with a high density of individuals, some other time a species frequently met may occur singly. The whole biomass of herb layer from the studied area divided by the total occurrence of individuals enables the calculation of the average individual biomass in individual associations. It appeared, for example, that the average individual in the herb layer of *Tilio-Carpinetum* weighs circa 3 times less, when compared with an average individual in coniferous forests, while nearly 10 times less, than in *Carici elongatae-Alnetum*.

Obtained numbers of individuals are sometimes surprising. And so, e.g. in the herb layer of *Tilio-Carpinetum*, with covering reaching on an average

Frequency, density and biomasses of various species in herb layer of *Carici elongatae-Alnetum*

Tab. IV

Species	Frequency in per cent		Average density per 1 m ²		No.***	Individual average growth in g	Net production in g/m ²	
	C*	D**	C	D			C	D
<i>Carex elongata</i>	25	11	1.2	1.8	20	5.69500	9.882	10.251
<i>Carex acutiformis</i>	50	29	20.0	7.1	58	1.34327	19.477	9.537
<i>Peucedanum palustre</i>	15	15	2.7	4.6	30	2.03133	0.060	9.344
<i>Dryopteris thelypteris</i>	70	49	126.0	48.0	504	0.11654	14.685	5.687
<i>Solanum dulcamara</i>	75	41	29.7	8.0	119	0.40596	12.077	3.248
<i>Calamagrostis canescens</i>	20	12	26.2	15.4	105	0.19333	5.075	2.977
<i>Glyceria fluitans</i>	5	5	5.2	5.8	31	0.47580	2.385	2.759
<i>Iris pseudoacorus</i>	10	7	0.7	1.0	20	2.42450	1.500	2.424
<i>Stachys palustris</i>	10	4	1.2	1.0	20	1.38450	1.637	1.384
<i>Myosotis palustris</i>	10	13	7.7	7.3	31	0.14032	1.087	1.024
<i>Sium latifolium</i>	10	10	0.7	1.9	20	0.48750	1.280	0.926
<i>Galium palustre</i>	65	40	26.5	21.3	106	0.03933	4.170	0.838
<i>Lysimachia thyrsiflora</i>	20	8	2.0	1.4	20	0.52600	1.867	0.787
<i>Dryopteris spinulosa</i>	5	3	2.0	1.2	20	0.62100	0.100	0.745
<i>Carex Hudsonii</i>	25	1	2.7	0.1	11	7.25454	19.950	0.725
<i>Moehringia trinervia</i>	5	7	0.7	2.8	20	0.22500	0.012	0.630
<i>Viola palustris</i>	5	9	0.5	4.4	20	0.12050	0.065	0.530
<i>Scutellaria galericulata</i>	5	5	1.2	1.5	20	0.31400	0.207	0.471
<i>Lysimachia vulgaris</i>	10	6	0.7	1.6	20	0.29450	0.047	0.471
<i>Deschampsia caespitosa</i>	5	2	0.2	0.2	9	2.14777	0.412	0.429
<i>Cardamine amara</i>	20	17	5.2	3.7	21	0.05619	0.295	0.208
<i>Ranunculus repens</i>	25	12	4.2	2.5	25	0.04780	0.191	0.119
<i>Lycopus europaeus</i>	30	9	9.7	1.0	39	0.09205	0.897	0.092
<i>Hottonia palustris</i>	5	7	0.5	2.2	22	0.02727	0.007	0.060
<i>Caltha palustris</i>	10	2	1.5	0.2	22	0.17045	0.102	0.034
<i>Scirpus silvaticus</i>	10	—	0.7	—	20	2.86800	0.390	—
Total			279.6	147.0			94.729	55.700

* Values obtained from permanent samples.

** Values obtained from random samples.

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

29%, which is rather low, per 1 m² there were recorded on an average 382 individuals, while in the richer vegetation not less than 912 individuals, what when converted into hectare gives 3.82 and 9.12 millions of individuals. If to this figure the number of saplings and shrubs is added then this number will be increased still by 150,000 individuals per hectare. Herb layer of *Pino-Quercetum*, *Carici elongatae-Alnetum*, and, particularly, *Vaccinio myrtilli-*

Pinetum appeared poorer; in the latter only almost one million of individuals or shoots per hectare has been recorded. The application of density method gives also the information about the abundance of shrubs or trees in shrub and herb layer (Tab. V). When one knows their density or annual increment value, one can attempt to evaluate their production.

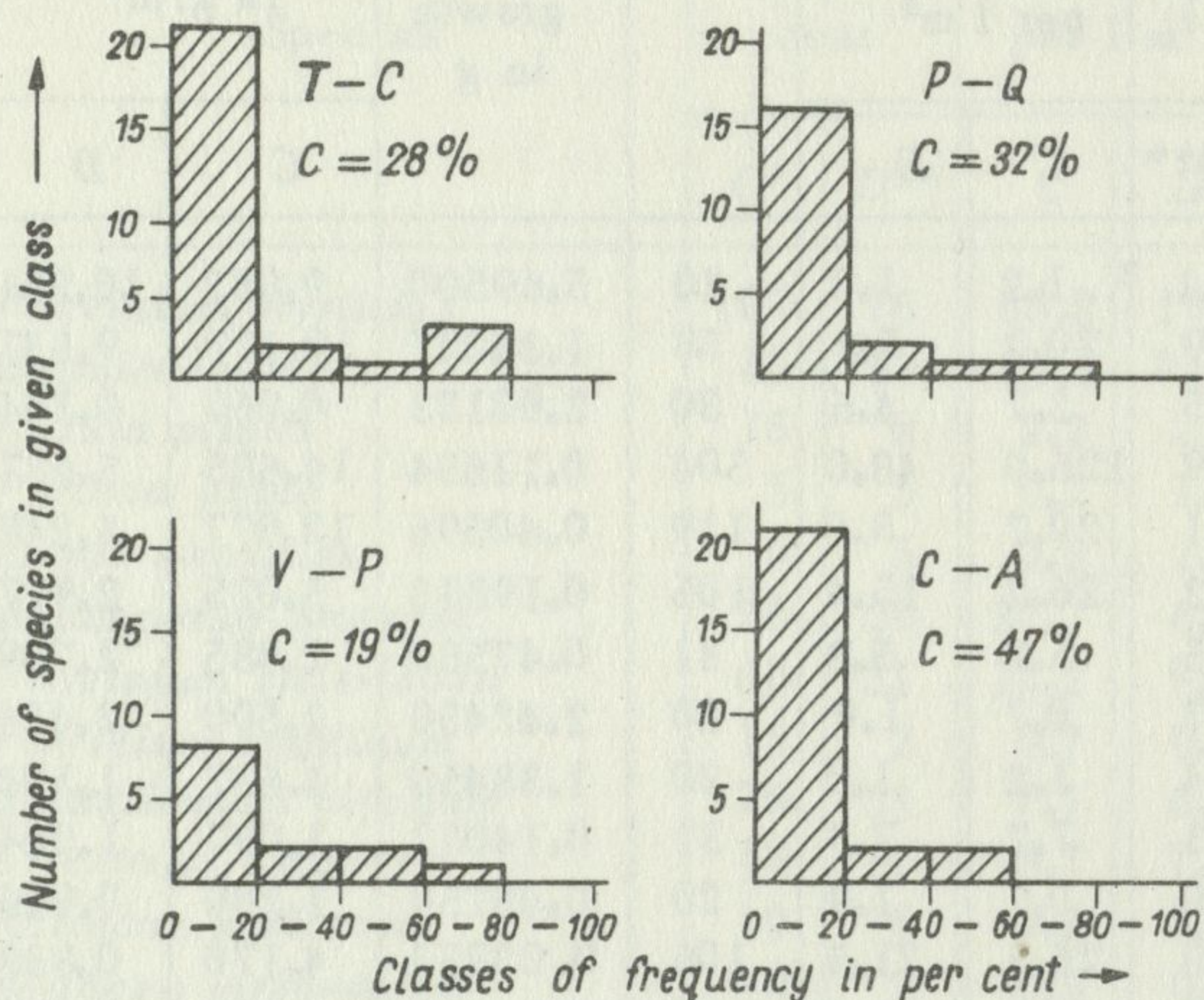


Fig. 1. Frequency diagrams of species in *Tilio-Carpinetum* (T-C), *Pino-Quercetum* (P-Q), *Vaccinio myrtilli-Pinetum* (V-P), and *Carici elongatae-Alnetum* (C-A)
C - average cover

Number of tree and shrub species in the shrub and herb layer of *Tilio-Carpinetum* (T-C), *Pino-Quercetum* (P-Q), and *Vaccinio myrtilli-Pinetum* (V-P) (data from random samples, converted to 100 m²)

Tab. V

Species	Number of individuals in association:		
	T-C	P-Q	V-P
<i>Frangula alnus</i>	26	91	125
<i>Quercus robur</i>	12	26	10
<i>Sorbus aucuparia</i>	10	7	6
<i>Corylus avellana</i>	26	10	—
<i>Carpinus betulus</i>	18	5	—
<i>Viburnum opulus</i>	5	3	—
<i>Populus tremula</i>	2	1	—
<i>Padus avium</i>	15	—	—
<i>Alnus glutinosa</i>	—	1	—
<i>Betula verrucosa</i>	—	—	9
<i>Betula pubescens</i>	—	—	1

Through the recording of the density of tree seedlings within individual associations, we tackle the problem of the natural regeneration of a stand, and thus to some extent we get the knowledge of succession trends of associations. In the herb layer of *Tilio-Carpinetum*, for example, there was found on an average more than 6 times more saplings of hornbeam per 10 m², than in the mixed, coniferous forest. Reversed relations, although not so strongly marked quantitatively, revealed self-regeneration and shrubs of *Frangula alnus*¹. In *Vaccinio myrtilli-Pinetum molinietosum* there was 5 times more of them, than in *Tilio-Carpinetum*, and almost twice as much as in *Pino-Quercetum*.

3.4. Weight structure of population

One of the most significant quantitative features with serious ecological and site-forming importance presents the standing crop. It is the best index of plant growth and the best basis for the estimate of production size. The mere presence of a species in given associations says very little about its

¹Latin names of plant species after Szafer, Kulczyński and Pawłowski (1953).

ecological role, it is only the strict analysis of its density and standing crop, which appraises it from an ecological standpoint. When one will analyze results concerning the course of biomasses, and strictly speaking, increments of individual populations, one will come to the fundamental conclusion concerning the regularity of the weight structure of population. It appears that only a small number of species (about 20–25%) presents the main, fundamental bulk of forest ground vegetation while remaining 75–80% of species constitute only 1/4 of the plant material in herb layer. In associations poor in respect to vegetation or site (e.g. in *Vaccinio myrtilli-Pinetum* and *Vaccinio myrtilli-Pinetum molinietosum*) the quantitative and weight domination of one or few only species is obviously marked. In floristically richer associations the main standing crop is distributed among the higher number of species. In this case distinct, decidedly dominant species are lacking. And so, in *Vaccinio myrtilli-Pinetum molinietosum* the main role is played by only 3 species, and out of them one, *Vaccinium myrtillus*, produces not less than 50% of the total standing crop. In *Pino-Quercetum* there are 4 species; the most important one comprises still 33% of the total standing crop of herb layer. In *Tilio-Carpinetum* there are 7 analogous species, while 10 of them in *Carici elongatae-Alnetum*. The most numerous population in both cases comprises about 18% of the total standing crop. Table VI contains the detailed analysis of the course of standing crop of herb layer in four associations. There were isolated in it 4 weight classes with stating number of species forming these classes. On the basis of population proportion in the total standing crop (increment) of herb layer there can be distinguished 3 groups of species. The first, most important group comprises species, which form the fundamental framework of herb layer. On the average they comprise about 25% of species list, but they are most significant in respect to weight, since on an average they represent 70–75% of the standing crop. These species may be called dominants. There can be temporary and permanent dominants among them (Sławiński 1950). Temporary dominants dominate decidedly in certain season of year, afterwards they die-off (e.g. geophytes from early spring period in the herb layer of *Tilio-Carpinetum* or beech forest). Permanent dominants prevailing throughout the whole vegetation season (as *Vaccinium myrtillus* in *Vaccinio myrtilli-Pinetum*) have the greatest significance. They may be determined as edificators or main components (Paczoski 1951). These are species which in ecological respect are most significant. Their enormous and decidedly prevailing over other populations standing crop with the definite chemical content, continuously affect the soil and environment, and shape them quite distinctly. Sporadic species, rather numerous (about 15–30%) form the extremally average group, which does not play almost any role in the standing crop and production. In our case they amounted only from 1 to 3% of the total standing crop. Finally, there could be distinguished the third, most important group (on an average 50% of all species) participating in 20–30% in the total standing crop.

Weight structure of herb layer in four associations

Tab. VI

Weight classes (g)	<i>Carici elongatae-Alnetum</i>				<i>Tilio-Carpinetum</i>				<i>Pino-Quercetum</i>				<i>Vaccinio myrtilli-Pinetum</i>			
	number of species		biomass		number of species		biomass		number of species		biomass		number of species		biomass	
		(%)	(g/m ²)	(%)		(%)	(g/m ²)	(%)		(%)	(g/m ²)	(%)		(%)	(g/m ²)	(%)
> 1.0	10	40	48.635	79	7	26	10.959	66	4	20	13.139	74	3	23	9.053	69
1.0-0.5	7	28	5.181	7	4	14	2.882	17	2	10	1.124	9	4	31	3.039	23
0.5-0.1	5	20	1.698	13	8	30	2.330	14	9	45	2.131	16	4	31	0.910	7
0.1 >	3	12	0.186	1	8	30	0.548	3	5	25	0.199	1	2	15	0.078	1
Total	25		55.700		27		16.719		20		16.593		13		13.080	

It results from the above considerations that in production estimation dominant populations with high, average individual weight and total standing crop are particularly important. These species are not numerous and in the determination of density and current increment they should receive a serious attention. Remaining 80% of species represent only 20–30% of standing crop. They often include abundant species with a high density, but low standing crop (e.g. *Oxalis acetosella*) and in spite of their decided, quantitative predominance their significance in the total production of biomass is low. And vice versa, sometimes rare species with high weight may significantly affect the production size.

Irrespectively to fact, whether one will deal with large or small, numerous or rare individuals, they all are treated with equal objectiveness in the method of random sampling and production estimation with the aid of density and average standing crop (average, individual increment).

3.5. Comparison of abundance and standing crop of populations in several associations

It is commonly known that not all populations develop themselves to an equal extent in various environments. Analysis of density and size of standing crop may serve as a good index of ecological conditions of an environment for the species studied. Several common species in few associations studied were compiled in Table VII and VIII to show the course of important quantitative characters of these populations in relation to association, and to determine thus roughly relatively optimal environment for them. For example, some species are more numerous in one environment, although they have lower average increments of individual biomass when compared with other environments, and vice versa. The fact of the occurrence of species with highest bulks and highest density in the definite association proves that here they find their ecological optima.

3.6. Fructification index

Fructification index determines the ratio between fructifying and not fructifying individuals. It is expressed by a fraction which states per what number of individuals falls one fructifying individual. The greater denominator, the lower degree of fructification (lower index). For example, in *Tilio-Carpinetum* in the case of *Oxalis acetosella*, there flowers one per 230 individuals (index $1/230$), in *Pino-Quercetum* already one per 65 individuals – $1/65$. Table IX states several such examples. It can be said generally that in many populations only not numerous individuals set fruits, the remainder depends on vegetative propagation. The highest number of species and in highest quantities flowers and fructifies in *Pino-Quercetum*. Fructification provides one of very important phenomena of vigour symptoms for species

Some quantitative characters of species common to *Tilio-Carpinetum* (T-C), *Pino-Quercetum* (P-Q), and *Vaccinio myrtilli-Pinetum* (V-P)

Tab. VII

Species	Frequency in per cent			Density per 10 m ²			Individual average biomass in g			Total biomass in g/10 m ²		
	T-C	P-Q	V-P	T-C	P-Q	V-P	T-C	P-Q	V-P	T-C	P-Q	V-P
<i>Anemone nemorosa</i>	79	18	6	732	112	20	0.01420	0.01300	0.03014	10.394	1.456	0.603
<i>Vaccinium myrtillus</i>	16	77	76	29	297	198	0.12052	0.16690	0.18067	3.495	49.569	63.776
<i>Majanthemum bifolium</i>	66	18	53	525	67	61	0.02980	0.03578	0.03387	15.645	2.397	2.066
<i>Luzula pilosa</i>	7	10	6	23	18	23	0.51736	0.62723	0.47571	11.899	11.290	10.941

Comparison of frequency, density, individual average biomass and total biomass for certain common species in associations studied

Tab. VIII

Associations and species	Frequency in per cent		Density per 10 m ²		Individual average biomass in g		Total biomass in g/10 m ²	
	T-C	C-A	T-C	C-A	T-C	C-A	T-C	C-A
<i>Tilio-Carpinetum</i> (T-C) <i>Carici elongatae-Alnetum</i> (C-A)	T-C	C-A	T-C	C-A	T-C	C-A	T-C	C-A
<i>Deschampsia caespitosa</i>	8	2	8	2	1.67000	2.14777	13.360	4.295
<i>Lysimachia vulgaris</i>	13	6	23	16	0.07325	0.29450	1.685	4.712
<i>Dryopteris spinulosa</i>	1	3	1	12	0.39000	0.62100	0.390	7.452
<i>Moehringia trinervia</i>	5	7	15	28	0.07023	0.22500	1.053	6.300
<i>Tilio-Carpinetum</i> (T-C) <i>Pino-Quercetum</i> (P-Q)	T-C	P-Q	T-C	P-Q	T-C	P-Q	T-C	P-Q
<i>Oxalis acetosella</i>	68	24	1,388	388	0.00566	0.00577	7.828	2.239
<i>Convallaria maialis</i>	10	12	44	38	0.30476	0.16362	13.409	6.218
<i>Viola silvestris</i>	20	3	38	10	0.10261	0.27232	3.899	2.723
<i>Pino-Quercetum</i> (P-Q) <i>Vaccinio myrtilli-Pinetum</i> (V-P)	P-Q	V-P	P-Q	V-P	P-Q	V-P	P-Q	V-P
<i>Melampyrum pratense</i>	52	20	284	63	0.13067	0.10490	37.110	6.609
<i>Pteridium aquilinum</i>	10	2	12	2	2.78476	1.79000	33.417	3.580
<i>Solidago virga-aurea</i>	9	2	11	2	0.45600	0.09000	5.016	0.180
<i>Molinia coerulea</i>	1	53	4	340	0.09258	0.04651	0.370	15.813
<i>Vaccinium vitis-idaea</i>	9	31	18	91	0.08350	0.06734	1.503	6.128
<i>Trientalis europaea</i>	25	37	34	71	0.01819	0.02195	0.618	1.558
<i>Festuca ovina</i>	8	5	9	13	0.51200	4.60800	4.608	9.412
<i>Scorzonera humilis</i>	1	4	1	5	0.19666	0.37901	0.197	1.895

in given environment. In the area studied, *Pino-Quercetum* appeared to create best conditions for the full development of many plants.

In respect to weight, the standing crop of fruits comprises a very small part of the actual production; under analyzed conditions it presents fractions of per cent (Tab. X). The possibility of an easy estimate of fruit production with the present method also supports it. The knowledge of the biomass of fruits and seeds is also important, because they present an important food item for many animals.

3.7. Current to old material ratio

In the method of production estimation on the basis of an analysis of differences in standing crops of plant material one takes into consideration

Fructification index of certain species in associations *Tilio-Carpinetum* (T-C), *Pino-Quercetum* (P-Q), and *Vaccinio myrtilli-Pinetum* (V-P) (data from random samples)

Tab. IX

Species	T-C	P-Q	V-P
<i>Anemone nemorosa</i>	1/732	—	—
<i>Galeobdolon luteum</i>	1/299	—	—
<i>Stellaria holostea</i>	1/261	—	—
<i>Oxalis acetosella</i>	1/230	1/65	—
<i>Luzula pilosa</i>	1/23	1/2	—
<i>Viola silvestris</i>	1/14	1/5	—
<i>Moehringia trinervia</i>	1/4	1/1	—
<i>Majanthemum bifolium</i>	1/105	1/34	1/61
<i>Vaccinium myrtillus</i>	—	1/32	1/28
<i>Festuca ovina</i>	—	1/9	1/13
<i>Trientalis europaea</i>	—	1/5	1/7
<i>Melampyrum pratense</i>	—	1/2	1/4
<i>Anthoxantum odoratum</i>	—	1/1	1/1

Biomasses of herb layer in associations examined (data on 20 permanent samples in grammes oven-dry weight per 4 m² and in percentages)

Tab. X

Association	A	B	C	D	B:A (%)	D:C (%)
	total	previous years	current year	fruits		
<i>Tilio-Carpinetum</i>	123.059	4.285	118.774	0.322	3.6	0.3
<i>Pino-Quercetum</i>	213.203	69.847	143.356	0.284	32.8	0.2
<i>Vaccinio myrtilli-Pinetum</i>	222.645	126.630	108.015	0.330	56.9	0.3
<i>Carici elongatae-Alnetum</i>	394.745	13.481	381.264	2.600	3.4	0.7

the total biomass, i.e. the one including both old biomass from previous years and the current one — from the current year. There are quite frequently to be met species, and even whole associations, in which the standing crop from previous years decidedly dominates over the current increment. This increases obviously the possibility of error in production estimate, since one deals in such cases with large biomasses and their large variation. In the present work, as it has been mentioned, the production estimate is based exclusively on the current year biomasses. There occurs, thus, need for the segregation of current year parts from these formed previously. In forest herb layer within majority of associations, there are few species partially or entirely winter-hard. In certain, however, association types, as for example in coniferous forests, built mainly of forbs, populations of plants with durable above-ground shoots dominate decidedly. Table X indicates that in the herb layer of *Tilio-*

Carpinetum and *Carici elongatae-Alnetum* the ratio of previous year biomass to the current year one is low and does not reach even 4%. On the other hand in *Pino-Quercetum* and particularly in *Vaccinio myrtilli-Pinetum molinietosum* the material from previous years comprises almost 60% of the total standing crop.

I shall not cite details on the manner of the differentiation and segregation of these standing crops from each other, because this matters deserves a separate elaboration. I would like to mention, that in the overwhelming majority old parts are easily recognizable and separable with the aid of both colour and morphological details and might be quantitatively estimated.

3.8. Estimate of the production of above-ground parts of herb layer

Two last columns in Tables I–IV present maximal increments of the standing crop of individual populations of herb layer in associations studied, expressed in grammes of dry weight per 1 m². Values in column C have been calculated on the basis of data from 20 permanent samples, while those in column D – from 100 random samples. Increments from permanent samples (C) were found directly through the analysis of maximal increments of individual populations in samples. Increments inserted in the last column (D) have been calculated undirectly from the index of average density (column IV from the left) and from the mean individual increment (column VI). The sum of maximal increments of all populations (species) provides the estimation of the size of net primary production of the herb layer studied.

The production of above-ground parts of vegetation has been calculated with the aid of method based upon the average, individual increment and average density of population and amounted to:

in association:	g/m ² (kg/ha)
<i>Tilio-Carpinetum</i>	16.72 (167.2)
<i>Pino-Quercetum</i>	16.59 (165.9)
<i>Vaccinio myrtilli-Pinetum</i>	13.08 (130.8)
<i>Carici elongatae-Alnetum</i>	55.70 (557.0)

The estimate of herb layer production in these same associations, but with the use of the direct analysis of increments from 20 permanent samples amounted to: 29.70, 35.83, 27.00, and 94.73 g/m², respectively, and thus it was by 170 to 206% higher (compare Tab. XI). Such an overestimation of values obtained from permanent plots concerns also other quantitative characters. And so – the average covering is in them by 121 to 221% higher, while the number of individuals from 190 to 376% higher, when compared with random samples. Only these two quantitative characters explain to a serious

extent differences obtained in production estimation with these two methods. In the selection of locations for permanent plots we tried to observe the principle of homogeneity and typical character of a stand. Thus samples were being established in spots with higher cover of vegetation and richer species composition. The best indication of this are average values of cover and individual number from permanent plots, rather distinctly exceeding similar characters from random samples. Another kind of samples was taken entirely randomly, by throwing circles within the whole phytocoenosis studied. In 100 throws there frequently occurred empty samples, i.e. samples without plants. This technique of random throws is, what is generally known, deprived of subjectivism and yields the average, actual picture of floristic and quantitative relations. The values obtained (very low after all: from 19 to 47%) of cover and density from these samples are the best indication that the herb layer studied is strongly impoverished and destroyed. The comparison of these two estimates obtained with two techniques proves, how serious influence is exerted by the way of sampling place selection and sample number on the final result. In this respect the techniques of random samples obtained in possibly great numbers and extensive range decidedly dominates over many others.

Cover, number of individuals and biomasses on permanent (C) and random (D) samples in herb layer in four associations

Tab. XI

Association	Average coverage in per cent			Number of individuals			Biomass		
				in m ²		$\frac{C}{D}$ in per cent	in g/m ²		$\frac{C}{D}$ in per cent
	C	D	$\frac{C}{D}$	C	D		C	D	
<i>Tilio-Carpinetum</i>	58	29	200	912	382	139	29.70	16.72	177
<i>Pino-Quercetum</i>	56	32	175	496	132	376	35.83	16.59	216
<i>Vaccinio myrtilli-Pinetum</i>	42	19	221	216	90	240	27.00	13.08	206
<i>Carici elongatae-Alnetum</i>	57	47	121	280	147	190	94.73	55.70	170

One may try to make results of the estimation from permanent samples closer to objective ones and introduce the correction for the average covering of herb layer from random samples. The general biomass calculated from permanent samples (B_c) with average cover (C_c) is corrected by mean cover from a high number of random samples (C_f). In this case the production (P) would be equal to the following proportion:

$$P = \frac{B_c \times C_f}{C_c} \quad (4)$$

Through the introduction of a correction on cover from random samples into results of permanent ones we come to production values, which are very close to those obtained from random samples. They amount to:

in association:	g/m ²
<i>Tilio-Carpinetum</i>	to 14.84 (lower by 13%)
<i>Pino-Quercetum</i>	to 19.75 (higher by 16%)
<i>Vaccinio myrtilli-Pinetum</i>	to 12.21 (lower by 7%)
<i>Carici elongatae-Alnetum</i>	to 78.11 (higher by 29%)

Generally speaking, differences are slight. Owing to this one can suggest for not specialists, who would like to get a rough estimation of herb layer production, the above, simplified method. It would consist also on an analysis of 20–40 permanent samples and 100 or more random throws with the difference that one does not record species, nor their numbers (density). One is restricted only to the selective clipping of plants in the phase of fructification from permanent plots with very accurate recording of herb layer cover in per cents. With random throws one is also limited to the evaluation of cover. Current year increments obtained from permanent plots with determined, average cover are corrected by the value of average cover from random samples (100 throws) according to the above-cited formula (4). Results obtained with the aid of this procedure, are obviously considerably less accurate.

3.9. Estimate of moss production

The problem of moss production estimate has been roughly approached in the present paper. The dry matter of mosses has been determined on permanent plots (Bc) with definite density (Cc). Mean cover by mosses (Cf) in associations studied was derived from 100 random throws. On this basis the standing crop of mosses in random samples was calculated:

$$Bf = \frac{Bc \times Cf}{Cc} \quad (2)$$

With such procedure we got following quantities of moss standing crop in grammes of dry matter per 1 m² in:

<i>Tilio-Carpinetum</i>	0.9 with 0.14% cover,
<i>Pino-Quercetum</i>	2.7 with 1.90% cover,
<i>Vaccinio myrtilli-Pinetum</i>	47.5 with 35.00% cover,
<i>Carici elongatae-Alnetum</i>	0.67 with 0.58% cover.

With the assumption that circa 1/3 of the standing crop falls to the current

year growth (data from moss analysis on meadow and only certain species in forest) the general production of mosses should be evaluated roughly on:

	g/m ²	in association:
0.3		<i>Tilio-Carpinetum</i>
2.7		<i>Pino-Quercetum</i>
16.0		<i>Vaccinio myrtilli-Pinetum</i>
0.2		<i>Carici elongatae-Alnetum</i> (in depressions)

3.10. Estimate of the size of plant fall

In all associations studied the size of leaf fall is correlated with seasonal variation. This fall is slight at the beginning of summer, increases slightly during this season and since September there occurs a rapid growth of curve, which reaches its peak in October and abruptly drops down in November (com-

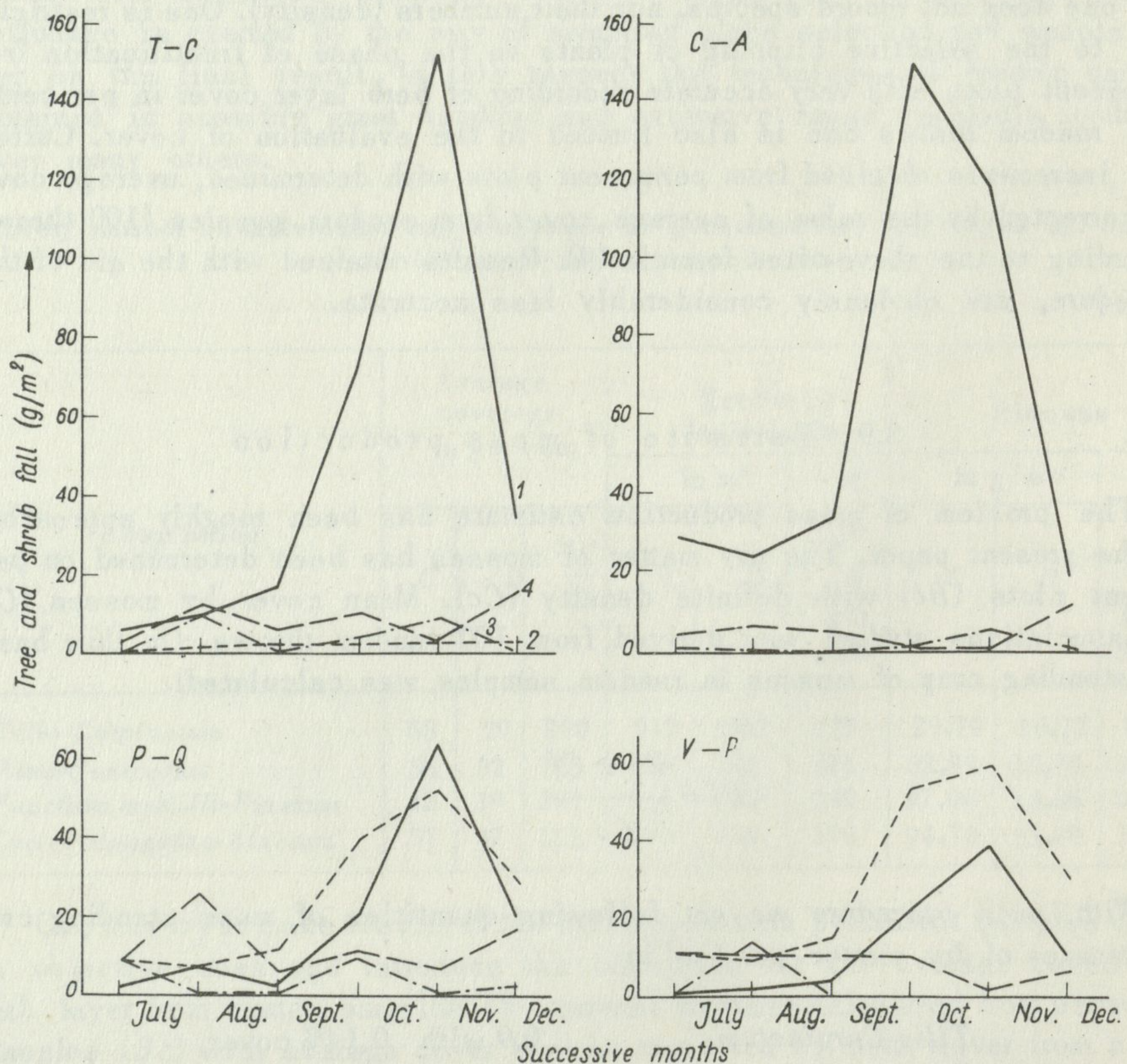


Fig. 2. Tree and shrub fall in *Tilio-Carpinetum* (T-C), *Carici elongatae-Alnetum* (C-A), *Pino-Quercetum* (P-Q), and *Vaccinio myrtilli-Pinetum* (V-P) during summer and autumn 1966

1 — leaves of deciduous trees, 2 — leaves of coniferous trees, 3 — fruits, 4 — plant debris

pare Fig. 2 and 3). The leaf fall in summer is several times smaller when compared with autumnal one. The amount of twig, bark, etc. fall is different. These curves have no distinct peaks. This fall is uniformly distributed throughout a year, and sometimes is higher in summer. The fall of fruits has similar distribution in time.

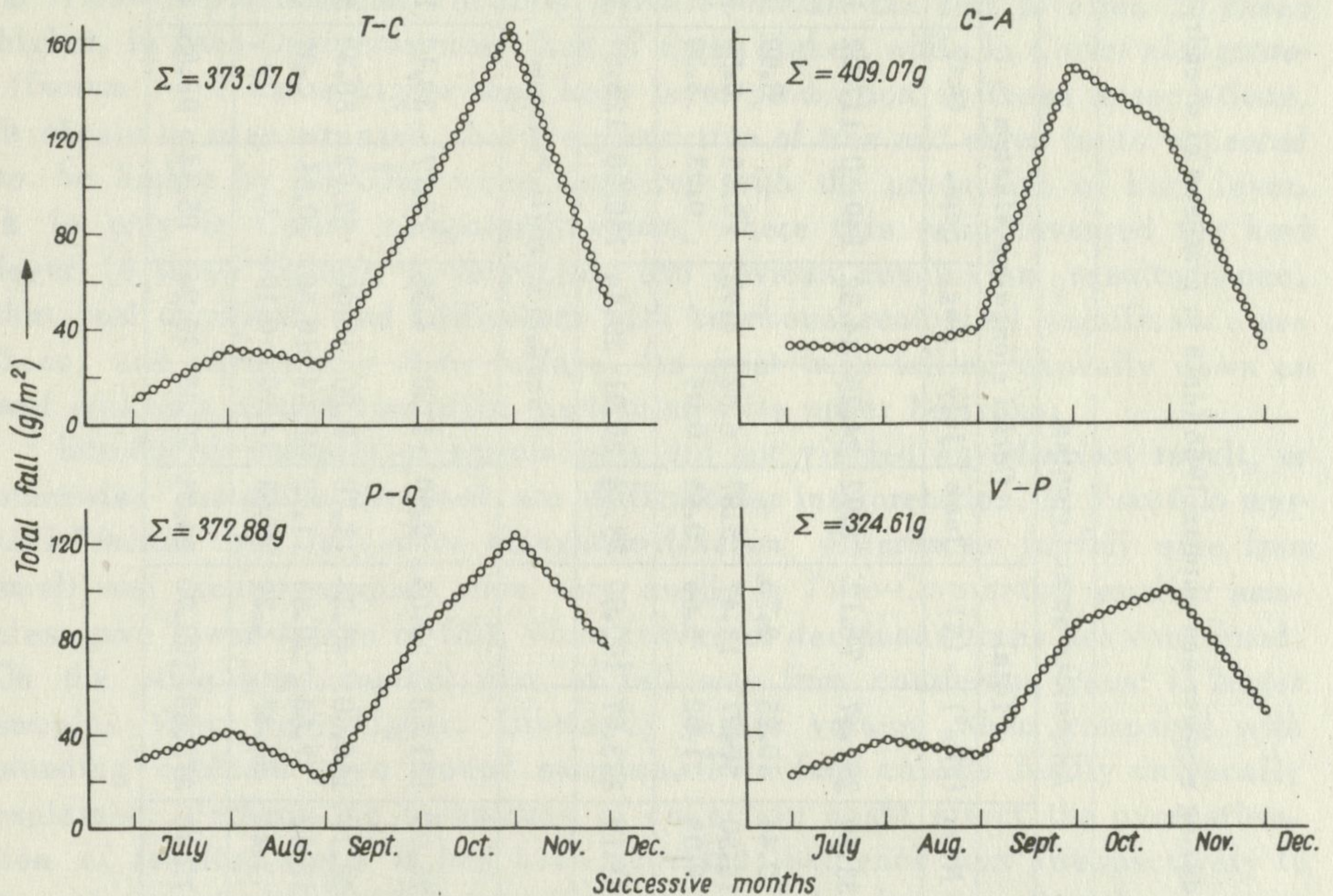


Fig. 3. Total tree and shrub fall in *Tilio-Carpinetum* (T-C), *Carici elongatae-Alnetum* (C-A), *Pino-Quercetum* (P-Q), and *Vaccinio myrtilli-Pinetum* (V-P) during summer and autumn 1966

In the total bulk of fall there dominate leaves, which in deciduous tress in overwhelming majority present the current year biomass, while in conifers — rather the biomass from previous years. The domination of leaves in the total volume of fall is enormous and ranges from 73 to 91%. These fluctuations are related with plant association (Tab. XII). Fruit fall reveals the lowest values. Proportions of deciduous and coniferous foliage in four associations studied present a good illustration of the species composition of stand. In *Carici elongatae-Alnetum* the stand is composed exclusively of deciduous trees, mainly of alder and hence coniferous leaves lack. In *Tilio-Carpinetum* the proportion of coniferous leaves is negligible and amounts to only slightly more than 3% of the total leaf fall. In *Pino-Quercetum* these proportions are almost equal, while in *Vaccinio myrtilli-Pinetum* coniferous leaves are twice as much in the fall (Fig. 2). The fall curve is more spread in *Vaccinio myrtilli-Pinetum*; it does not form any pointed peak. This can be explained by the specific property of pine needles, which have the more uniform fall.

Plant fall from tree and shrub layers in four associations during summer and autumn 1966 (data in grammes of oven-dry weight per 1 m²)

Tab. XII

Kind of fall	Associations and months																	
	<i>Tilio-Carpinetum</i>						Total		<i>Carici elongatae-Alnetum</i>						Total			
	June	July	Aug.	Sept.	Oct.	Nov.	(g/m ²)	(%)	June	July	Aug.	Sept.	Oct.	Nov.	(g/m ²)	(%)		
Leaves of deciduous trees	6.00	10.00	16.92	73.10	152.05	33.40	291.47	78.12	28.92	24.25	34.52	149.50	117.02	19.20	373.41	91.28		
Leaves of coniferous trees	0.57	0.90	0.92	2.87	2.55	2.44	10.25	2.75	—	—	—	—	0.99	—	0.99	0.24		
Plant debris	3.45	12.10	6.60	10.02	2.80	15.30	50.27	13.47	3.87	6.62	4.92	0.55	0.50	11.27	27.73	6.78		
Fruits	0.50	8.90	0.06	3.15	8.42	0.05	21.08	5.66	0.65	0.04	—	0.03	5.30	0.92	6.94	1.70		
Total	10.52	31.90	24.50	89.14	165.82	51.19	373.07	100.00	33.44	30.91	39.44	150.08	123.81	31.39	409.07	100.00		
	<i>Pino-Quercetum</i>									<i>Vaccinio myrtilli-Pinetum</i>								
Leaves of deciduous trees	2.27	7.47	2.77	20.45	63.72	25.05	121.73	32.64	0.90	2.20	4.55	22.77	38.17	10.40	78.99	24.34		
Leaves of coniferous trees	9.35	7.52	11.72	39.37	52.27	29.77	150.00	40.24	11.70	9.80	15.00	52.02	58.32	31.35	178.19	54.89		
Plant debris	8.82	26.37	6.75	11.50	6.92	17.32	77.68	20.83	11.12	10.65	10.50	10.55	2.37	6.72	51.91	15.99		
Fruits	9.03	0.42	0.23	10.35	0.20	3.24	23.47	6.29	0.63	14.70	0.19	—	—	—	15.52	4.78		
Total	29.47	41.78	21.47	81.67	123.11	75.38	372.88	100.00	24.35	37.35	30.24	85.34	98.86	48.47	324.61	100.00		

In *Pino-Quercetum* and in *Tilio-Carpinetum* the fall was almost identical and amounted to some 273 g/m². For the period since June to November it reaches the lowest values in *Vaccinio myrtilli-Pinetum*, since some 225 g/m², while the highest ones in *Carici elongatae-Alnetum* — circa 410 g/m².

The comparison of the fall size with herb layer production is just surprising. In *Tilio-Carpinetum* and *Vaccinio myrtilli-Pinetum* the fall is circa 20 times higher, in *Pino-Quercetum* more than 17 times higher, while in *Carici elongatae-Alnetum* — 7 times higher than herb layer production in these associations. It should be also stressed, that the production of tree and shrub fruits appeared to be higher by 15–30%, when compared with the production of herb layer. It is only in *Carici elongatae-Alnetum*, where this ratio favoured the herb layer (8 times higher). A very clear and obvious conclusion results hence, that real dominants and edificators with enormous ecological significance are trees, and particularly their foliage. Its great bulk falling annually down on soil will form it most distinctly, particularly its upper horizons.

Introduced variants of sample size did not yielded any distinct result, or otherwise questions involved are difficult for interpretation. In *Vaccinio myrtilli-Pinetum* and in *Carici elongatae-Alnetum* differences in fall size from small and greater samples were very small. In *Tilio-Carpinetum* smaller samples gave lower values of fall, when leaves of deciduous trees are concerned. On the other hand another size of fall was from coniferous trees: in larger samples they were higher. Distinctly higher values, when compared with standing catchers gave ground samples. This fact can be hardly univocally explained. Perhaps the techniques of collection might affect the overestimation of results, since it has been accepted that each part irrespectively to its size was included, if it even touched the circle. It seems that the greatest influence on results had the situation of sample in relation to trees. Samples close to trees gave, as a rule, higher values of fall, than those distant from trees.

There arises suggestion for future production studies to take much care and deal much more accurately with the estimation of this part of primary production, which size exceeds at least several times other components of plant production. Relatively very high biomass of fruits also inclines to a better elaboration of procedure of field analysis in this sphere.

3.11. The size of production (compilation)

In the present elaboration we tried to evaluate the size of production of above-ground parts of herbaceous plants and mosses in herbage cover and that of fall from trees and shrubs in four forest associations. Table XIII presents the general comparison of values for the plant production studied. The size of the production is for each association given in g/m² and in kcal/m². The value of fall includes only fruits and leaves as biomass, which

can be considered as the current year production. The bulk of plant remnants, bark, dead twigs, etc. were excluded, since in greater part they do not constitute the biomass produced during the current year. In the lowest column total value of production with total fall is given. In the conversion of dry biomass values into calories there has been accepted the index - 1 g of biomass = 4.35 gcal after Golley (1961), and Wiegert and Evans (1964).

Summary of net production in four associations

Tab. XIII

Kind of production	<i>Carici elongatae- -Alnetum</i>		<i>Tilio-Carpine- -tum</i>		<i>Pino-Querce- -tum</i>		<i>Vaccinio myrtilli-Pinetum</i>	
	g/m ²	kcal/m ²	g/m ²	kcal/m ²	g/m ²	kcal/m ²	g/m ²	kcal/m ²
Leaf and fruit fall	381.34	1.659	322.80	1.404	295.20	1.284	272.70	1.186
Herbs	55.70	0.242	16.72	0.073	16.59	0.072	13.08	0.057
Mosses	0.20	0.001	0.30	0.001	2.70	0.012	16.00	0.069
Total	437.24	1.902	339.82	1.478	314.49	1.368	301.78	1.312
Total value of production together with whole fall	464.97	2.023	390.09	1.697	392.17	1.706	353.69	1.538

It appeared that the highest production of both herb layer and the fall of leaves and fruits from trees and shrubs was found in *Carici elongatae-Alnetum*. It amounts to more than 4,370 kg of dry mass per 1 ha. The lowest value occurred in *Vaccinio myrtilli-Pinetum* - slightly more than 3,000 kg/ha. Reversed relations reveals the production by mosses (Tab. XIII).

I shall not carry out any comparative analysis of results obtained in the present work with those obtained by other authors, since divergencies in production estimate, undoubtedly rather serious, hardly could be explained. We do not know, whether they result from the application of various methods, or from different vegetation relations dependent upon the whole complex of local environmental factors.

I cannot omit, however, the problem of similarity of results between the present and the work carried out on the same area in 1964 (Traczyk and Traczyk 1967). In general, we find a considerable divergence of estimates with the use of similar techniques. With the use of 20 permanent samples (1966) results were very similar to those from 1964 (Tab. XIV). The same situation is found in the case of random samples (in 1966) and the introduction of correction concerning covering to results from 1964, the correction obtained from random throws, from the area of 400 m². Two first techniques included samples with seriously greater covering and density, following two techniques, based on random samples with much lower covering and density, resulted

in considerably lower estimation of production. It results hence that the selection of places for sampling and the number of samples very significantly affects results of production estimate, at any rate to a considerably greater extent than other procedural elements.

Comparison of net production obtained from permanent and random samples during 1964 and 1966 (data in grammes oven-dry weight per 1 m²)

Tab. XIV

Association	Permanent samples		Random samples	
	1964	1966	1964	1966
<i>Tilio-Carpinetum</i>	28.11	29.70	13.59	16.72
<i>Pino-Quercetum</i>	27.03	35.83	17.93	16.59
<i>Vaccinio myrtilli-Pinetum</i>	24.38	27.00	15.44	13.08
<i>Carici elongatae-Alnetum</i>	105.00	94.73	94.59	55.70

4. SUMMARY

1. In the work a considerably modified harvest method was used. It depends on the determination of density and actual increments of individual populations of herb layer. Increments are expressed by the value of the index of average individual growth. This index multiplied by the value of density equals to the production of population.

2. The density plays first class role in the method discussed. Owing to this analysis one can in an objective way get the most reliable illustrations of numbers within all populations occurring in the herb layer.

3. Numbers of individuals are frequently surprising. For example, in the herb layer of *Tilio-Carpinetum* with covering amounting on an average to 29%, and thus relatively poor, there occurred about 4 millions of individuals per 1 ha, while in the rich herb layer not less than 9 millions of individuals. Herb layer in *Vaccinio myrtilli-Pinetum*, with only less than one million of individuals per hectare, appeared to be poorer.

4. Density analysis enables also to obtain data concerning the abundance of shrubs and tree regeneration.

5. Biomass provides one of most important quantitative features. The mere presence of species in definite association does not characterize its ecological significance. It is only the careful analysis of its biomass and density, which evaluates him in ecological aspect. The fact of the occurrence of species with the highest bulk and density in definite association evidences that it is just here, where they find their ecological optima.

6. The total biomass of herb layer divided by total occurrences of individuals enables to calculate the average biomass of individual in subsequent associations. It appeared that the average individual in herb layer of *Tilio-Car-*

pinetum weighs circa 3 times less than an average individual in *Vaccinio myrtilli-Pinetum*, and almost 10 times less than that in *Carici elongatae-Alnetum*.

7. It has been found that only a slight number of species (about 20–25%) comprises the main bulk of herb layer, remaining species form only 1/4 of the plant material in herb layer. Interesting enough that in floristically and in respect to site poor associations (e.g. in *Vaccinio myrtilli-Pinetum molinietosum*) there is marked the extremal quantitative and weight domination of one or only few species. In floristically richer associations the main biomass of herb layer is distributed among the higher number of species. Table VI contains the detailed analysis of herb layer biomasses in associations studied.

8. The ratio between the current year and old biomass is different in relation to association. In the herb layer of *Tilio-Carpinetum* and *Carici elongatae-Alnetum* the previous year biomass does not reach even 4%. On the other hand in *Vaccinio myrtilli-Pinetum* it reaches not less than 60% of the total biomass of herb layer (Tab. X).

9. Most species and in highest numbers flower and fructify in *Pino-Quercetum*. On the area studied this association provides best conditions for the full development of many plants.

10. The production of aerial parts of herb layer, calculated on the basis of an average individual increment and density amounted to:

in association:	kg/ha
<i>Carici elongatae-Alnetum</i>	557.0
<i>Tilio-Carpinetum</i>	167.2
<i>Pino-Quercetum</i>	165.9
<i>Vaccinio myrtilli-Pinetum</i>	130.8

The production of mosses amounts to: 2, 3, 27, and 160 kg/ha, respectively. The production of above-ground parts of herbaceous plants is quite opposite to the size of moss production.

11. The estimate of herb layer production in these same associations with the use of direct analysis of increments from 20 permanent samples appeared to be from 170 to 206% higher (Tab. XI). The reason of this was the fact that permanent samples were taken from places with a higher cover of herb layer and a more abundant species composition (from homogeneous and typical in phytosociological viewpoint places). The comparison of these two estimates proves how serious effect upon final results has the way of sampling place selection and number of samples. It seems, that the method of random samples taken in great numbers and broadly spread, yields satisfactory results.

12. The size of plant fall from trees and shrubs amounted in kilograms of dry matter per 1 hectare to:

in association:

- 4,100 *Carici elongatae-Alnetum*
 3,730 *Tilio-Carpinetum*
 3,720 *Pino-Quercetum*
 3,250 *Vaccinio myrtilli-Pinetum* (compare Tab. XII)

13. The fall from trees and shrubs in *Tilio-Carpinetum* and in *Vaccinio myrtilli-Pinetum* appeared to be about 20 times higher than herb layer production, while in *Pino-Quercetum* – more than 17, and in *Carici elongatae-Alnetum* – 7 times higher. This casts light on the enormous role, which may be played by the litter in forest communities due to its volume.

14. In future the estimation of plant fall, the size of which frequently surpasses by several times other components of plant production, should receive more keen attention.

I appreciate highly the cooperation of H. Traczyk, M. Sc., L. Puszkarska, M. Sc., and U. Plewczyńska, M. Sc. in studies.

REFERENCES

1. Braun-Blanquet, J. 1964 – Pflanzensociologie – Wien, New York, 865 pp.
2. Golley, F. B. 1961 – Energy values of ecological materials – Ecology, 42: 581–584.
3. Lieth, H. (editor), 1962 – Die Stoffproduktion der Pflanzendecke. Vorträge und Diskussionsergebnisse des internationalen ökologischen Symposiums in Stuttgart-Hohenheim vom 4–7 Mai 1960 – Stuttgart, 156 pp.
4. Medwecka-Kornaś, A. 1965 – Zagadnienia botaniczne w Międzynarodowym Programie Biologicznym – Wiad. bot. 9: 3–13.
5. Ovington, I. D. 1962 – Outline of general procedure to determine organic production of woodlands – (mimeographed).
6. Paczowski, J. 1951 – Dzieła wybrane – Warszawa, 392 pp.
7. Petruszewicz, K. 1966 – Niektóre pojęcia w badaniach produktywności wtórnej – Kosmos, A, 15: 581–599.
8. Rajchel, R. 1965 – Net primary productivity of the herb layer in two associations of the Ojców National Park (Southern Poland) – Fragm. Flor. Geobot. 11: 121–150.
9. Sławiński, W. 1950 – Podstawy fitosocjologii. III. – Monografie i Podręczniki UMCS, 1: 275–336.
10. Sočava, V., Lipatova, V., Groškova, A. 1962 – Opyt učeta polnoj produktivnosti nadzemnoj časti travjanogo pokrova – Bot. Ž. 47: 473–484.
11. Szafer, W., Kulczyński, S., Pawłowski, B. 1953 – Rośliny polskie – Warszawa, 1020 pp.
12. Traczyk, H., Traczyk, T. 1965 – Charakterystyka fitosocjologiczna terenów badawczych Instytutu Ekologii PAN w Dziekanowie Leśnym (Puszcza Kampinowska) – Fragm. Flor. Geobot. 11: 547–562.
13. Traczyk, H., Traczyk, T. 1967 – Tentative estimation of the production of herb layer – Ecol. Pol. A, 15: 823–835.

14. Wiegert, R. G., Evans, F. C. 1964 — Primary production and the disappearance of dead vegetation on an old field in Southeastern Michigan — *Ecology*, 45: 49–63.

BADANIA NAD OCENĄ PRODUKCJI RUNA I WIELKOŚCIĄ OPADU ROŚLINNEGO

Streszczenie

W pracy przedstawiono wyniki badań nad oceną produkcji runa oraz wielkością opadu roślinnego w czterech zespołach leśnych Kampinoskiego Parku Narodowego: *Tilio-Carpinetum*, *Pino-Quercetum*, *Vaccinio myrtilli-Pinetum* i *Carici elongatae-Alnetum*.

Zastosowano znacznie zmodyfikowaną metodę żniwną, polegającą na ustaleniu zagęszczenia oraz aktualnych przyrostów poszczególnych populacji runa. Przyrosty populacji wyrażają się wielkością wskaźnika przeciętnego przyrostu osobniczego. Wskaźnik ten, pomnożony przez wartość zagęszczenia, równa się produkcji populacji.

Zagęszczenie odgrywa pierwszorzędną rolę w zastosowanej metodzie. Dzięki tego rodzaju analizie można uzyskać na obiektywnej drodze najwierniejszy obraz liczebności w obrębie wszystkich występujących w runie populacji.

Liczebności osobników okazały się niejednokrotnie zaskakujące. W runie *Tilio-Carpinetum*, przy pokrywaniu wynoszącym średnio 29%, a więc stosunkowo ubogim, wystąpiło na 1 ha około 4 000 000 osobników, a w runie bogatszym aż ponad 9 000 000 osobników. Uboższe były runa boru świeżego, gdzie zanotowano tylko około 1 000 000 osobników lub pędów na 1 ha.

Analiza zagęszczenia pozwoliła również na uzyskanie danych dotyczących obfitości krzewów i podrostu drzew.

Za jedną z najbardziej istotnych cech ilościowych uznano biomasę, gdyż sama obecność gatunku w danym zbiorowisku bardzo mało mówi o jego roli ekologicznej, a dopiero ścisła analiza biomasy i zagęszczenia wartościuje go w aspekcie ekologicznym. Fakt występowania gatunków o największych masach i największym zagęszczeniu w określonym zbiorowisku dowodzi, że w nim właśnie znajdują się ich optima ekologiczne.

Całość biomasy runa podzielona przez sumę wystąpień osobników pozwoliła na obliczenie przeciętnej biomasy osobnika w poszczególnych zbiorowiskach. Okazało się, że przeciętny osobnik w runie grondu waży około 3-krotnie mniej niż przeciętny osobnik w borach, a blisko 10-krotnie mniej niż w olsie.

Stwierdzono, że tylko niewielka liczba gatunków (około 20–25%) stanowi główną masę runa leśnego; pozostałe gatunki tworzą zaledwie 1/4 część masy roślinnej runa. W ubogich florystycznie i siedliskowo zbiorowiskach (np. w borach czernicowych i trzęślicowych) zaznacza się wybitna dominacja ilościowa i wagowa jednego lub zaledwie kilku gatunków. W bogatszych florystycznie środowiskach główna biomasa runa rozkłada się na większą ilość gatunków. Dokładną analizę kształtowania się biomas runa w badanych zespołach zawiera tabela VI.

Stosunek biomasy tegorocznej do biomasy dawnej kształtuje się różnie, zależnie od zbiorowiska. W runie *Tilio-Carpinetum* i *Carici elongatae-Alnetum* zeszłoroczna biomasa nie osiąga nawet 4% a w *Vaccinio myrtilli-Pinetum* aż 60% ogólnej biomasy runa (tab. X).

Stwierdzono, że najwięcej gatunków i w największych ilościach kwitnie i owocuje w *Pino-Quercetum*. Zbiorowisko to stwarza w badanym terenie najlepsze warunki dla pełnego rozwoju wielu roślin.

Produkcja części nadziemnych runa, obliczona na podstawie przeciętnego przyrostu osobniczego oraz gęstości wyniosła:

w zespole:	kg/ha
<i>Carici elongatae-Alnetum</i>	557,0
<i>Tilio-Carpinetum</i>	167,2
<i>Pino-Quercetum</i>	165,9
<i>Vaccinio myrtilli-Pinetum</i>	130,8

Produkcja mchów w poszczególnych zespołach wynosiła odpowiednio: 2, 3, 27 oraz 160 kg/ha. Produkcja części naziemnych roślin zielnych kształtowała się więc wręcz odwrotnie do wielkości produkcji mchów.

Wielkość produkcji runa w tych samych zbiorowiskach, przy zastosowaniu bezpośredniej analizy przyrostów z 20 prób stałych, okazała się od 170 do 206% wyższa (tab. XI). Przyczyna tego tkwi w fakcie pobrania prób stałych z miejsc o większym pokrywaniu runa i bogatszym składzie gatunkowym (z miejsc jednorodnych i typowych w znaczeniu fitosocjologicznym). Porównanie tych dwu ocen dowodzi jak wielki wpływ na wielkość ostatecznych wyników posiada sposób wyboru miejsc do pobierania prób oraz ilość prób. Wydaje się, że metoda prób losowych, pobranych w dużej ilości i z rozległego rozrzutu, daje zadowalające wyniki.

Wielkość opadu roślinnego z drzew i krzewów, badana metodą chwytaczy (koło drucziane obszyte workiem i przymocowane do słupka), kształtowała się w kilogramach suchej masy na 1 hektar:

w zespole:	
<i>Carici elongatae-Alnetum</i>	4 100
<i>Tilio-Carpinetum</i>	3 730
<i>Pino-Quercetum</i>	3 720
<i>Vaccinio myrtilli-Pinetum</i>	3 250 (tab. XII)

Opad z drzew i krzewów w gronzie i w borze okazał się około 20 razy większy niż produkcja runa, w borze mieszanym — ponad 17, a w olesie — 7 razy większy. Rzucą to światło na ogromną rolę, jaką, z uwagi na swoją masę, może odgrywać ściółka w zbiorowiskach leśnych.

Autor sądzi, że w przyszłości należałoby zająć się bardziej wnikliwie oceną opadu roślinnego, którego wielkość przewyższa często kilkanaście razy inne elementy składowe produkcji roślinnej.

AUTHOR'S ADDRESS:
 Dr. Tadeusz Traczyk,
 Institute of Ecology,
 Polish Academy of Sciences,
 Warszawa, ul. Nowy Świat 72,
 Poland.