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Head: Dr. Tadeusz Traczyk

Tadeusz TRACZYK

STUDIES ON THE PRIMARY PRODUCTION
IN MEADOW COMMUNITY*

Results of 2-year studies on the primary production of a meadow (*Stellario-Deschampsietum*) are given. Apart of a brief, phytosociological characteristics, there has been in detail described the procedure, changes of plant standing crops, floristic analysis, statistical variation of samples, the disappearance rate of dead material and several ways of production estimate. It was found that divergencies in production estimates are rather high and depend upon the method of calculation. Difficulties, mostly procedural, connected both with the techniques of material collection and with the utilization of data for production calculations, are stressed. Method of production estimate on the basis of the direct analysis of increase in plant standing crop, is preferred.

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*The work was done within the International Biological Programme in Poland.

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4. Summary

1. DESCRIPTION OF COMMUNITY

Studies have been carried out on Strzeleckie Meadows, in the north-eastern part of Kampinos Forest, close to the Field Station of the Institute of Ecology, Polish Academy of Sciences, near Warsaw. These meadows were not cultivated since nearly ten years. In 1965, owing to author's suggestion, they have been included into the area of strict reserve of the name of Prof. Roman Kobendza (Sieraków reserve). The detailed, phytosociological characteristics of meadow with charting of associations in a scale of 1:2,500 preceded works on the production. Results of phytosociological work have been published separately (Traczyk 1966).

One meadow community from the order *Molinietalia*, related to the association *Stellario-Deschampsietum* Freitag 1957, has been selected for studies. The vegetation of this community is dominated first of all by *Carex fusca*¹, *C. panicea*, *Deschampsia caespitosa*, and *Festuca rubra*. The dense turf of mosses form *Climacium dendroides* and *Aulacomium palustre*.

Soils occupied by *Stellario-Deschampsietum* were classified to peat humus soils (Musierowicz 1958). Below the gray-brown humus horizon, 20 cm deep, there is to be found strongly gleyed medium sand with rusty stains and spots (G_0) and a bluish loose sandy soil (G_r). Gley formation results from seasonal fluctuations in ground water with a table at the depth of 40–80 cm. Rather high water level affects very obviously also the mosaic pattern of meadow sod. Even slight depressions in microrelief flooded with water favour

¹Names of species after Szafer, Kulczyński and Pawłowski (1953).

the development of species from the order of *Caricetalia fuscae*. The spatial variation in vegetation required an adequate selection of sample areas.

2. METHODS

2.1. Analysis of above-ground parts

2.1.1. Selection of stand

Harvest method has been used for studies. It consists in the direct measurement of plant standing crop from strictly determined area and at established interval of time.

Owing to the fact that results of production works are not referred to the whole meadow as a plant formation, but to strictly determined, with the aid of phytosociological methods, association or lower taxonomic unit, meadow stands with complex floristic composition were avoided in the selection of samples. The selection of stand was thus not random in this respect. This concerned also areas within the phytocoenosis of the studied community, where depressions, transition zones, trampled, rooted places, etc. were excluded, and sampling was restricted to stands homogeneous from phytosociological standpoint.

2.1.2. Period of sampling

Field works undertaken during the spring of 1964 have been completed in summer of 1966. In the first year of study there were taken 8 series of samples during the period from May until November, in 1965 – 6 samples, while in the last year – only two (dates of sampling are given in Table I). Thus it included the period of two annual cycles with the duration of 365 days each. These periods do not correspond with calendar years.

2.1.3. Number and size of samples

Twenty sites with the area of circa 20 m² each have been established within the community studied. From each site there were taken, at monthly, sometimes longer, intervals, several samples of various size. In the first year of studies two kinds of samples have been taken: circular ones with the area of 1/6 m² and square ones with the area of 1/10 m². During the next year square plots were excluded in order to avoid edge effect (Van Dyne, Vogel and Fisser 1963) and four circles with the area of: 250, 750, 2,500, and 5,000 cm² were used (the purpose of such arrangement was to find if there occurs any strict correlation between the size of sample and standing crop). These circles were arranged concentrically, smaller inside increasing ones. Clipping of plants has been started with the smallest circle and com-

pleted on the largest one. Standing crop from each sample was collected separately. First two samples with the total area of 1,000 cm² presented the fundamental sample and were segregated (similarly as square samples from 1964), while remaining ones served exclusively for the estimate of general standing crop. Sorted fundamental samples, with the area of 1,000 cm² each, taken at definite time intervals, were called series. Each series consisted altogether of 20 samples including 2 m² of meadow sod.

2.1.4. Techniques of sampling and segregation of material

Whole plant cover was clipped at the soil level with scissors from each sample established with the aid of frame. Fall down parts and dead material from the previous year were carefully collected. The whole biomass was put to igelite bags and placed in refrigerators after transportation to laboratory. The standing crop from fundamental samples (1,000 cm²) was sorted into 3 categories:

- a. green material, which has been segregated into species,
- b. dead material,
- c. mosses (without segregation into dead and green material).

Segregated material was dried in paper bags at the temperature of 85°C during 48 hours and then weighed with the accuracy to the nearest 0.01 g. Analysis carried out with the aid of such techniques gave the possibility of the observation of variation in standing crops in samples from one series and enabled the estimate of the proportions of standing crop of individual species in each sample.

2.1.5. Analysis of growth in mosses

Mosses were collected from each fundamental sample without any analysis of increment. As a result these data concerned the total standing crop of mosses per definite area. In order to determine what a per cent of the total standing crop of mosses constituted the current growth, there were taken additionally 20 circular samples, at monthly intervals from July until September, 1965. The size of sample amounted to 250 cm² (18 cm in diameter). Within each sample we tried to separate the current growth from the remaining standing crop. The current growth could be easily distinguished by its vividly green colour. Moreover, with a skillful, light pulling with pincette they can be separated at their basis from remaining parts of previous years. This concerns at least studied here species of *Climacium dendroides* and *Aulacomium palustre*. From the comparison of current and older growth the coefficient in per cents has been determined. This coefficient allows to estimate the current production of mosses.

2.2. Analysis of underground parts

Most difficulties are involved in the examination of underground parts of meadow plants. The isolation of single individuals in densely compacted

sod is really impossible. The worse is the matter with the separation of current year standing crop of roots from the standing crop of previous years. In this connection until the reliable techniques for the estimation of root production will be prepared, we decided to obtain at least rough data about the growth of roots on the basis of a difference in standing crop from two sample series. One series has been taken at autumn, another one in the full swing of summer of the next year. Each series consisted of 10 soil monoliths with the area of 1,000 cm² (block of 33.3 × 30 cm in area and 30 cm in depth). It appeared that this depth is entirely sufficient, since the overwhelming majority of roots does not reach deeper than 15–20 cm. After the removal of sod, the monolith was cut into small slices and air dried. Afterwards soil was sieved and the root mass impured still with soil was rinsed in water and after cleaning dried until the constant weight.

2.3. Disappearance of plant material

There have been carried out also preliminary experiments on the direct estimate of disappearance rate for plant material, i.e. green and dead material of vascular plants and mosses. Dried to the constant weight material was placed in 10 g portions to plastic bags with 2 mm screen mesh. Each category was represented by 10 bags (altogether 30). These bags were placed on meadow after the removal of vegetation from these spots. At two week intervals (during the late summer and at longer intervals – during autumn) bags were cleaned of plants growing through them in order to prevent the eventual increase in their bulk. These trials were established on October 30, 1964. The first series of samples was taken for analysis with the beginning of September, 1965, i.e. after 10 months, while the other after 14 months. From the decrease in bulk it was concluded about the disappearance rate for individual categories during the given period. Besides of direct measurements of losses in plastic bags there was used also the dead material from 20 fundamental samples in individual series. On the basis of these data there were calculated instantaneous daily rate of disappearance (r_i) according to the formula after Wiegert and Evans (1964):

$$r_i = \frac{\ln (W_0 : W_1)}{t_i - t_0} \quad (1)$$

where: \ln – natural logarithm, W_0 – standing crop of dead material at the time t_0 , W_1 – standing crop of dead material at the time t_1 , t_0 – date of the establishment of experiment of earlier recording, t_1 date of later recording, $t_1 - t_0$ – period of disappearance duration in days.

The techniques of dead material collection differed from the paired-plots design described by above-mentioned authors (Wiegert and Evans 1964).

2.4. Analysis of site conditions

During the study period there were taken also measurements of ground waters, precipitations and temperatures with standard procedure. During years 1965 and 1966 phenological observations were taken.

3. RESULTS

3.1. Standing crops of above-ground parts

3.1.1. Green material

Table I contains the comparison of mean values of dry standing crops expressed in grams per 1 square meter and in per cents. These values concern the green and dead material of vascular plants, mosses, and the total above-ground material. The course of changes in standing crops within distinguished categories during the period of two years illustrates the Figure 1.

Standing crops of green herbs, dead herbs, mosses and total vegetation (expressed in g/dry weight/1 m² and in percentages)

Tab. I

Year	Date	Green herbs		Dead herbs		Mosses		Total (g/m ²)
		(g/m ²)	(%)	(g/m ²)	(%)	(g/m ²)	(%)	
1964	May 16	57.8	7.8	297.2	39.3	401.7	51.1	756.7
	June 2	85.0	10.6	260.9	32.7	452.5	56.7	798.4
	June 17	131.2	15.2	272.6	31.6	457.4	52.2	861.2
	July 3	160.4	20.3	224.5	28.4	405.8	51.3	790.7
	Aug. 4	163.3	24.7	151.5	22.9	345.8	52.4	660.5
	Sept. 2	148.3	19.1	262.0	33.8	365.4	47.1	775.7
	Oct. 1	77.8	11.3	288.9	41.8	323.6	46.9	689.6
	Nov. 3	23.0	4.2	290.0	44.1	334.3	51.7	662.3
Mean		105.8	14.0	225.9	35.0	385.8	51.0	749.4
1965	April 12	26.6	3.5	312.6	41.3	419.4	55.2	758.6
	May 16	52.0	6.9	279.7	37.4	416.6	55.7	748.3
	July 4	162.3	25.7	197.9	31.3	271.8	43.0	632.0
	Aug. 12	193.6	27.1	241.2	33.7	280.2	39.2	715.0
	Sept. 20	129.6	18.0	334.2	46.6	254.4	35.4	718.2
	Dec. 22	59.0	7.8	393.7	51.8	307.3	40.4	760.0
Mean		103.8	15.0	293.2	40.0	324.9	45.0	722.0
1966	April 19	32.6	3.7	394.6	44.9	452.2	51.4	879.4
	May 18	103.3	11.8	358.3	41.1	410.0	47.0	871.6

Changes in standing crop of green biomass give a reliable picture concordant with the development of meadow vegetation in the course of year. Since spring until July there occurs rather rapid increase of green biomass.

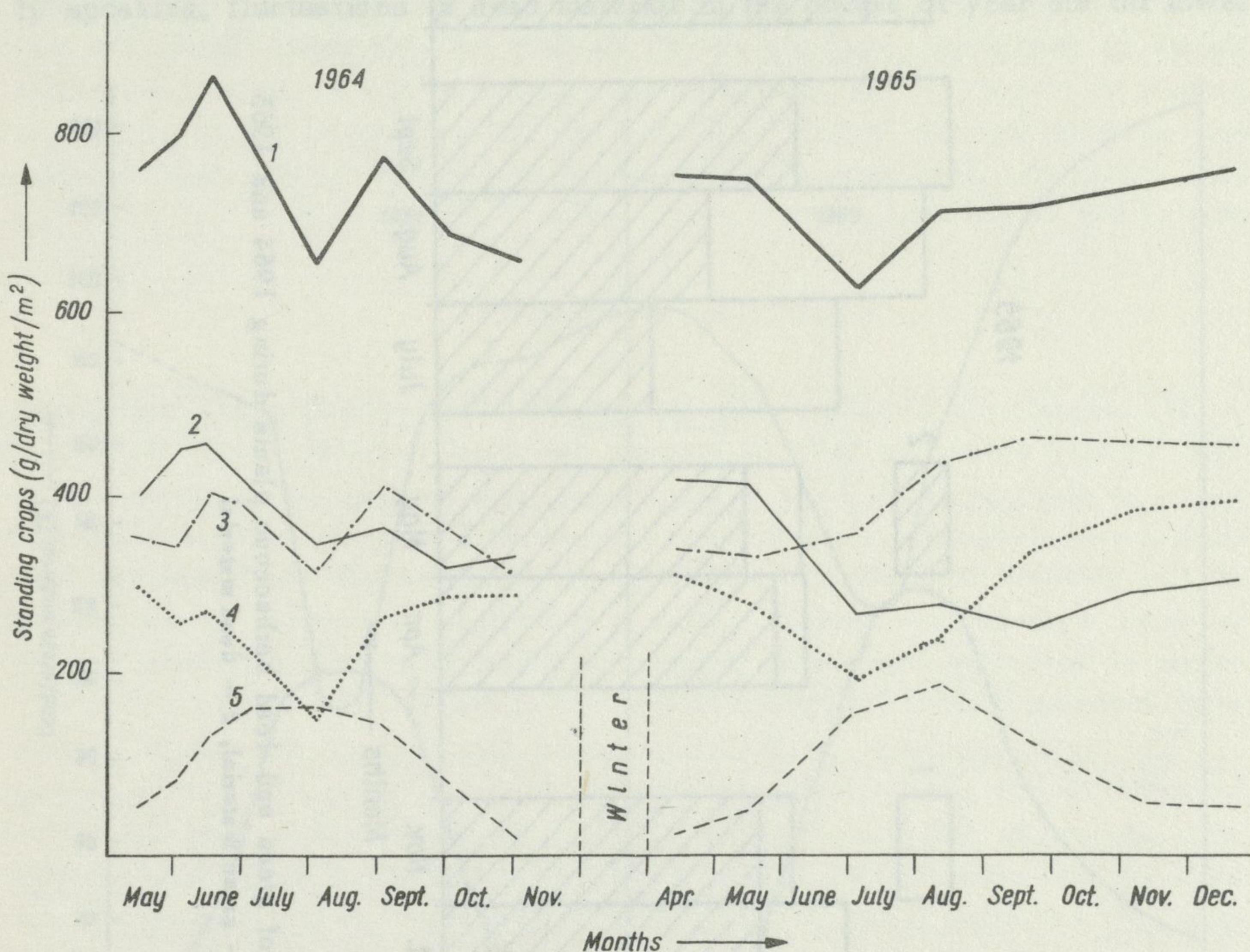


Fig. 1. Ovendry weights of standing crops for green and dead herbs, mosses, and total vegetation during 1964-1965

1 - total, 2 - mosses, 3 - herbs (dead and green material), 4 - dead material. 5 - green material

The peak standing crop occurred at the beginning of August and amounted to 163.3 g/m² in 1964, while to 193.6 g/m² in the next year. Since August until October one can note massy disappearance of plants what is distinctly reflected by the decrease of green biomass and a rapid increase in the dead one. The standing crop of green material during a summer six or even seven times exceeds the minimal standing crop for autumn and winter period. The average contribution of green material of herbaceous plants presents a negligible part of the total standing crop of the meadow vegetation studied. It amounts on the average only to nearly 15% and fluctuates from 3.5 to 27.1%.

3.1.2. Dead material

Dead material has an opposite course than the green one (Fig. 2 and 3). Peak values are noted, of course, during autumn, winter and spring, while

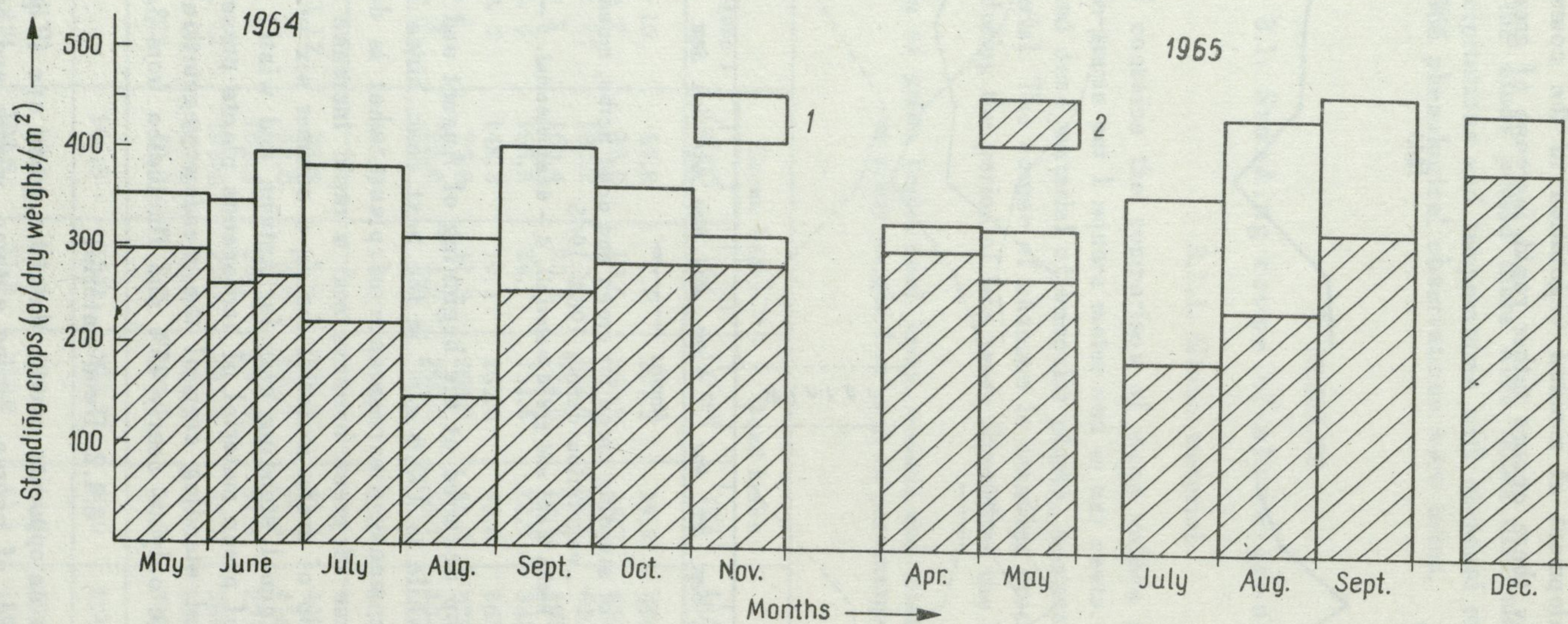


Fig. 2. Changes in standing crops of green and dead herbaceous plants during 1964 and 1965
1 - green material, 2 - dead material

lowest ones – in the full swing of summer. Characteristic drop in dead material, occurring from spring to summer, is caused by rather high rate of its decomposition, with simultaneous complete or only slight dying of green plants. Generally speaking, fluctuations in dead material in the course of year are far lower

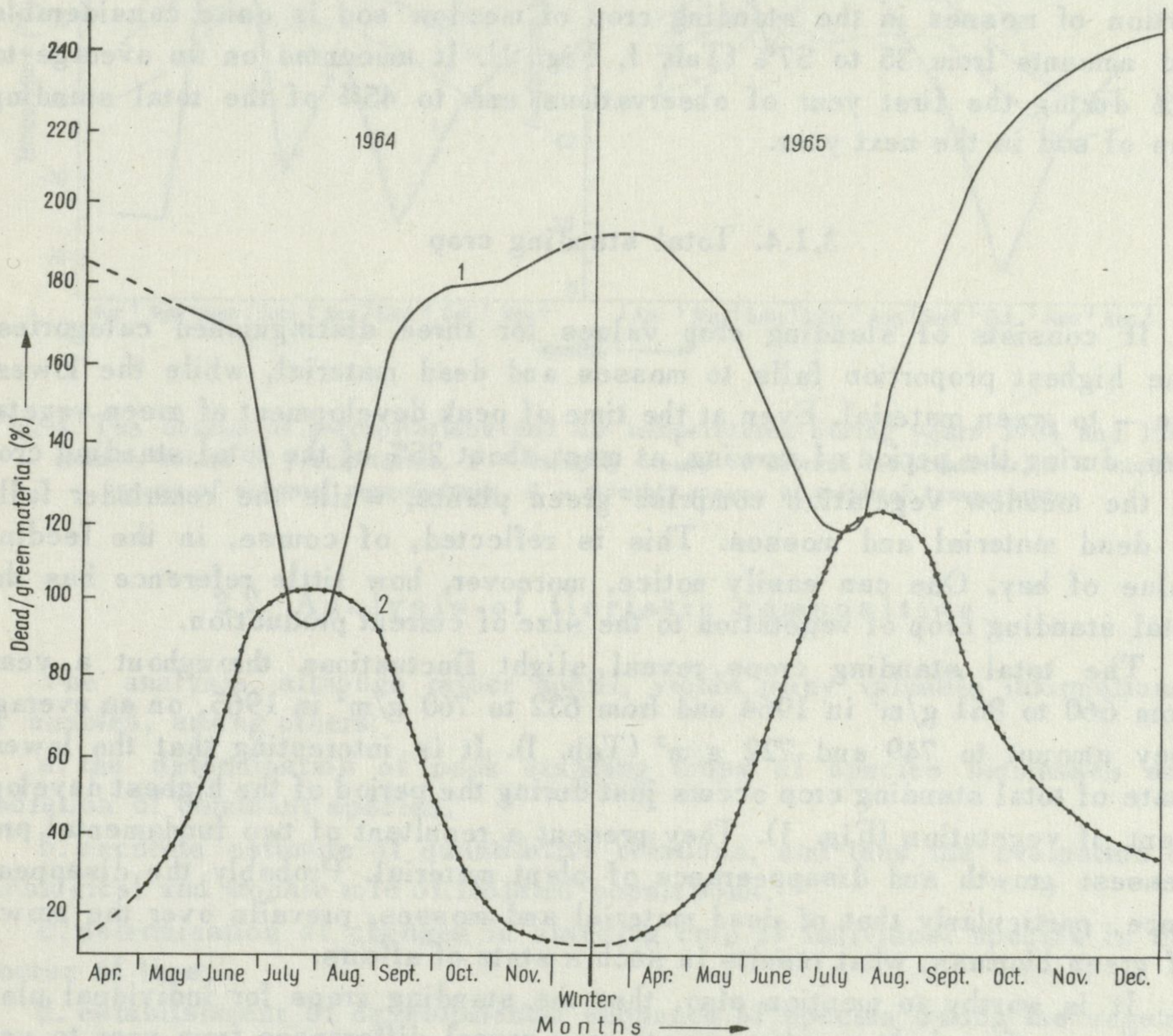


Fig. 3. The ratio between dead and green material
1 – dead material, 2 – green material

than those in green material. The maximal value, occurring in autumn, only twice exceeds the summer minimum. The stock of dead material in the crop of general sod is always rather big and amounts on an average to 35–40%.

3.1.3. Mosses

In the course of two years long observations the same regularity of changes in the standing crop of mosses is repeated. The highest standing crop is recorded during spring and early summer, and followed by a decline. Since July until the end of year the crop is maintained without any serious fluctuations. Spring, peak values prove that during this period there occurs growth

in mosses and a very low decomposition of older parts. During the summer, in spite of the further growth, mosses die-off severely due to drought, what results in the lowering of the total standing crop. During autumn both the growth and dying-off cease almost completely and therefore their average status is maintained until the spring on more or less equal level. The proportion of mosses in the standing crop of meadow sod is quite considerable and amounts from 35 to 57% (Tab. I, Fig. 1). It amounted on an average to 51% during the first year of observations and to 45% of the total standing crop of sod in the next year.

3.1.4. Total standing crop

It consists of standing crop values for three distinguished categories. The highest proportion falls to mosses and dead material, while the lowest one – to green material. Even at the time of peak development of green vegetation, during the period of mowing, at most about 25% of the total standing crop of the meadow vegetation comprise green plants, while the remainder falls to dead material and mosses. This is reflected, of course, in the feeding value of hay. One can easily notice, moreover, how little reference has the total standing crop of vegetation to the size of current production.

The total standing crops reveal slight fluctuations throughout a year: from 660 to 861 g/m² in 1964 and from 632 to 760 g/m² in 1965, on an average they amount to 749 and 722 g/m² (Tab. I). It is interesting that the lowest state of total standing crop occurs just during the period of the highest development of vegetation (Fig. 1). They present a resultant of two fundamental processes: growth and disappearance of plant material. Probably the disappearance, particularly that of dead material and mosses, prevails over the growth of green biomass, what results in such a state of affairs.

It is worthy to mention also, that the standing crops for individual plant groups or the whole meadow growth may reveal differences from year to year (Fig. 1). There can occur an acceleration or delay in the process of production, dying-off and disappearance of plant biomass in the course of years. These differences are probably caused by the variation in site factors, and mostly in climatic ones. Among the complex of ecological factors the most important seem to be precipitations, which jointly with temperature are decisive for the water balance of a meadow. The distribution and amount of precipitation, particularly during spring and summer, when a rapid development of vegetation occurs, may decide to a serious extent about the production of sod during the recorded period. Rather obvious correlation between precipitations and the formation of some standing crops during vegetation seasons results from the comparison of Figure 4 (where values of precipitations and temperatures in 1964 and 1965 are inserted) with the Figure 1 (presenting changes in standing crops of vegetation).

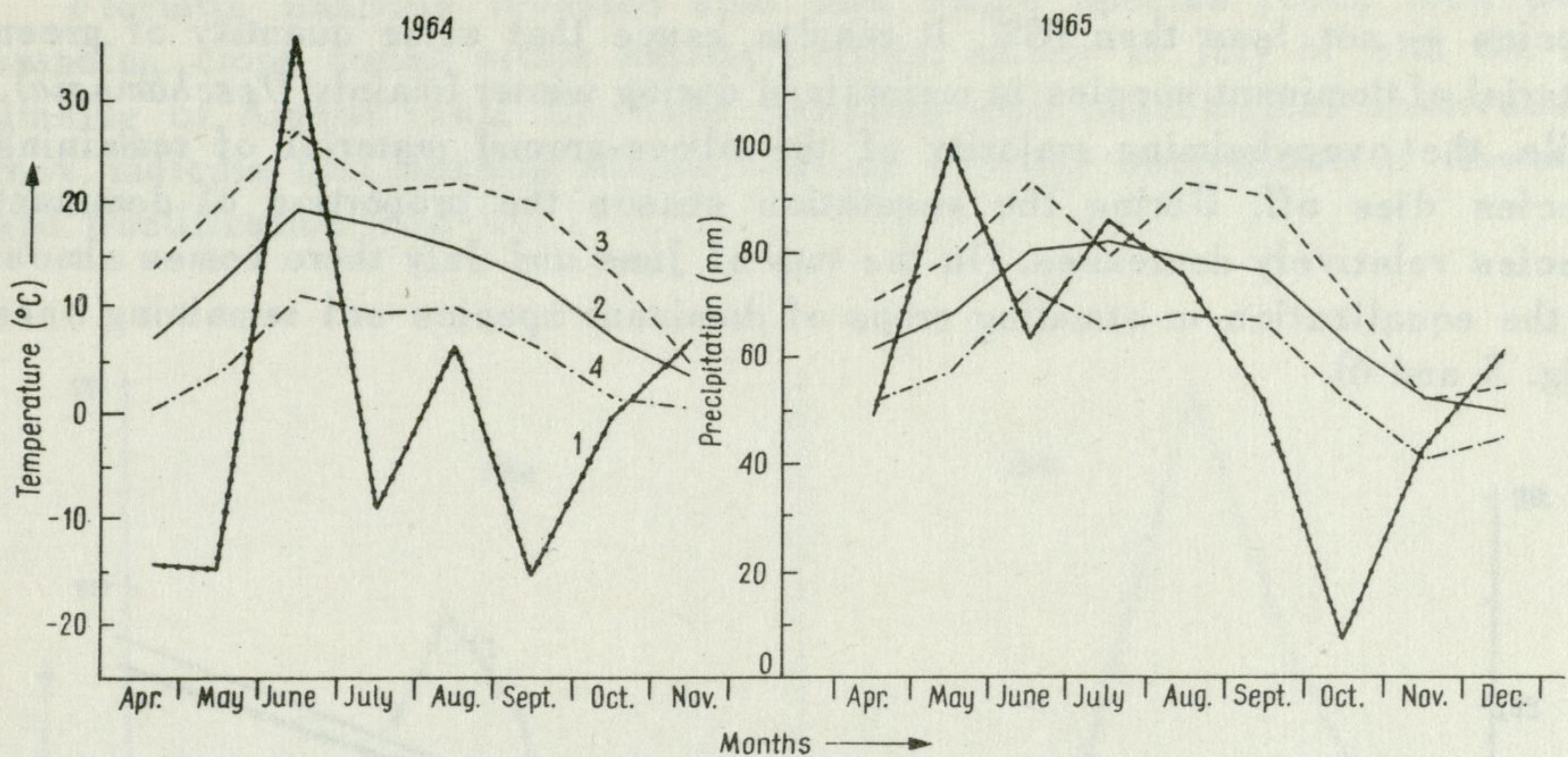


Fig. 4. The course of precipitations and air temperatures during years 1964 and 1965
 1 – monthly totals of precipitation, 2 – monthly means of diurnal temperatures, 3 – monthly means of maximal temperatures, 4 – monthly means of minimal temperatures

3.2. Analysis of floristic composition

The analysis, although rather uphill, yields many valuable informations; it enables, among others:

- a. the determination of peak standing crops of species biomasses and isolation of dominant species,
- b. accurate estimate of quantitative relations, and thus the evaluation of ecological and trophic role of isolated populations,
- c. determination of changes in standing crop of individual species in the course of time,
- d. establishment of developmental sequence of species during the vegetation period as well as the rate of their growth and dying-off,
- e. calculation of net production through totalling of peak standing crops of species biomasses,
- f. evaluation of feeding value of hay,
- g. the determination of the most favourable period for haymaking.

In the studied meadow sod the decided prevalence in numbers have *Carex fusca*, *C. panicea* (treated together in the analysis), *Deschampsia caespitosa* and *Festuca rubra*. Out of the total number of 46 herbaceous species, contributing to the vegetation of the meadow studied, not less than 65% of green material falls on an average to the mentioned four species. It is obvious that the ratio is subjected to alterations throughout a year, what is distinctly illustrated by Figure 5. Beyond the vegetation season there dominate decidedly dominant species. The green material of 42 herbaceous species comprised during winter only to about 17% of the green material, while that of 4 dominant

species — not less than 83%. It results hence that some quantity of green material of dominant species is maintained during winter (mainly *Deschampsia*), while the overwhelming majority of the above-ground material of remaining species dies off. During the vegetation season the proportion of dominant species relatively decreases. On the turn of June and July there comes almost to the equalization in standing crops of dominant species and remaining ones (Fig. 5 and 6).

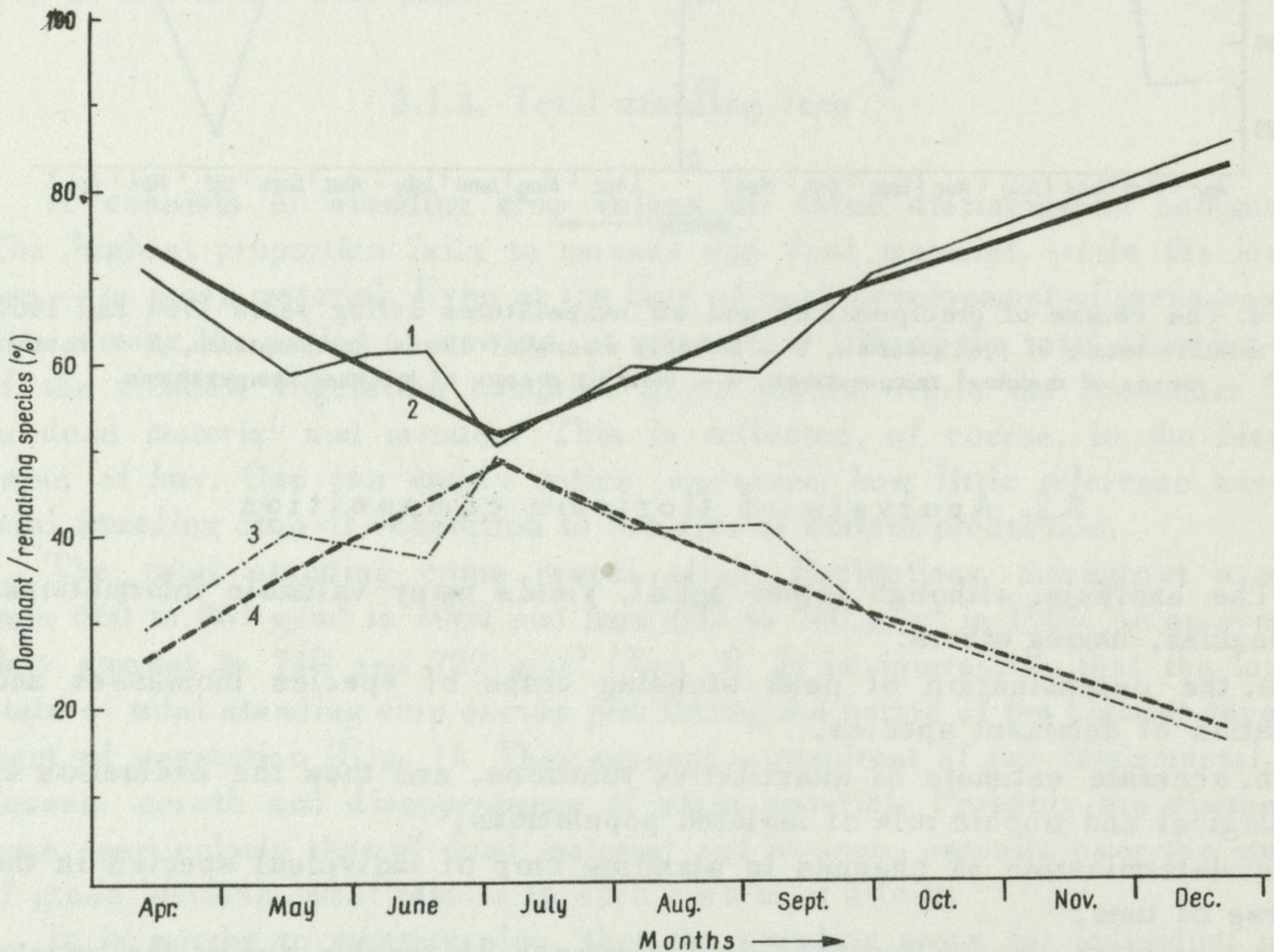


Fig. 5. The ratio between the standing crop of green material for four dominant species: *Carex fusca*, *C. panicea*, *Deschampsia caespitosa*, and *Festuca rubra*, and the standing crop of remaining species from meadow sod during years 1964 and 1965

1, 2 — standing crop of four dominant species: 1 — in 1964, 2 — in 1965; 3, 4 — standing crop of remaining species: 3 — in 1964, 4 — in 1965

It is worthy mentioning that curves of changes in standing crop of species result from changing of standing crops found at the time of sampling. During a year there were only 6 (in 1965) or 8 (in 1964) such dates. Established thus the standing crops are connected into line and the curve of development and dying off for species is constructed. It is worthy to stress, that almost all standing crops for species give curves with single top, which illustrate well the actual development of plants on meadows. This fact also supports the method used here.

Floristic analysis revealed also that single species reach their peak standing crops during rather similar periods, mainly in July or with the beginning of August (Tab. II). When compared with phenological observations they indicate that maximal states coincide with the phenophase of flowering and fructification (Fig. 7).

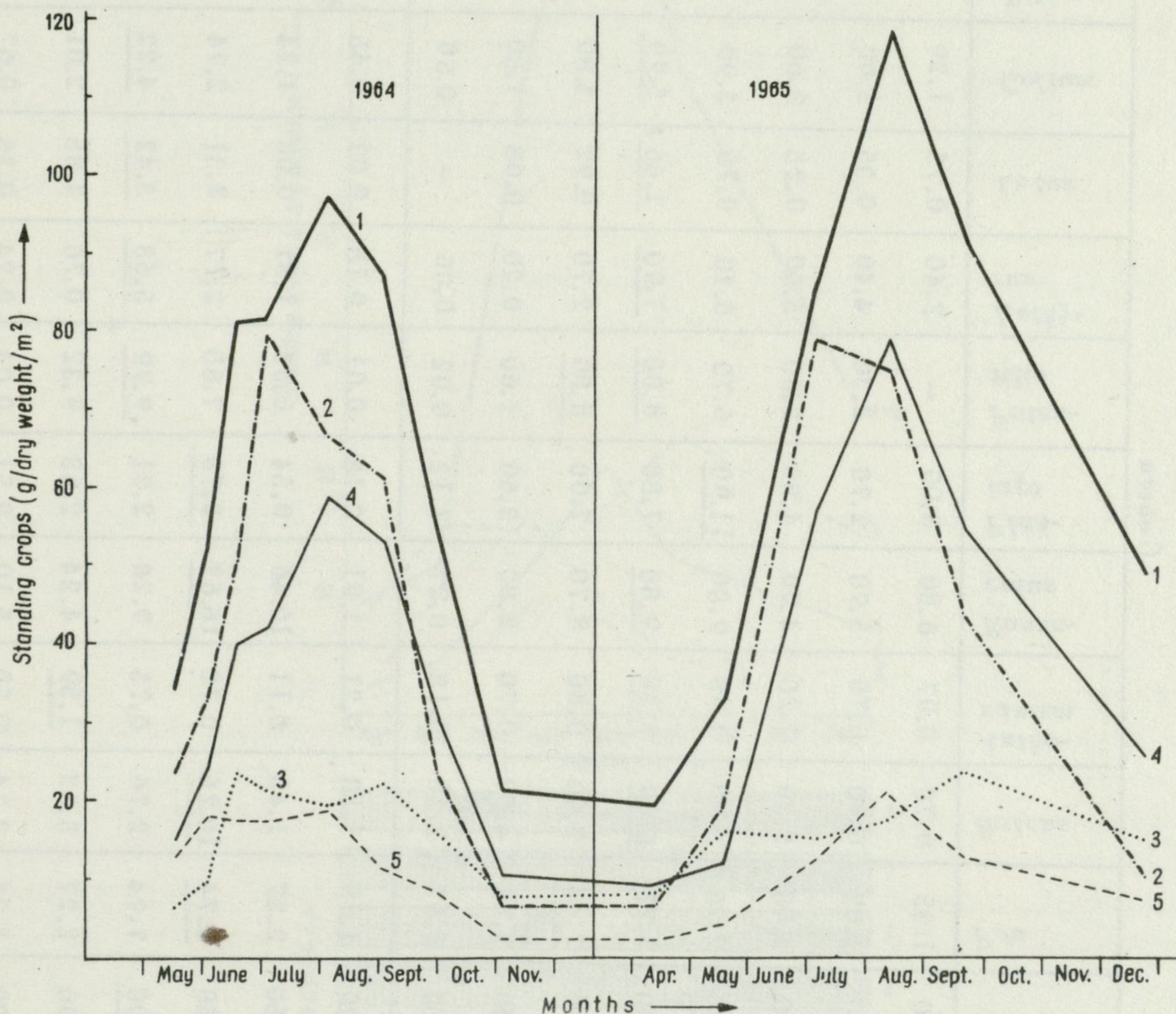


Fig. 6. Standing crops of more important species and groups of species

1 - standing crop of four dominant species (see Fig. 5), 2 - standing crop of remaining species, 3 - standing crop of sedges (*Carex fusca*, *C. panicea*), 4 - standing crop of *Deschampsia caespitosa*, 5 - standing crop of *Festuca rubra*

In spite of fact that the peak standing crop of herbs occurs in the beginning of August, the most favourable period for mowing would be the end of June or beginning of July, when the floristic composition of vegetation is most diversified and the less valuable, when feeding quality is concerned, sedges and *Deschampsia caespitosa* do not reach their peak standing crops (Fig. 5).

Standing crops of the important genera in individual series during 1964 and 1965 (data in g/dry weight/1 m²)

Tab. II

Year	Date	Genera														
		<i>Carex</i>	<i>Deschampsia</i>	<i>Festuca</i>	<i>Poa</i>	<i>Holcus</i>	<i>Anthoxanthum</i>	<i>Ranunculus</i>	<i>Plantago</i>	<i>Potentilla</i>	<i>Lathyrus</i>	<i>Lotus</i>	<i>Galium</i>	<i>Filipendula</i>	<i>Rumex</i>	<i>Ophio-glossum</i>
1964	May 16	15.00	6.20	13.00	1.35	0.70	0.07	6.80	3.00	—	2.40	0.75	1.20	—	2.40	0.70
	June 4	24.30	9.80	18.10	1.02	0.90	0.70	5.90	2.70	2.30	4.40	0.35	3.00	0.53	2.10	0.90
	June 17	40.00	<u>23.30*</u>	17.70	2.08	2.20	1.20	4.90	4.80	3.80	5.60	0.25	3.60	1.09	2.40	1.00
	July 3	42.10	21.40	17.60	2.28	3.60	1.90	9.80	<u>11.90</u>	6.70	5.70	0.70	3.90	0.43	<u>4.30</u>	<u>1.70</u>
	Aug. 4	<u>58.80</u>	19.20	<u>19.00</u>	1.27	<u>6.00</u>	<u>2.30</u>	<u>9.80</u>	7.80	<u>8.80</u>	<u>7.90</u>	<u>1.66</u>	<u>5.90</u>	0.68	4.00	0.80
	Sept. 3	53.40	22.10	11.50	<u>7.44</u>	3.00	0.80	8.70	7.00	<u>8.80</u>	2.70	0.92	3.80	<u>2.60</u>	2.00	1.20
	Oct. 1	30.30	15.90	8.40	2.42	4.60	0.70	2.80	3.60	1.60	0.20	0.08	1.80	0.41	0.20	0.04
	Nov. 4	10.90	7.80	2.50	0.67	2.10	0.18	0.27	1.13	0.02	0.06	—	0.60	—	0.28	—
1965	April 12	9.30	8.20	2.20	1.18	1.13	0.21	1.91	0.18	0.01	0.18	0.03	0.45	—	0.37	—
	May 18	12.40	15.90	4.50	2.37	1.45	0.11	10.46	0.54	0.03	1.51	0.08	1.24	0.76	2.10	0.14
	July 4	56.90	15.20	12.50	<u>8.74</u>	<u>10.26</u>	0.72	<u>16.63</u>	<u>2.78</u>	7.85	2.77	2.31	2.94	<u>4.49</u>	<u>3.36</u>	<u>1.96</u>
	Aug. 12	<u>79.00</u>	17.60	<u>21.00</u>	7.94	2.76	0.75	9.28	2.21	<u>9.99</u>	<u>5.63</u>	<u>3.42</u>	<u>4.22</u>	4.12	1.66	1.14
	Sept. 20	54.70	<u>23.80</u>	12.90	2.27	3.53	<u>1.59</u>	4.24	2.63	9.32	0.76	2.85	2.01	4.49	0.76	0.40
	Dec. 22	25.70	15.20	7.80	3.93	2.34	0.50	5.10	0.51	0.04	0.24	0.35	0.67	0.27	0.67	—

*Numbers underlined denote the maximal biomass of green material of given genus.

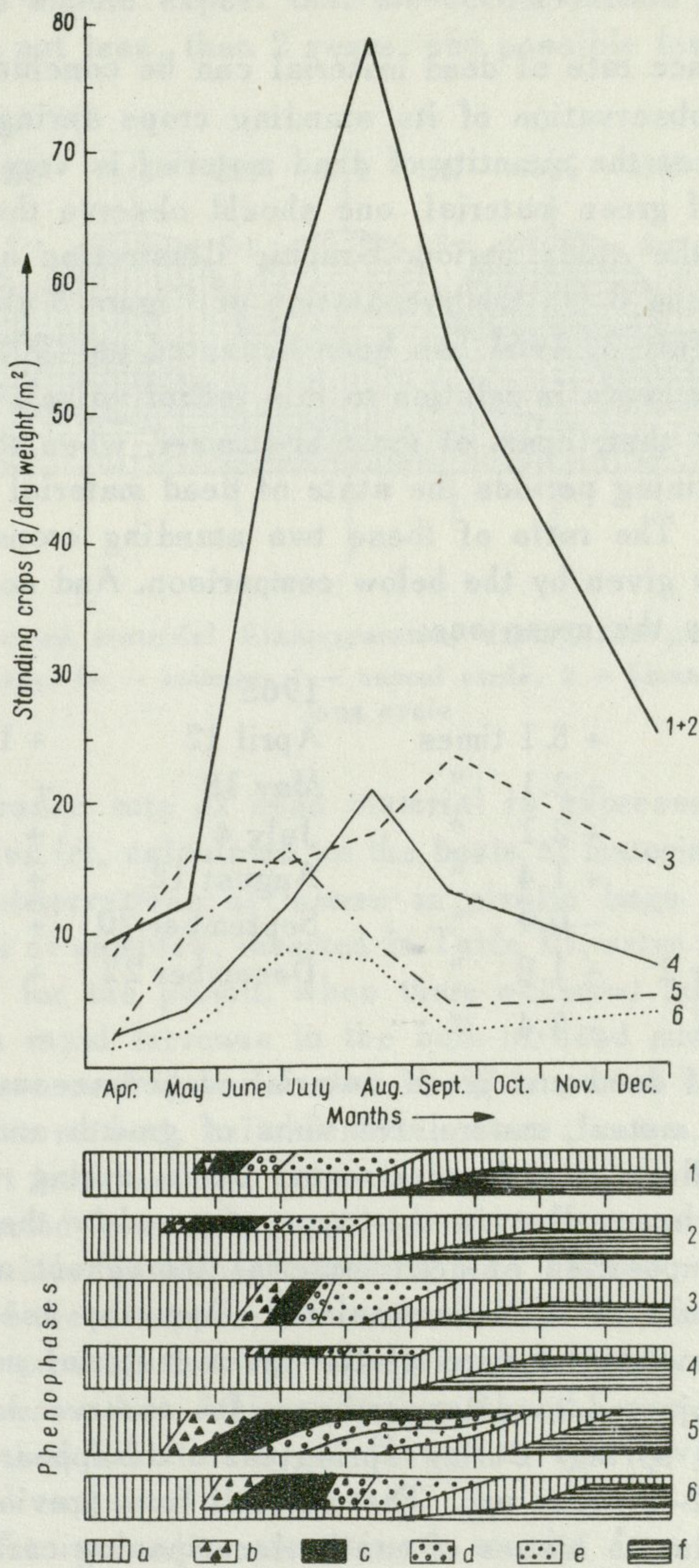


Fig. 7. Changes in standing crops and phenology of more important species from meadow sod in 1965

1 - *Carex fusca*, 2 - *C. panicea*, 3 - *Deschampsia caespitosa*, 4 - *Festuca rubra*, 5 - *Ranunculus acer*, 6 - *Poa pratensis*. Phenophases: a - stage of green leaves, b - flower buds, c - flowering, d - young fruits, e - ripe fruits, f - yellowing of leaves

3.3. Disappearance of dead material

The disappearance rate of dead material can be concluded, apart of direct experiments, from observation of its standing crops during a year within individual series. Since the quantity of dead material is very strictly connected with the quantity of green material, one should observe the formation of both parameters during the study period. Graphic illustration of this relationship present Figures 2 and 3 (in the preparation of Figure 3 the standing crop of green material on July 3, 1964 has been accepted as 100% and other values are presented in per cents in relation to this initial value). From these figures it results obviously that, apart of the mid-summer, when the ratio is more or less equal, in remaining periods the state of dead material decidedly exceeds the green material. The ratio of these two standing crops within individual series is accurately given by the below comparison. And so, the dead material was greater (+) than the green one:

1964		1965	
May 16	+ 5.1 times	April 12	+ 11.7 times
June 2	+ 3.1 "	May 18	+ 5.4 "
June 17	+ 2.1 "	July 4	+ 1.2 "
July 3	+ 1.4 "	August 12	+ 1.2 "
August 4	- 0.9 "	September 20	+ 2.6 "
September 2	+ 1.8 "	December 22	+ 6.7 "
October 1	+ 3.4 "		

Measurements of dead and green material of herbaceous plants rather closely illustrate the mutual, natural relations of growth and disappearance of vegetation, as well as its developmental cycle during vegetation season. One can conclude hence that in this type of meadow there never comes to the complete decomposition of dead material throughout a year, but always rather remarkable part of it is accumulated. One may assume thus, that the current year dead material formed of the green material not used by people, not at once is subjected to disappearance. Its reserve does not decompose during winter until spring. During spring there disappear first of all older parts coming from 2-3 years ago. The material from previous year crop loses its weight mainly due to losses of easily decomposing carbohydrates, organic acids, etc. The overwhelming majority of this material composed of lignin and cellulose undergoes a period of preliminary "maceration" and only in a next year the decay rate is higher, although probably not until the end of year. One can imagine that the cycle of complete decomposition of dead material from its formation until complete disappearance lasts for several years. Before this cycle is completed a new bulk of dead material is laid each year on older ones. Scheme of such three years long cycle is presented on Figure 8. Results of an experiment on the rate of dead material decomposition in screen mesh plastic bags (Tab. IV) also suggest the 3 years or longer cycle of its disappearance. Dead parts of vascular plants after 14 months lost only 48%

of their bulk. One should expect that the decomposition period for remaining mass will last for not less, than 2 years, and possibly longer.

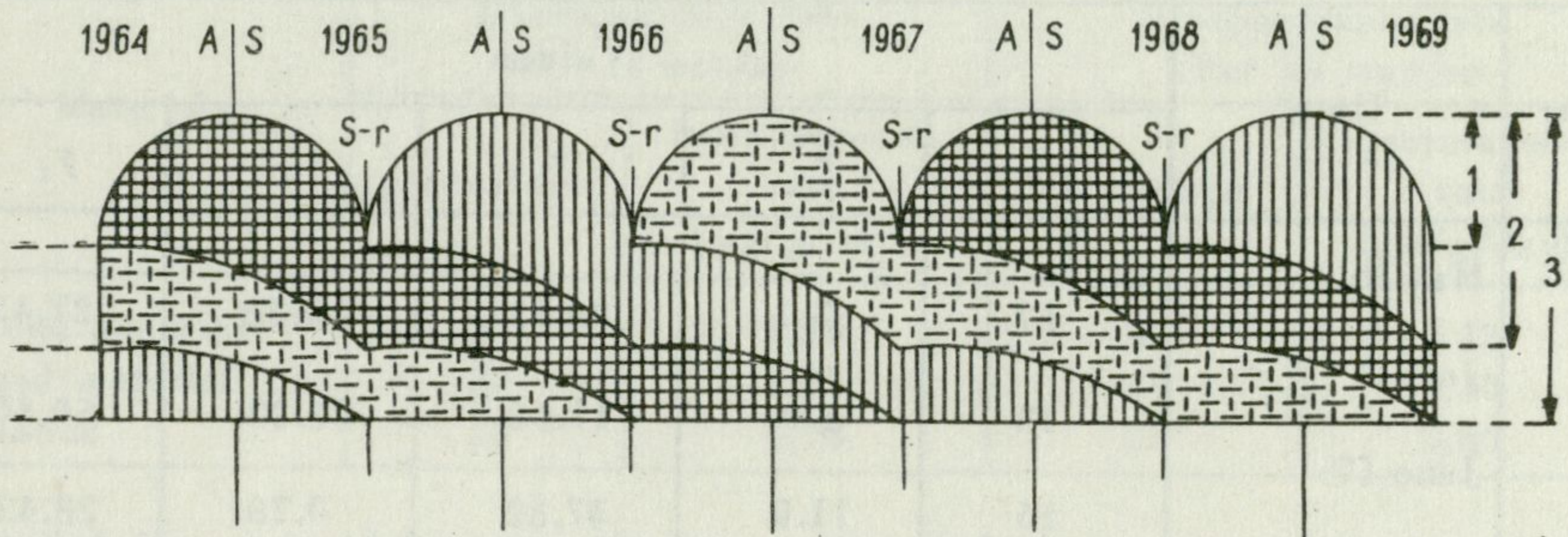


Fig. 8. Scheme of dead material disappearance during the period of several years
A - autumn, S - spring, S-r - summer, 1 - annual cycle, 2 - biannual cycle, 3 - three years long cycle

The disappearance rate of dead material is expressed also by so-called disappearance index (r), calculated on the basis of material from sample series and from direct observations of losses in plastic bags. Results of calculations from a series of samples, inserted in Table III, arise serious reservations, particularly these for the period, when there occurred rapid dying off plants, and due to this a rapid increase in the bulk of dead material (compare rapid growth in the curve on Figures 1 and 3). This period did not yielded, with the use of present method, reliable data, since losses, which occurred undoubtedly, were at least several times lower than increments of dead material. Results for the period from spring until summer, when mortality of green plants was negligible, while decomposition rate was high - seem to be reliable. The comparison of the disappearance rate of dead material from sample series and plastic bags proves, that the disappearance index, on an average, was in the first case more than 4 times higher than the one calculated from data of the second method (plastic bags). Wiegert and Evans (1964) obtained similar results and explained their causes.

There were obtained also approximate results from the experiment with plastic screen mesh bags, aimed at the examination of the disappearance rate of material in three distinguished categories: green material, dead material of vascular plants and mosses (compare Tab. IV). It appeared that green parts of vascular plants are subjected to a more rapid decomposition, than dead ones. Mosses disappear at about twofold slower rate than herbaceous plants. Rather casual dates of sampling precluded the observation of disappearance rate for these biomasses in relation to season. This is why in 1966 long-termed experiments on plant material disappearance rate were established in order to elucidate this problem.

It is worthy to mention also that on reserved meadows, where the plant

Daily disappearance rate, mortality and growth of herbaceous plants (data in g/dry weight/1 m²)*

Tab. III

Year	Date	Values				
		t_i	r_i	x_i	d_i	y_i
1964	May 16	—	—	—	—	—
		17	7.7	36.53	0.23	27.43
	June 2	15	2.9	11.60	23.30	69.50
	June 17	16	11.9	47.32	0.78	28.42
	July 3	32	12.2	73.39	0.39	3.29
	Aug. 4	29	18.9	113.32	223.82	208.82
	Sept. 2	29	3.3	26.33	52.53	-17.97
	Oct. 1	32	0.2	1.74	3.54	-54.26
	Nov. 3	160	0.5	22.51	45.11	0.00
	April 12	35	4.6	49.03	7.13	32.53
	May 16					
Total		365				300.70
1965	April 12	35	—	—	—	—
	May 16	47	7.3	82.05	0.35	110.65
	July 4	38	5.2	43.56	0.23	31.53
	Aug. 12	40	8.0	92.67	185.67	121.67
	Sept. 20	63	0.8	19.05	78.55	7.95
	Dec. 22	116	0.1	4.57	4.48	0.00
	April 19	26	3.7	33.99	2.69	73.39
		May 16				
Total		365				345.19

*Explanations of signs: t_i — a time interval (in days), r_i — instantaneous daily disappearance rate, x_i — amount of dead material disappearing during an interval, d_i — mortality of green material, y_i — growth of above-ground vegetation.

Disappearance rate of green material, dead material and mosses (from mesh bags)

Tab. IV

Materials	Disappearance rate after 10 months		Disappearance rate after 14 months	
	percentage	instantaneous rate (mg/g/day)	percentage	instantaneous rate (mg/g/day)
Green material	32	1.70	56	2.13
Dead material	22	1.25	48	1.40
Mosses	19	0.78	23	0.80

material is not used by man, the expenditure of plant material has a different form, when compared with utilized meadows. When the expenditure of net primary production is splitted into three streams: 1) utilization by man, 2) consumption by herbivores, 3) disappearance on the way of dying off and further decomposition by reducers, on reserved meadows the overwhelming majority of dead material flows to other trophic levels by the third stream, while on utilized meadows – by the first one. This is reflected decidedly by the circulation of organic matter in these two, differently used, communities.

3.4. Sample variation

Plant communities occur in nature in a form of stands (phytocoenoses). Each stand of this heterogeneous plant web is other and never entirely repeated in details.

It is just this spatial variation of phytocoenoses, which enormously complicate studies on primary production. Each plant stand differs from others not only with floristic composition, but first of all with quantitative relations – mass. These facts to a serious extent decide about the reliability of results. One should thus put a question, how great is this variation and whether the material collected with the aid of the method used in the present paper is sufficient and representative.

Recently discussed calculations were based on mean values from 20 basic samples in individual series. Now we have to determine what is the range of sample variation in series in respect to floristic similarity and size of biomasses. For this purpose several statistical methods were employed. The first one consisted in the calculation of the coefficient of floristic similarity. It was calculated according to Jaccard and Steinhaus formula (Sławiński 1950):

$$S = \frac{2c}{a + b} \cdot 100 \quad (2)$$

where: S – coefficient of floristic similarity expressed in per cents, c – number of species common for the compared samples, a – number of species in the first sample, b – number of species in the second sample.

The per cent proportion of similarity classes is presented in Table V, while the graphic illustration of this similarity present Czekanowski's diagram (Fig. 9). The degree of floristic similarity has been calculated only as an example for two series from 1965, for the beginning of vegetation season (April 12) and for the period of peak development of vegetation (August 12). In the summer series there was no single pair of samples, which had identical floristic composition, while in the spring series only 4% of cases revealed the similarity from 90 to 100%. Similarity classes from 60 to 80% were most numerous, while coefficients lower than 50% did not occurred at all. Generally, rather great differences in the floristic composition of compared samples were found.

Coefficient of floristic similarity of samples

Tab. V

Coefficient of similarity in per cent	Frequency of samples in per cent	
	in April	in August
51– 60	14	16
61– 70	33	42
71– 80	32	38
81–100	4	—

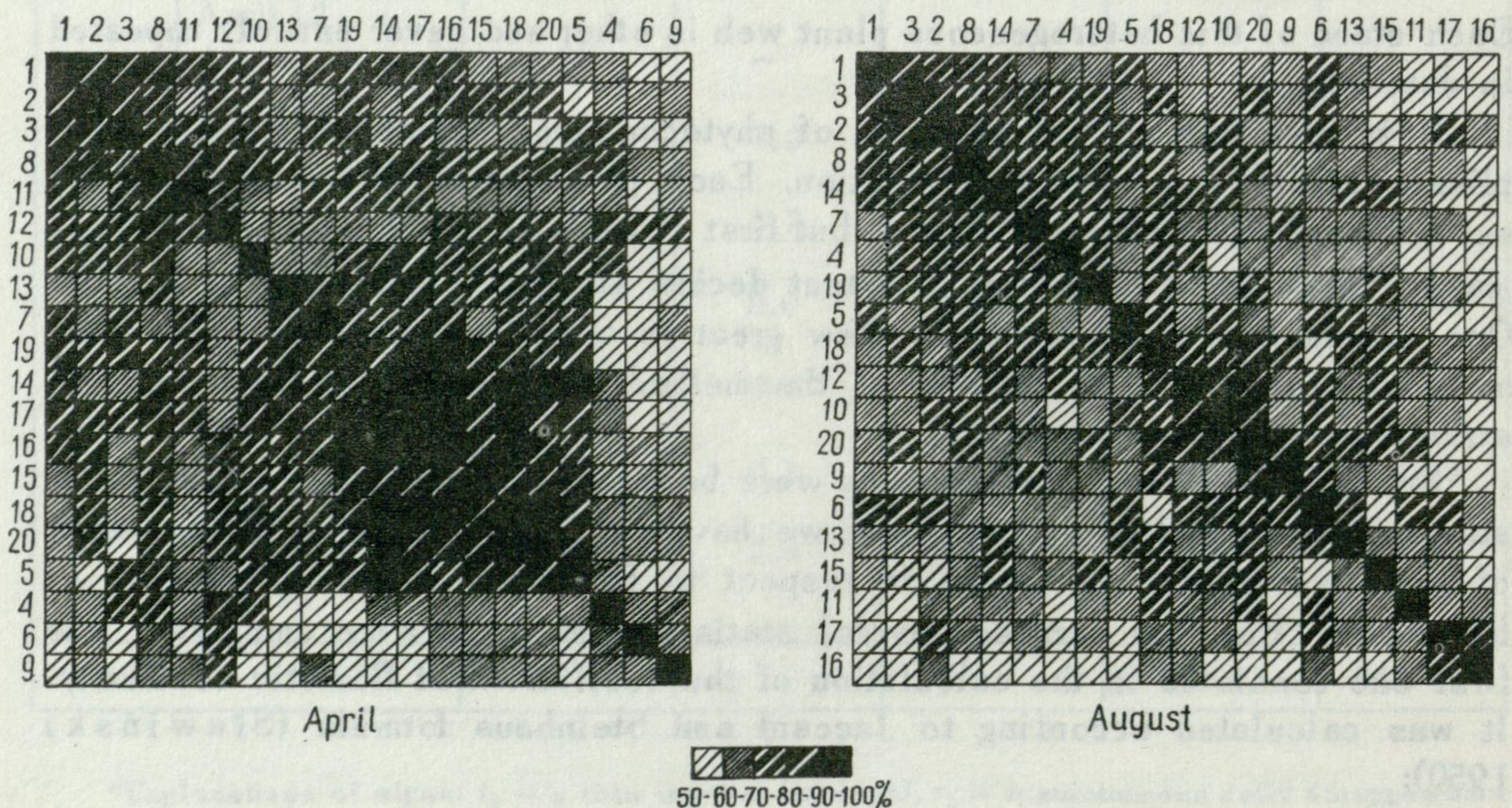


Fig. 9. Table of floristic similarity coefficients in samples in two series, from April and August, 1965 (diagram after Czekanowski)

It appeared also, that the way of spatial distribution of samples does not at all affect their variation, since samples taken in close vicinity did not revealed higher similarities than samples distant from each other by several hundreds of meters and vice versa.

The above analysis concerned only the combination of species, and did not allowed for the quantitative variation in biomasses. Figures 10 and 11

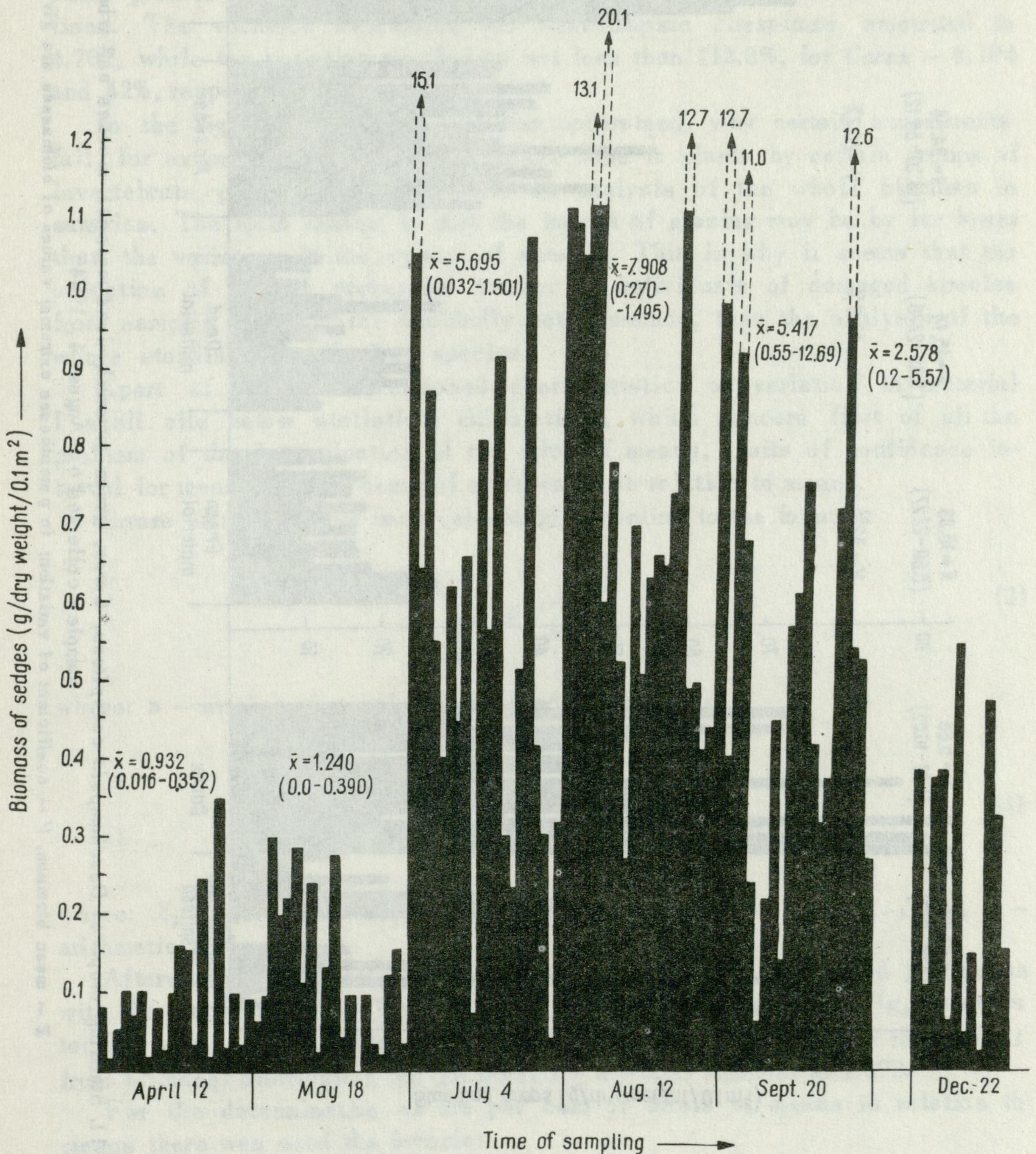


Fig.10. Green biomass of sedges in individual samples in 1965

\bar{x} - mean biomass of sedges from one series; in parentheses extremal values are given

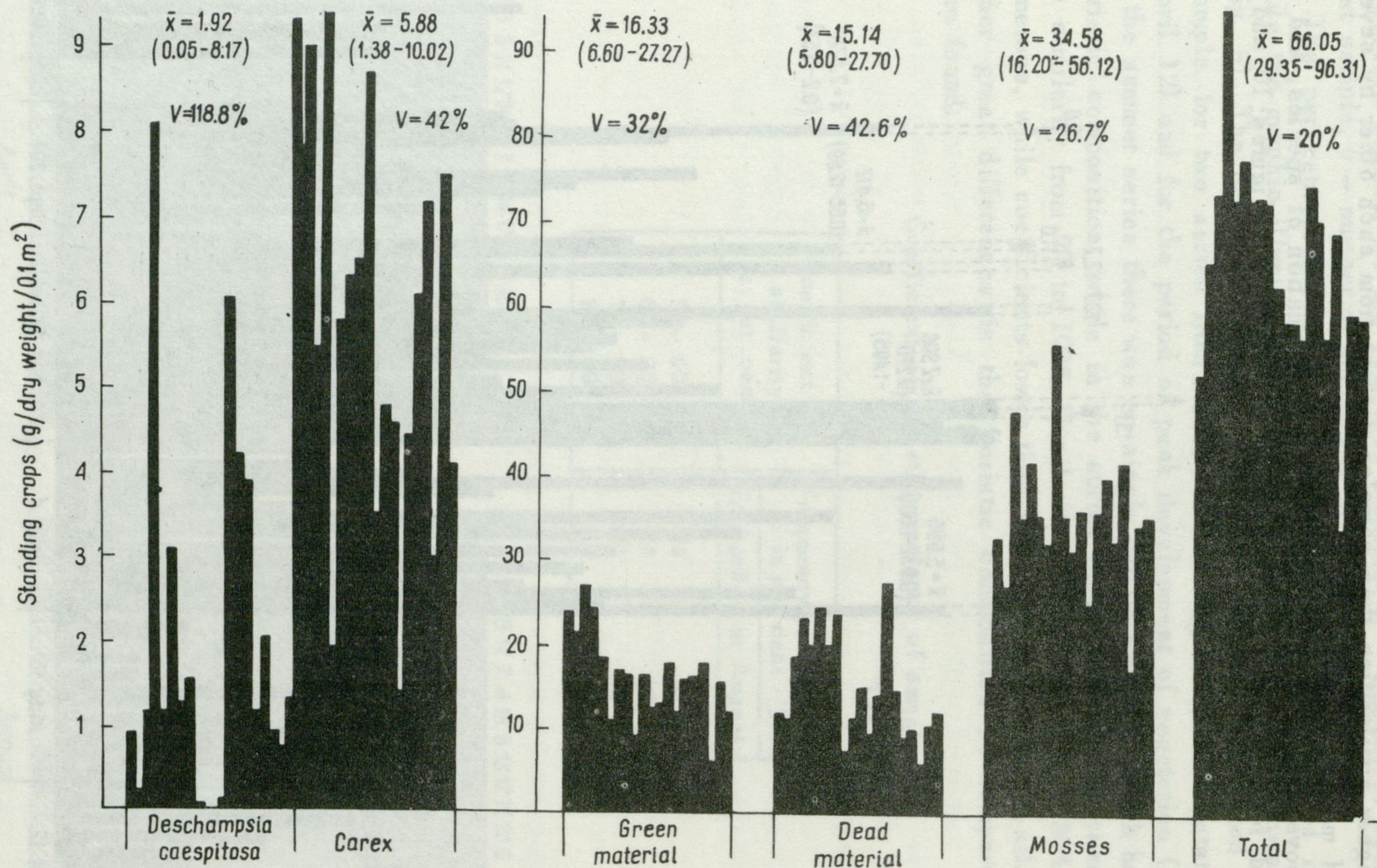


Fig. 11. Standing crops of *Deschampsia caespitosa*, *Carex*, green material, dead material, mosses and whole vegetation in samples collected on August 4, 1964

\bar{x} - mean biomass, V - coefficient of variation; in parentheses extremal values of biomasses are given

well illustrate the above variation. Figure 10 presents the diagram of variation in biomass of sedges (*Carex fusca* and *C. panicea*) in series from 1965, while Figure 11 – the biomass of *Deschampsia caespitosa*, *Carex* and isolated categories (i.e. green and dead material, mosses) in one series of samples from August 4, 1964. It appears that the variation in the biomass of single species in samples is very great, in one sample it may be several times greater than in the other. Isolated plant categories reveal low fluctuations. The variance calculated for *Deschampsia caespitosa* amounted to 4.702, while the variation coefficient not less than 112.8%, for *Carex* – 6.104 and 42%, respectively.

In the light of the above one can understand, why certain experiments fail, for example, the one on the damage done in plants by certain groups of invertebrate phytophages, based on an analysis of the whole biomass in samples. The main reason is that the impact of grazing may be by far lower than the variation in the volume of species. This is why it seems that the selection of strictly prescribed number of individuals of damaged species from samples presents the decidedly better method, than the analysis of the whole standing crop of given species.

Apart of the above-mentioned characteristics of variation in material I shall cite below statistical calculations, which concern first of all the problem of the determination of the error of means, limits of confidence interval for means and per cents of mean errors in relation to means.

Errors of means have been calculated according to the formula:

$$\sigma_{\bar{x}} = \frac{\sigma}{\sqrt{n}} \quad (3)$$

where: n – number of samples, σ – standard deviation:

$$\sqrt{\frac{1}{n} \sum_i^n (X_k - \bar{x})^2} \quad (4)$$

where: X_k – standing crops in individual samples ($k = 1, 2, \dots, 20$), \bar{x} – arithmetic mean.

Afterwards, limits of confidence interval have been calculated for means with the probability $\alpha = 0.95$; it has been found that the upper limit (g_1) amounts to: $\bar{x} + \sigma_{\bar{x}} \cdot t$, while the lower one (g_2) amounts to: $\bar{x} - \sigma_{\bar{x}} \cdot t$, while the value t from t-Student distribution for the level $1 - \alpha = 0.05$ amounts to 2.093.

For the determination of the per cent of errors of means in relation to means there was used the formula:

$$\frac{\sigma_{\bar{x}}}{\bar{x}} \cdot 100 \quad (5)$$

Statistical variation of green and dead material, mosses and total vegetation in 1964 and 1965*

Tab. VI

Year	Date	Green material					Dead material					Mosses					Total				
		\bar{x}	$\sigma_{\bar{x}}$	g_1	g_2	$\frac{\sigma_{\bar{x}}}{\bar{x}} \cdot 100$	\bar{x}	$\sigma_{\bar{x}}$	g_1	g_2	$\frac{\sigma_{\bar{x}}}{\bar{x}} \cdot 100$	\bar{x}	$\sigma_{\bar{x}}$	g_1	g_2	$\frac{\sigma_{\bar{x}}}{\bar{x}} \cdot 100$	\bar{x}	$\sigma_{\bar{x}}$	g_1	g_2	$\frac{\sigma_{\bar{x}}}{\bar{x}} \cdot 100$
1964	May 16	5.78	0.47	6.77	4.78	8.27	29.72	4.91	40.00	19.43	16.54	40.18	1.97	44.31	36.04	4.91	75.67	3.90	83.84	67.51	5.16
	June 2	8.50	0.63	9.82	7.17	7.46	26.09	2.65	31.64	20.53	10.17	45.25	2.74	50.98	39.76	6.05	79.85	3.25	86.66	73.03	4.07
	June 17	13.11	1.00	15.21	11.00	7.65	27.27	1.91	31.26	23.27	7.01	45.74	3.09	52.22	39.25	6.76	86.12	2.96	92.33	79.90	3.45
	July 3	16.04	1.61	19.41	12.66	10.05	22.45	1.93	26.50	18.39	8.64	40.58	3.14	47.15	34.00	7.74	79.07	4.70	88.01	69.22	5.95
	Aug. 4	16.33	1.17	18.78	13.87	7.17	15.15	1.44	18.16	12.13	9.52	34.58	2.06	38.89	30.26	5.96	66.05	2.96	72.24	59.85	4.48
	Sept. 3	14.83	1.09	17.11	12.54	7.36	26.20	1.65	29.65	22.74	6.30	36.54	2.88	42.58	30.49	7.89	77.58	3.64	85.21	69.94	4.69
	Oct. 1	7.78	1.08	10.04	5.51	13.89	28.82	1.26	31.47	26.16	4.39	32.36	2.27	37.11	27.60	7.03	68.97	2.81	74.85	63.08	4.08
	Nov. 4	2.80	0.31	3.45	2.14	11.26	29.00	1.61	32.37	25.62	5.56	34.43	2.79	40.28	28.57	8.12	66.24	3.34	73.23	59.24	5.05
1965	April 12	2.66	0.25	3.17	2.12	9.59	31.26	1.44	34.27	28.24	4.61	41.94	3.07	44.38	35.49	7.34	75.49	2.89	81.55	69.42	3.84
	May 18	5.20	0.40	6.04	4.35	7.72	27.97	1.76	31.65	24.28	6.30	41.66	2.97	47.88	35.43	7.13	75.00	3.38	82.08	67.91	4.51
	July 4	16.23	1.40	19.17	13.23	8.67	19.79	1.39	22.70	16.87	7.05	27.18	2.43	32.26	22.09	8.94	63.37	2.28	68.15	58.58	3.61
	Aug. 12	19.36	1.41	22.31	16.40	7.30	24.12	1.52	27.30	20.93	6.30	28.02	1.24	30.62	25.41	4.43	71.50	2.14	75.98	67.01	2.99
	Sept. 20	12.96	1.25	15.59	10.32	9.71	33.42	2.24	38.11	28.72	6.71	25.44	2.89	31.50	19.37	11.40	72.81	3.59	80.33	65.28	4.93
	Dec. 22	5.90	0.36	6.66	5.13	6.20	39.37	1.12	41.73	37.00	2.86	30.73	1.73	34.36	27.09	5.65	76.01	2.15	80.51	71.50	2.83

*Explanations of signs: \bar{x} - arithmetic mean, $\sigma_{\bar{x}}$ - error of mean, $\frac{\sigma_{\bar{x}}}{\bar{x}} \cdot 100$ - per cent of mean error in relation to mean, $g_1 = \bar{x} + \sigma_{\bar{x}} \cdot t$, $g_2 = \bar{x} - \sigma_{\bar{x}} \cdot t$, $t = 2.093$.

Results of these calculations are presented in Table VI. These data were used for the application of graphic method (compare Łuczak and Wierzbowska 1959). The method consists in the determination of extreme curve in relation to the empirical curve (Fig. 12). On this basis one can conclude,

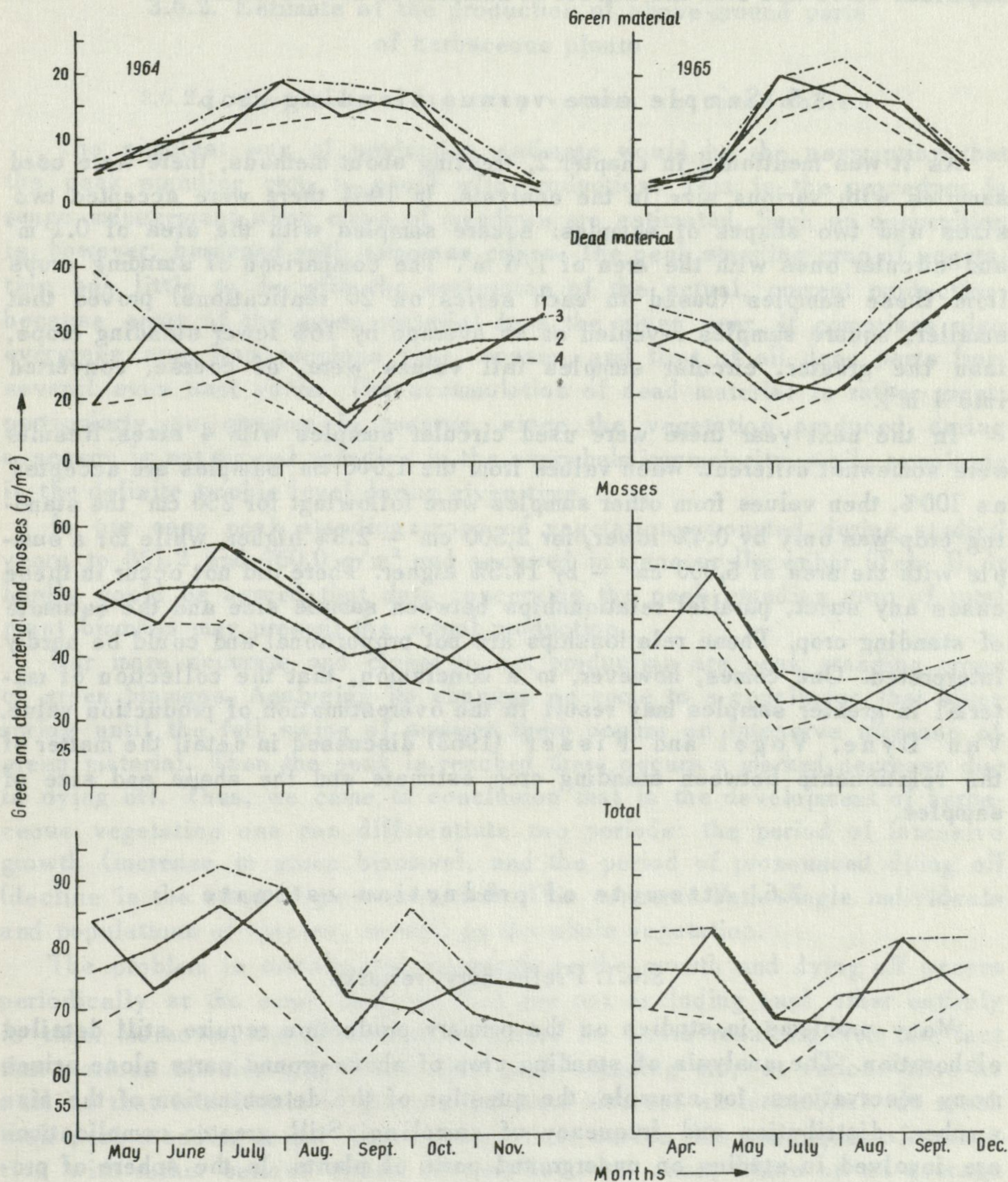


Fig. 12. Quantitative variation of green and dead material, mosses, and total vegetation during years 1964-1965

1 - empirical curve, 2 - extremal curve, 3, 4 - limiting curves

whether the number of samples taken (in our case 20) is sufficient for the comprehension of the actual variation in plant biomass in the meadow studied. It appeared that when the per cent of deviation of mean error from the mean fluctuates from 3 to 10% (calculated for the level of significance = 0.05), then the extreme curve does not differ fundamentally in its course from the empirical curve and thus the number of samples is not too small.

3.5. Sample size versus standing crop

As it was mentioned in chapter 2, treating about methods, there were used samples with various size in the analysis. In 1964 there were accepted two sizes and two shapes of samples: square samples with the area of 0.1 m^2 and circular ones with the area of $1/6 \text{ m}^2$. The comparison of standing crops from these samples (based in each series on 20 replications) proved that smaller, square samples revealed on an average by 16% lower standing crops, than the greater, circular samples (all values were, of course, converted into 1 m^2).

In the next year there were used circular samples with 4 sizes. Results were somewhat different. When values from the $1,000 \text{ cm}^2$ samples are accepted as 100%, then values from other samples were following: for 250 cm^2 the standing crop was only by 0.4% lower, for $2,500 \text{ cm}^2$ – 2.8% higher, while for a sample with the area of $5,000 \text{ cm}^2$ – by 14.5% higher. There did not occur in these cases any strict, parallel relationships between sample size and the estimate of standing crop. These relationships are not proportional and could be hardly interpreted. One comes, however, to a conclusion, that the collection of material in greater samples may result in the overestimation of production value. Van Dyne, Vogel and Fisser (1963) discussed in detail the matter of the relationship between standing crop estimate and the shape and size of samples.

3.6. Attempts of production estimate

3.6.1. Preliminary remarks

Many problems in studies on the primary production require still detailed elaboration. The analysis of standing crop of above-ground parts alone arises many reservations, for example, the question of the determination of the size, number, distribution and frequency of sampling. Still greater complications are involved in studies on underground parts of plants. In the sphere of production estimate there arise similar difficulties. Data cited in previous chapters dealt, as a rule, with standing crops. Sample series taken at definite time intervals enabled the comprehension of changes in these standing crops during a year. On this basis one could obtain the picture of developmental dynamics

for meadow vegetation, evaluate the role of individual species in the standing crop of vegetation, etc. At present we come to the question: what is the ratio between standing crop and production, or how to calculate production on the base of changing standing crops?

3.6.2. Estimate of the production of above-ground parts of herbaceous plants

3.6.2.1. Peak standing crop versus net production

The simplest way of production estimate would be the assumption that the peak standing crop is equal with production. This is the procedure in range management when crops of meadows are estimated. Such an assumption is, however, burdened with numerous errors. The peak standing crop of vegetation has little to do with the estimation of the actual, current production, because apart of the green material from the given year, it comprises also evergreen crop from previous year, mosses, and first of all dead parts from several even past years. The accumulation of dead material is rather great, particularly on meadow in reserve, since the vegetation produced during a season is not mowed and dies in the overwhelming majority, while remaining in the definite trophic level during given time.

In our case peak standing crops of vegetation amounted during studied years to 861.2 and 760.0 g/m² and occurred in June or December (Tab. I). It hardly could be agreed that data concerning the peak standing crop of total plant biomass may present the actual production.

Far more accurate and closer to net production are peak standing crops of green biomass. Analyzing its changes we come to a conclusion that since spring until the full swing of summer there occurs an intensive increase of green material. When the peak is reached there occurs a marked decrease due to dying off. Thus, we came to conclusion that in the development of herbaceous vegetation one can differentiate two periods: the period of intensive growth (increase in green biomass), and the period of pronounced dying off (decline in the state of green material). This concerns both single individuals and populations of species, as well as the whole vegetation.

The problem is complicated inasmuch as the growth and dying off occurs periodically at the same time, as they are not excluding each other entirely in time. Moreover, we do not account also for errors resulting from the fact that various species may reach their peak standing crop at various time as well as that individuals of given population also not simultaneously do reach their peak standing crops. Above reservations burden this techniques of estimation with rather serious errors. In our, however, case, where on an average almost 70% of green material is comprised by few dominant species, one can assume that the maximum of green biomass is conditioned mainly by the peak standing crop of these few species. The more, that maximal states of the

majority of plants coincide almost at the same time with the peak for dominant species (Tab. II). Undoubtedly the estimation of primary production on the basis of the peak standing crop of green biomass is underestimated by values resulting from dying off plants before the peak is reached as also from plant increment following this period. Due to these respects it can be only a rough value when compared with the actual production.

3.6.2.2. Net production versus sum of peak standing crops of individual species

The assumption that the sum of peak standing crops of all species is equal with the production, also arises reservations. Such a hypothesis would be right, if the vegetation studied consists of several species with a low density. There would be possible then to determine peak standing crops for each individual. Actually, in meadow communities and, in general, in nature such an ideal state of studies is impossible. One should restrict oneself, therefore, to the determination of the peak standing crop of the whole population of definite species. In this case we are not sure, however, whether all individuals from given population reached it already, since the development of individuals is not simultaneous. We are satisfied in this case with some average value. The error resulting from such procedure would not be after all great, because population in given environment reaches such state most often in masses. Worse is the fact that we are not sure, whether these peak standing crops are actual in the series, or caused by the spatial variation of vegetation. We should be aware that the distribution of individuals is not uniform, but in clumps, and in this situation a higher density of individuals in few samples of given series is enough to cause that the peak standing crop of definite population falls just to this series. Data obtained in this work generally contradict, however, this possibility. Peak standing crops for the overwhelming majority of species occur only once a year in July or the beginning of August, so they are rather probable and concordant with the natural development of plants (data from Table II and Figures 6 and 7 provide the good illustration for this fact). When we shall add that more than 40% of green biomass falls to two species of sedges, which reach their peak standing crops almost simultaneously with the majority of other species (what was mentioned already), then this manner of estimate seems to be far better than the former one. The summing of peak standing crops of species would give the production of herbaceous plants within limits of 205 g/m² in 1964 (i.e. by 22% higher than the peak standing crop) and 230 g/m² in the following year (25.5% higher than the peak standing crop of green material in 1965).

3.6.2.3. Production versus sum of losses

Knowing the initial and final state of biomass, as well as all losses one can calculate the production (P) according to the formula cited by Petrusiewicz (1967):

$$P = \Delta b + D \quad (6)$$

where: Δb – change of biomass presenting the difference between states of the initial and final biomass, D – sum of losses.

With the use of data presented in Figure 13 one can calculate the production according to the above formula (6) on the basis of losses of both dead and green material. When we put into the formula (6) data concerning the dead material, then the production during the period of 170 days (May 16 – November 3, 1964) and 224 days (April 12 – December 22, 1965) amounts to 164.6 g/m² and 195.8 g/m², respectively. When we put there values concerning the green material, one will obtain production value equal to 175.1 g/m² (in 1964) and to 167.0 g/m² (in 1965).

Standing crops at the beginning and completion of measurements play an important role in these calculations. These values depend to a serious degree upon the date of the beginning and completion of observations and upon rates of dead material decomposition and green material dying off. The method not always gives good results, because it does not allow for losses of dead material during the period of massy dying of green plants, as also losses of plants during their growth. It assumes that the growth and dying off are processes excluding each other in time, what is obviously wrong. In conclusion it is not adequate for our material.

3.6.2.4. Production versus sum of increments in green material

This techniques of estimation has been presented by Wiegert and Evans (1964). It is based on few fundamental parameters: on the knowledge of the disappearance rate of dead material in definite period (or so-called instantaneous daily rate of disappearance (r_i)) as well as on the knowledge of changes in standing crops of living and dead biomasses during the period studied. Using these data one calculates:

- a. amount of dead material disappearing during an interval (x_i),
- b. mortality of green material (d_i).
- c. vegetation growth (y_i).

Wiegert and Evans (1964) describe in detail the way of the calculation of these values and this is why I shall restrict myself to the fundamental statement that the increase in green material for definite period is equal to the difference in green biomass at the end and at the beginning of observations (Δb_i) plus the amount of green matter, which died off (d_i), according to the formula:

$$y_i = \Delta b_i + d_i \quad (7)$$

Through the summation of green material increments (y_i) during individual periods we come to the estimation of net primary production.

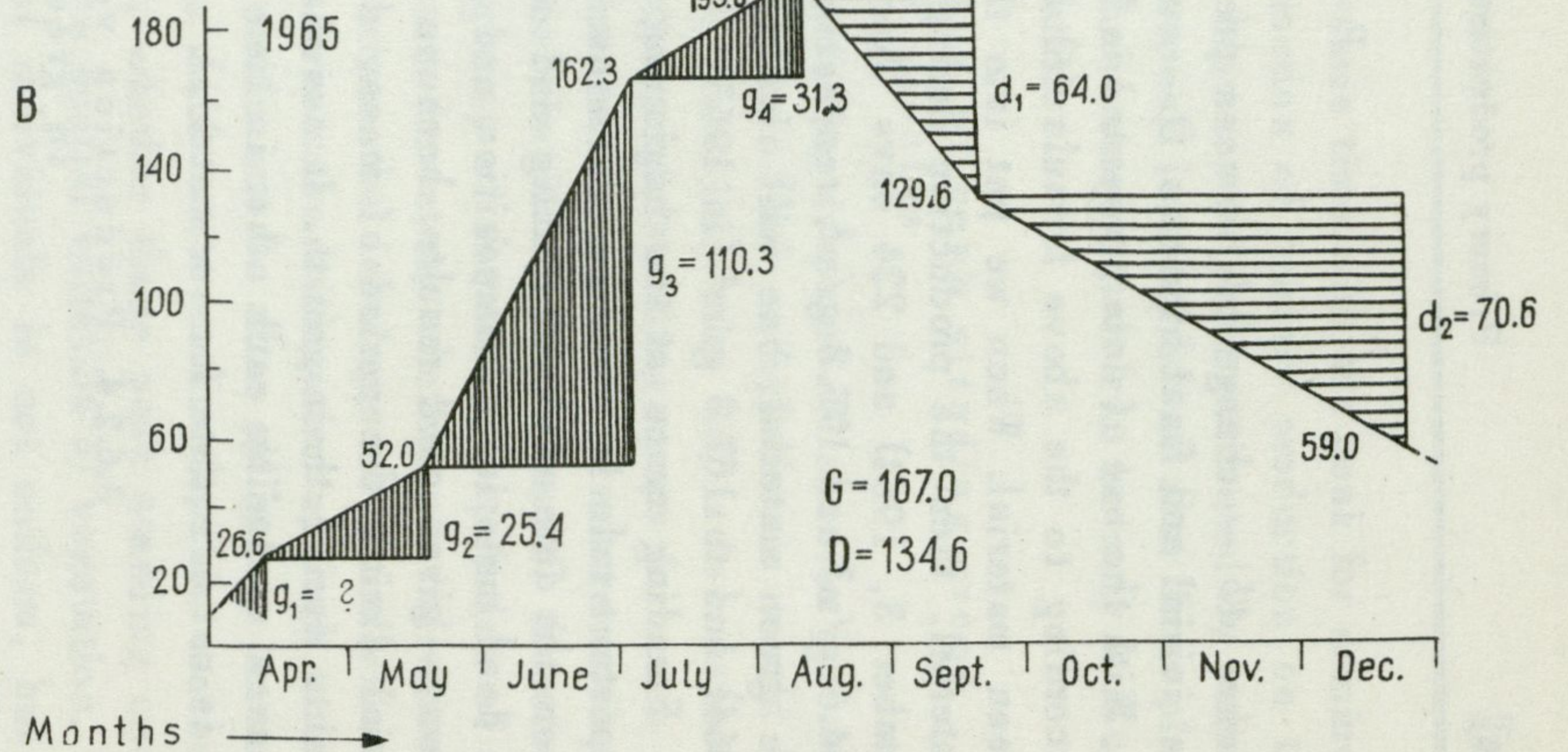
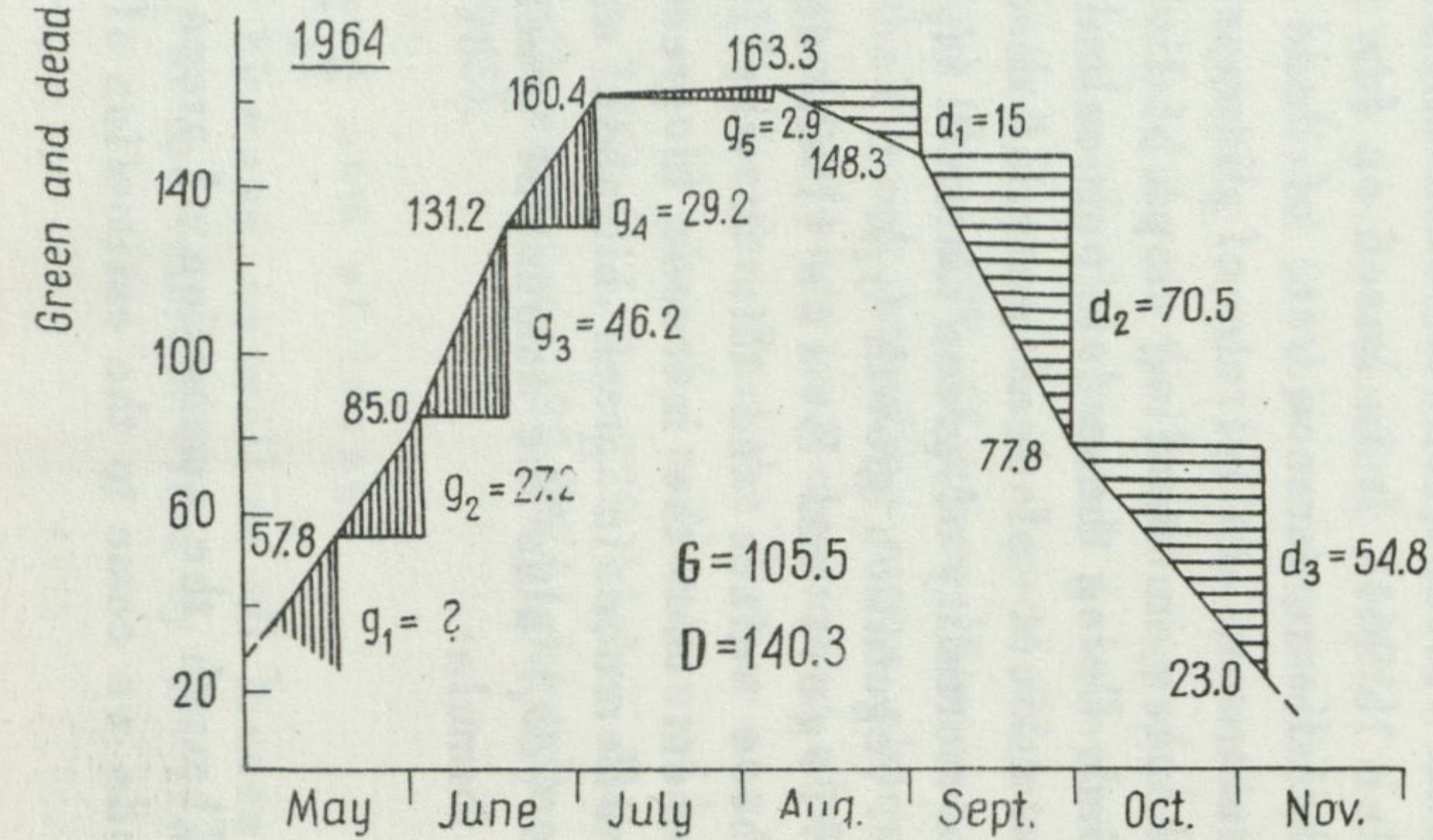
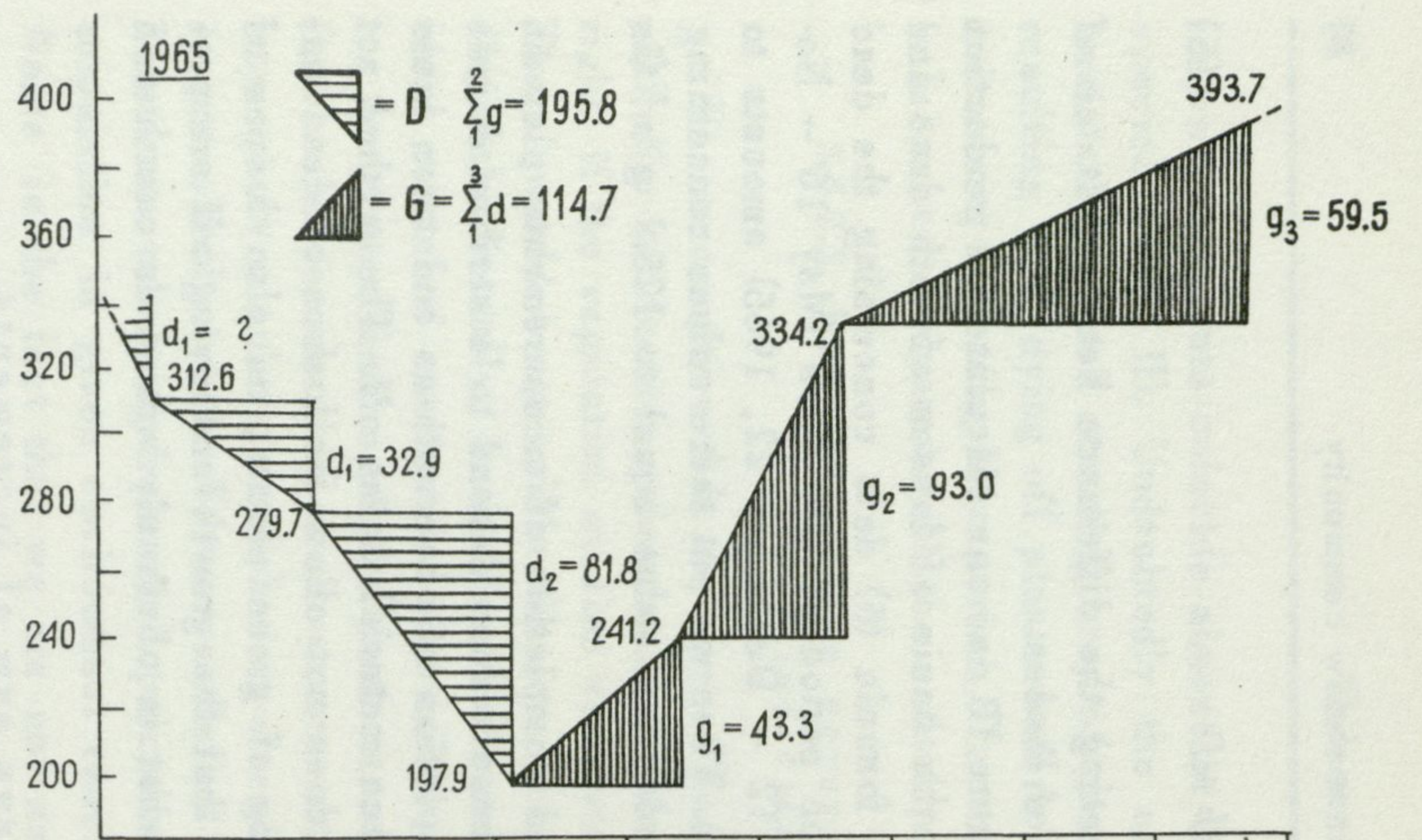
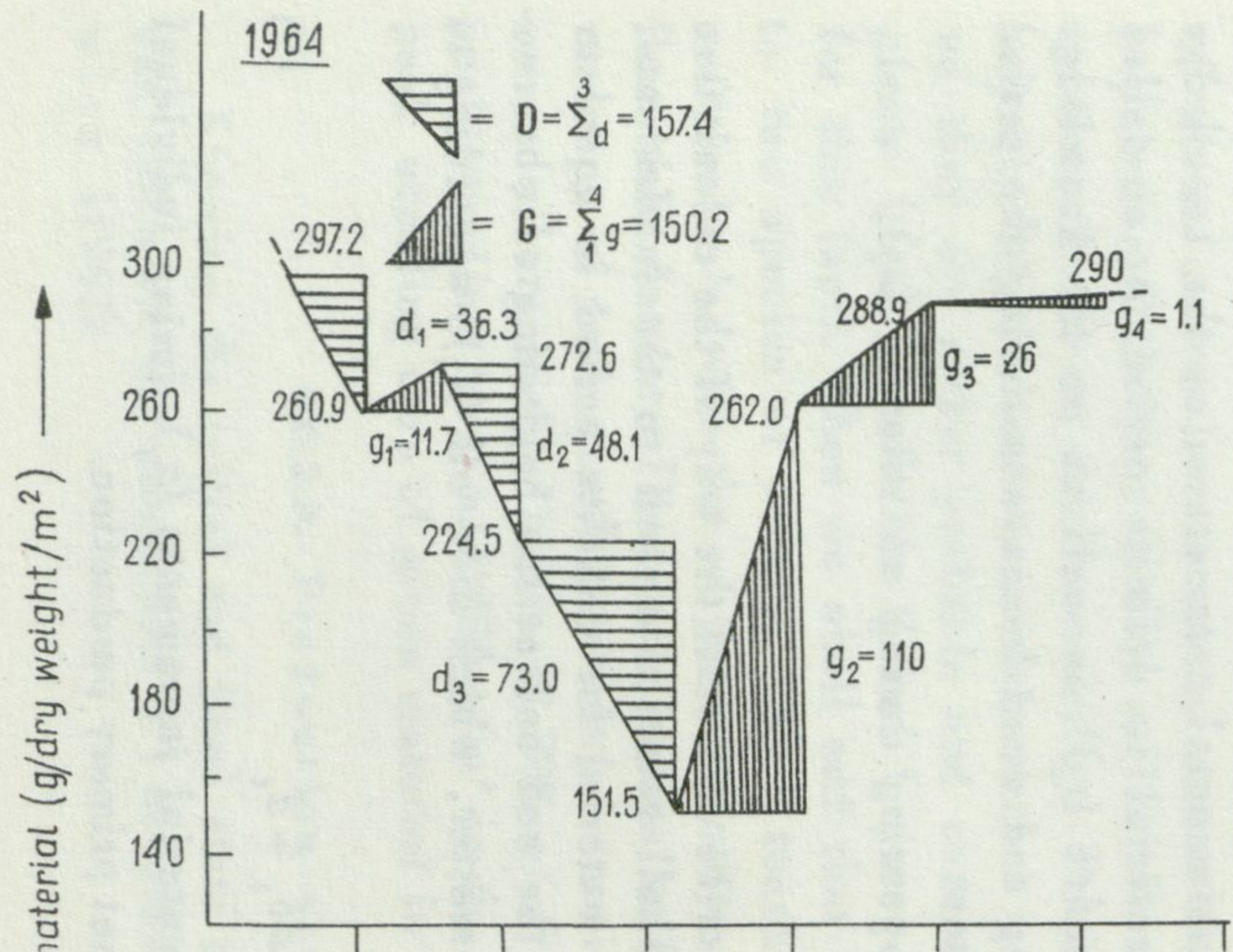


Fig. 13. Increments and losses in dead (A) and green (B) material during years 1964–1965

g – increments, d – losses, G – total increment, D – total loss

Table III presents the production estimate calculated in the above manner for two periods numbering to 365 days each. These periods — as it has been mentioned — are not concordant with calendar years: they began with the beginning of spring and completed at the same time of the following year. The value of production amounted for the first period to 300.70 g/m², for the second one — 345.19 g/m². If the production estimate would be limited to only 170 days in 1964 and 224 days in 1965 (periods of study), then it would amount to slightly less, namely: 268.17 and 304.33 g/m². We can see that also the problem of study period has some bearing in this method. One comes, for, to the question, if observations during vegetation season are sufficient, or production results should be presented for the period of the whole year. If the second alternative is accepted, then we do not know when to start and when to complete the collection of data. It seems that the duration of study should be connected adequately with the developmental cycle of meadow, and not with the beginning and end of calendar year. Studies should be started, then, just before the beginning of vegetation development, i.e. in early spring and completed in the similar season of the following year. Resulting, 365-day period will be well adapted to fundamental, developmental stages of vegetation. Results obtained for this period will reveal a good balance. Data for a calendar year, although concern also the period of 365 days, do not present, however, any natural value, but that delimited by the time of study. Moreover, the beginning and completion of work during winter is purposeless and just impossible.

In the course of analysis of green matter increment values (y_i) during two years (Tab. III and Fig. 14) one can easily note that the highest increment in standing crop occurs during the period from August until September. In the first period it amounted to 208.32 g/m² and thus it was more than 5 times greater than the increment in June, and nearly 70 times greater than that in July, what is an obvious nonsense. During the another period these relations were markedly lower. These values to a serious extent increased the general result of production. Because, according to the formula (7) the increment consists of not only the increment of green matter, but also its mortality (d_i) and disappearance rate (r_i), hence large changes in standing crops of both living and dead material very seriously affect the estimation of production size. The enormous increase in dead material from August to December visible in Figure 13 was most probably a result of sample heterogeneity, and not of the value concordant with the natural development of vegetation. This is supported by the comparison (for this period) of green material losses and dead material increment (Fig. 14) as well as by the analysis of standing crops from individual samples from this period. In the series from August 4 there were found not less than five samples with dead material amounting to less than 100 g/m², while seven below 150 g/m². The highest dead material amounted to only 272 g/m². The average dead material in this series was equal to only 151.5 g/m². In another series from September 2 there was found no one sample

below 150 g/m^2 , while seven of them had the size above 300 g/m^2 , hence the mean $- 262 \text{ g/m}^2$ and an enormous change of dead material states amounting

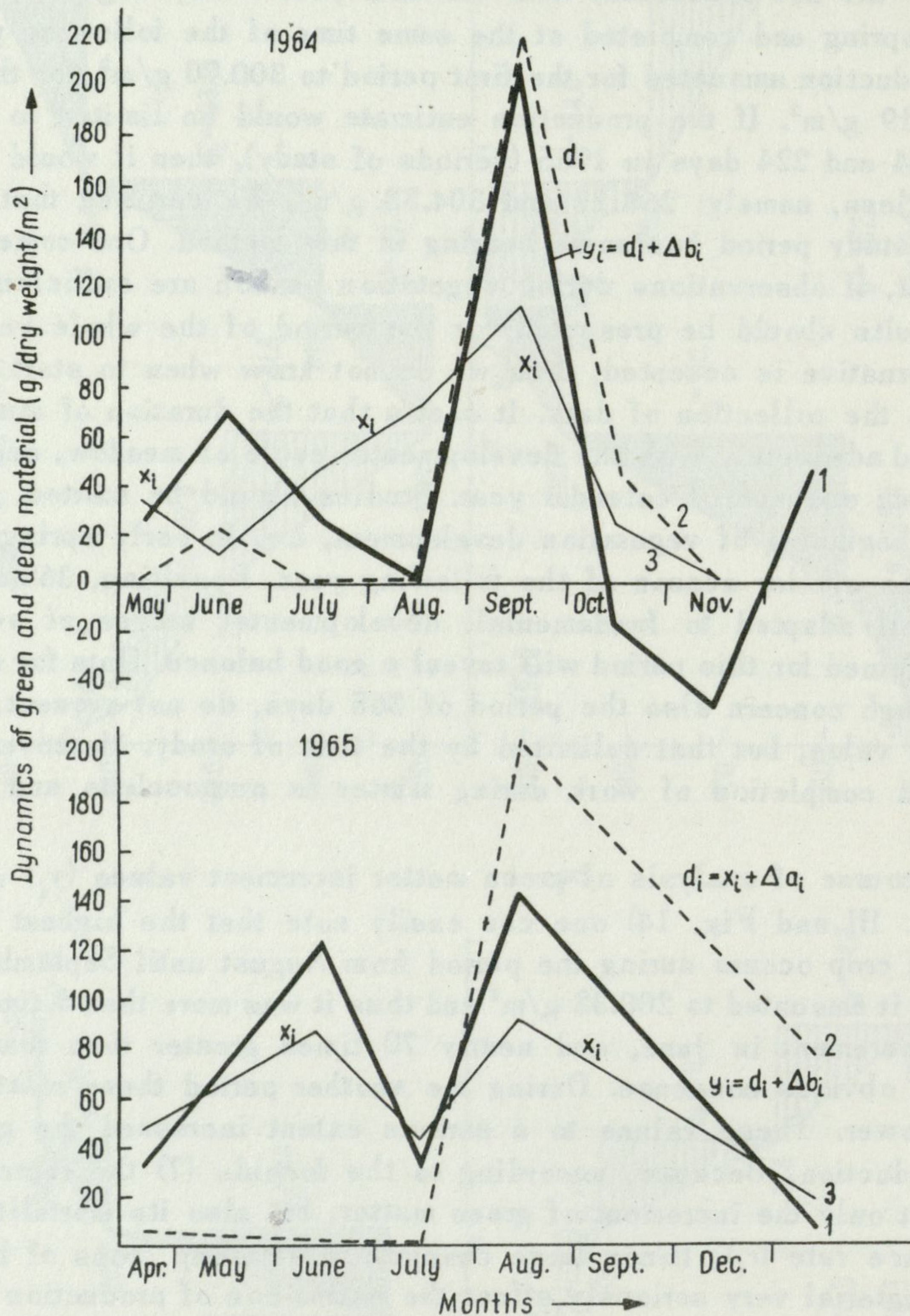


Fig. 14. Dynamics of growth and mortality of green material and the disappearance of dead material during the period of 1964-1965 (data from Table III)

1, y_i - growth of green material, 2, d_i - mortality of green material, 3, x_i - dead material disappearance, $\Delta a_i = a_t - a_{t_1}$, $\Delta b_i = b_t - b_{t_1}$ (a_t , a_{t_1} - standing crops of dead material at time t and t_1 , b_t , b_{t_1} - standing crops of green material at time t and t_1)

to 110 g/m^2 . It may be that this rapid growth resulted also partially from the dying off evergreen material from the previous year. Whatever is the situation

it is a fact that this laborious way of production estimate creates great possibilities of errors. Negative values of increments from October to November in 1964 (Tab. III and Fig. 14) are also incredible.

3.6.2.5. Production versus quantity of dead material disappearance

Another way of primary production estimation suggested also by Wiegert and Evans (1964) consists in the utilization of data which concern only changes in dead material status and the rate of its decomposition. In the previous formula (7) ($y_i = \Delta b_i + d_i$) the increment in green material is equal to the difference between the final and initial state ($\Delta b = b_n - b_0$) plus the quantity of green material dead - $d_i = (a_n - a_0) + x_i$.

This equation developed and summing up all increments from subsequent periods gives the formula:

$$\sum_{i=1}^n y_i = (b_n - b_0) + (a_n - a_0) + \sum_{i=1}^n x_i \quad (8)$$

In balanced ecosystems differences in final and initial standing crops both in green and dead material are close to zero, since the quantity of green material produced throughout a year has to die, similarly the dead has to disappear. Consequently, the quantity of dead plant material, which disappeared during, e.g. a year should be equal to the quantity of material produced during this period. On this principle the following formula is based:

$$\sum_{i=1}^n y_i = \sum_{i=1}^n x_i \quad (9)$$

The most important value in production estimation with this techniques becomes thus the quantity of disappearing dead material - x_i . The value is calculated according to the formula:

$$x_i = \frac{a_i + a_{i-1}}{2} \cdot r_i \cdot t_i \quad (10)$$

where: a_i - standing crop of dead material at the end, a_{i-1} - standing crop of dead material at the beginning, r_i - instantaneous daily rates of disappearance of dead material (compare formula (1)), t_i - a time interval in days.

One may base himself also on the mean, annual value for dead material crop =

$$\sum_{i=1}^n \frac{a_i + a_{i-1}}{2} \cdot \frac{t_i}{365} \quad (11)$$

and the mean, annual instantaneous rate of disappearance =

$$\sum_{i=1}^n (r_i \cdot t_i) \quad (12)$$

Several samples of dead material taken during a year give the possibility of the calculation of average standing crop of dead material. This value multiplied by the average, annual coefficient of disappearance enables to calculate the sum of dead material disappearing after a year and thus to estimate the production. The estimation of production as a sum of dead material values for the period of 170 days in 1964 amounted to 310.23, while for the period of 365 days – to 381.77. This estimate is thus considerably higher, than the sum of increments in green material (268.17 and 304.33). In the next year similar data amounted to 286.36 and 257.89 g/m², so they were lower than the sum of green material increments (304.33 and 345.19 g/m², respectively).

On the basis of the annual, mean value of dead material: 255.9 g/m² and of the mean, annual instantaneous rate of disappearance ($r = 8.2$) the production for 170 days in 1964 would amount to 356.7 g/m², while for 224 days in 1965 – to 341.5 g/m² (mean dead material = 293.2; $r = 5.2$; $t = 224$). Results are, thus, not concordant. Generally, the size of production, according to these formulae, depends mainly upon: the size of dead material standing crop, rate of disappearance, duration of study period. They all involve some reservations. It seems that the sum of increment during a year is not always equal to the sum of losses, since not always the green material produced during the given year dies entirely, similarly as the dead material does not disappear at once, but may be accumulated even during several years. Formulae given by Wiegert and Evans (1964) may be used mainly in such ecosystems, where the rate of production and disappearance of biomass is rapid and the cycle of plant matter circulation does not exceed one year, where does not occur the accumulation of green material, and particularly dead one from several years, as it occurs in strictly reserved meadow ecosystems. Here the rate of disappearance of dead material is rather slow and prolonged during two, three or more years. The reserve of such material, although revealing a regular cycle of growth and disappearance, is always several times greater, when compared with standing crops of green material.

Final results of the estimation of production of above-ground parts of herbaceous plants obtained with above-described techniques are presented in Table VII. These results are by no means concordant and it hardly can be decided, which are the most proper without reservations. Undoubtedly two

Comparison of production estimates for above-ground parts of vascular plants*

Tab. VII

	1	2	3	4	4a	5	5a	6
Year	max. standing crop	$\Delta B + D$	\sum of max. standing crops of species	$\sum y_{170}^{244}$	$\sum y_{365}$	$\sum x_{170}^{244}$	$\sum x_{365}$	
1964	163.3	153.5	204.9	268.2	300.7	310.2	381.8	356.7
1965	193.6	199.4	230.4	304.3	345.2	286.4	275.9	341.5

*Columns:

- 1 - production value equal to maximal standing crop,
- 2 - production value calculated on the basis of formula (6): $P = \Delta b + D$,
- 3 - production value calculated by summing up maximal standing crops of species,
- 4 - total growth of green material during 170 days in 1964 and 224 days in 1965 (Tab. III),
- 4a - total growth of green material during periods of 365 days (Tab. III),
- 5 - total disappearing dead material during 170 (1964) and 224 (1965) days,
- 5a - total disappearing dead material during periods of 365 days,
- 6 - production value calculated from mean mass of dead material and mean annual instantaneous rate of disappearance (r) for periods of 170 days in 1964 and 270 days in 1965.

first estimates (columns 1 and 2 in Table VII) and three last ones (columns - 5, 5a, 6) are least probable; first one are underestimated, while the latter - overestimated. Differences between these two groups of estimates amount much more than 100%. Particularly the acceptance of dead material, its standing crop and disappearance rate, as a basis for calculations is very risky in the situation studied, due to difficulties in the determination of the instantaneous rate of disappearance as also due to fact that the growth of vegetation takes several months in a year, while its dying and disappearance - several years. Much more favourable in the comparison of production values calculated from peak standing crop of green biomass of a species (column 3 in Table VII) as well as from plant increments determined according to the formula (7) (column 4 in Table VII). Differences between these estimates amount for the first year of studies to 30%, while for the second - to 23%. One can generally state, that estimates based on the sum of vegetation increments seem to be more real.

3.6.3. Moss production

The moss layer on meadow studied consists of two species of mosses: *Climacium dendroides* and *Aulacomium palustre*. They are perennial plants. Already in spring on previous year twigs there appear vividly green, current

year shoots. These shoots grow during spring and summer and reach their maximal increments in the full swing of summer (July, August). In this situation there arose the possibility of the separation of current year increment and the determination of the weight proportion between them and the biomass of mosses from previous years (procedure of sampling and the separation of current year mass was described in paragraph 2).

It appeared that in July the current year standing crop constituted 41% of the total standing crop, in August – 35%, in September – 36%. On the average 37% of moss biomass in summer falls to the current year production. It is obvious that this coefficient will be subjected to changes throughout a year. In spring, when increments begin to be formed, it will be small. Along with the growth of mosses it will be increased. In autumn it may be the highest, due to the decrease in previous year biomass. The value of this coefficient obtained for the period of full development of the moss layer of current year presents to some extent an average and representative magnitude. Knowing this coefficient one can estimate the current year production of mosses in relation to the mean biomass of mosses for a year. Doing so, moss production in 1964 would amount to 143.2 g/m², while in 1965 – 120.2 g/m². This estimate seems to be much more reliable than the one based on general standing crop of mosses, strictly: on the difference between the maximal and minimal standing crop during a year.

3.6.4. Root production

The separation of current year root mass from their older parts, similarly as it was in the case of moss analysis, is very difficult, if not impossible. This is why in the examination of underground parts the estimate techniques was used. It was based on the hypothetical difference in biomasses in two periods, namely at the period of minimal and maximal standing crop. After the vegetation season, in October 1964, the standing crop of underground parts was examined. It was assumed that it will be maintained until the beginning of vegetation season of the next year. This will be the minimal standing crop. It amounted to 520 g when converted into 1 m². This is mean value obtained from 10 samples (border values of biomasses fluctuated from 39 to 105.5 g/0.1 m²). In next June, in the full swing of vegetation, we expected maximal increments of root bulk. Having this in regard we took the second, analogous series of root samples in mid-June. The mean value of dry root biomass amounted then to 822.8 g/m² (extremal values fluctuated from 41.3 to 149.2 g/0.1 m²). From the differences in biomasses collected in summer and autumn we concluded about the increment in root bulk. The difference amounted to 302.8 g/m². The result obtained presents an approximate value, because: 1) one does not know, whether really minimal and maximal states of root biomass occur in periods of sampling, and 2) number of samples was undoubtedly too low, while their variation in respect to biomass – too high. The estimate may

be close to the value corresponding with production, although strictly speaking it is merely a change in biomass - ΔB (compare Petruszewicz (1967)).

3.6.5. Primary production - compilation

In the estimation of primary production with harvest method it should be remained that we do not allow for at least two values; respiration, i.e. energy spent by vegetation on maintenance and losses of plant biomass resulting from various activity of animals (Varley 1967). This will constitute thus the net primary production (Odum 1960, Petruszewicz 1963 and 1967) reduced by the value of losses caused by phytophages or broadly - heterotrophs.

In Table VIII there are compiled rough results of net production of three basic categories: above-ground parts of vascular plants, their underground parts (roots) and moss production. For above-ground parts of plants there were accepted production values calculated with Wiegert and Evans (1964) method (sum of increments) for two full study periods consisting of 365 days each. Combined with the production of roots and mosses the total net primary production of the meadow studied would amount to 746.7 g/m² for 1964, while to 768.19 g/m² for 1965. Assuming that the caloric value of 1 g of dry plant material is equal to circa 4.35 gcal (Golley 1961, Wiegert and Evans 1964) then the production in two studied periods would amount to 3.248 and 3.348 kcal/m². When the estimation is limited to 170 days in 1964 and 270 days in 1965, then the production would be lower and amount to 714.17 g/m² or 3.107 kcal/m² and to 727.33 g/m² or 3.170 kcal/m², respectively. Thus the total production of vegetation on the meadow studied approximately does not exceed much values of 700 g/m² in dry matter or 3 kcal/m². Out of this, about 450 g/m² or 2 kcal/m² falls to above-ground parts of herbaceous plants and mosses.

Summary of net production

Tab. VIII

Material	Years			
	1964		1965	
	g/m ²	kcal/m ²	g/m ²	kcal/m ²
Shoots	300.70	1.308	345.19	1.502
Roots	302.80	1.317	302.80	1.317
Mosses	143.20	0.623	120.20	0.529
Total	746.70	3.248	768.19	3.348

4. SUMMARY

The present paper was intended to be a procedural attempt and as such consciously aimed at coming in a specific research work across many difficult and discussive matters involved in studies on primary production. This may explain the undertaking of numerous clues (particularly when the evaluation of techniques and possibilities of the application of formulae are concerned), from which many were not worked out in details, but only outlined. Nevertheless, some obtained results deserve the attention.

1. It results from the analysis of standing crops that the average contribution of the green biomass represents only a small portion of the total biomass of meadow studied. Even during the period of the peak development of vegetation at the utmost 25% of the total biomass fall to herbaceous plants, while the remainder – to one year or older dead plant parts and mosses. This is reflected, of course, by the feeding value of hay.

2. The above analysis permits also the conclusion that the total biomass of vegetation has little connection with the size of current production.

3. Out of the total number of 46 species of herbaceous plants, representing the vegetation of the meadow studied, four dominant species, i.e. *Carex fusca*, *C. panicea*, *Deschampsia caespitosa*, and *Festuca rubra* take on an average 65% of the green material, and out of them two sedges take more than 40%.

4. Almost all specific biomasses give single peak curves, which well reflect the development of plants on the meadow. Specific analysis revealed that individual species reach their peak standing crops in rather similar period, mainly in July or August.

5. In spite of the fact that the peak standing crop of green biomass occurs at the beginning of August, the most favourable period for mowing would be the end of June or beginning of July, when the species composition of meadow is most diversified, and the less valuable as fodder sedges and *Deschampsia caespitosa* do not reach still their peak standing crops (Fig. 5).

6. The cycle of the full decomposition of dead plant material is in the meadow studied prolonged for few years.

7. Estimates of the disappearance rate for dead material are different in relation to the techniques used. The coefficient of disappearance calculated for data from plastic screen mesh bags appeared to be four times lower than the coefficient of disappearance calculated from measurements of dead material crops from sample series.

8. There were discussed several ways of production estimates to indicate which of them is most adequate. Discrepancies in estimations are rather serious (Tab. VI). It seems that estimates based upon the sum of increments (formula (7)) are most reliable, although they are also burdened with reservations.

9. The total net production of the meadow studied has been estimated

on 746.7 g/m² (7,467 kg/ha) in 1964, while 768.19 g/m² (7,682 kg/dry matter/ha) in 1965 (Tab. VIII).

10. It has been shown also how many procedural inadequacies are to be overcome in studies of this kind. The greatest trouble of procedural character causes the spatial variation in vegetation. In this connection we are not sure, whether changes found in standing crops, their ups and downs, on the basis of which we conclude about the production and circulation of plant material in definite ecosystem, are a strict reflection of real facts, or to some extent (we do not know what?), are they a matter of chance, since samples are on each occasion taken from other locations. These locations may differ (and do differ even considerably) both in the species composition, in numbers of plants, and in the size of plant biomass.

11. There arises thus suggestion to take the possibly greatest and statistically sufficient number of samples in series – even if it will be on the expense of sampling frequency – in order to eliminate thus to the utmost the casualness and to make means being a basis for production estimate values really representative for the ecosystem studied.

12. The stressing of weak points of the discussed procedure enables to plan further works on the refinement of procedure. It seems, that one should aim at the estimate of production on the basis of the direct analysis of green material increments (since increments are decisive for the size of production) and not on the basis of indirect estimation of increments calculated from changes in mean standing crops of green and dead material.

13. At the present stage of research one feels a lack of sufficiently good techniques for the estimation of production of underground parts of plants. This problem requires the serious intensification of works in this field.

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BADANIA NAD PRODUKCJĄ PIERWOTNĄ ZBIOROWISKA ŁĄKOWEGO

Streszczenie

Niniejsze opracowanie należy do serii badań w zakresie produktywności ekosystemów lądowych, podjętych przez Instytut Ekologii PAN w ramach Międzynarodowego Programu Biologicznego. Przedstawiono w nim wyniki dwuletnich badań (1964–1965) nad produkcją pierwotną zbiorowiska łąkowego rzędu *Molinietalia*, zbliżonego do zespołu *Stellario-Deschampsietum* Freitag 1957.

Badania zlokalizowano na Łąkach Strzeleckich położonych w północno-wschodniej części Puszczy Kampinoskiej w pobliżu Stacji Terenowej Instytutu Ekologii PAN w Dziekanowie Leśnym. Łąki te nie były użytkowane od około dziesięciu lat. Prace nad produkcją poprzedzone zostały badaniami fitosocjologicznymi przy uwzględnieniu kartowania zbiorowisk łąki w skali 1:2500. Wyniki tych badań zostały opublikowane w oddzielnej pracy (Traczyk 1966).

W badaniach zastosowano metodę zniwną, polegającą na bezpośrednich pomiarach biomasy roślinnej z ściśle określonych powierzchni w ustalonych odstępach czasu. Na próby wybrano płyty jednorodne pod względem fitosocjologicznym.

W obrębie badanego zbiorowiska wytyczono 20 stanowisk, każde o powierzchni około 20 m², z których pobierano (przeważnie w miesięcznych odstępach) po jednej próbie kolistej o powierzchni 1 000 cm². Z prób tych wycinano nożyczkami, tuż przy samej glebie, całą masę roślinną oraz zbierano opadłe części roślin i zeszłoroczny materiał martwy.

Materiał roślinny, z każdej próby oddzielnie, segregowano na trzy kategorie:

- a. biomasa zieloną, którą sortowano na gatunki (rośliny naczyniowe),
- b. części martwe (rośliny naczyniowe),
- c. mchy (bez rozdzielania części martwych od zielonych).

Posegregowany materiał suszono w temperaturze 85°C przez 48 godzin, a następnie ważono z dokładnością do 0.01 g.

W celu ustalenia, jaki procent ogólnej masy mchów stanowiły przyrosty tegoroczne, pobierano dodatkowo po 20 prób kolistych o powierzchni 250 cm² (średnica: 18 cm), raz w miesiącu w ciągu lipca, sierpnia i września. Z każdej próby starano się oddzielić przyrosty tegoroczne od reszty masy. Z porównania mas przyrostów tegorocznych i części starszych ustalono procentowy współczynnik przyrostów, który pozwala na ocenę tegorocznej produkcji mchów.

Badania części podziemnych roślin łąkowych narażały najwięcej trudności metodycznych. Dla uzyskania orientacyjnych danych o przyroście korzeni, na pod-

stawie różnicy stanów biomas z dwóch serii prób, pobrano jedną serię prób w jesieni, drugą – w pełni lata następnego roku. Na każdą serię składało się 10 monolitów glebowych o powierzchni 1 000 cm² i głębokości 30 cm. Po oddzieleniu darni, monolit krajano na drobne pasy i suszono na powietrzu. Następnie odsiewano glebę, przemywano wodą masę korzeniową i suszono ją do stałej wagi.

Przeprowadzono również wstępne doświadczenia nad bezpośrednią oceną tempa rozkładu trzech kategorii masy roślinnej: masy zielonej roślin naczyniowych, masy martwej roślin naczyniowych oraz całkowitej masy mchów. Wysuszony do stałej wagi materiał układano porcjami po 10 g, w torebkach wykonanych z siatek plastikowych o średnicy oczek równej 2 mm. Każda kategoria roślin reprezentowana była przez 10 takich torebek. Torebki te wyłożono na łące po poprzednim usunięciu roślinności z miejsc wyłożenia. Pierwszą serię prób wzięto do analizy po 10, a drugą po 14 miesiącach. Z ubytku mas wnoszono o tempie rozkładu poszczególnych kategorii za dany okres. Oprócz bezpośrednich pomiarów ubytków w siatkach plastikowych wykorzystano również materiał martwy z 20 prób podstawowych z poszczególnych serii. Na podstawie tych danych obliczono współczynniki tempa rozkładu masy martwej (r_i) z wzoru Wiegerta i Evansa (1964).

W ciągu okresu badań dokonywano również pomiarów wód gruntowych, opadów i temperatur. W latach 1965 i 1966 przeprowadzano obserwacje fenologiczne.

Dane dotyczące średnich wartości stanów biomas suchej, wyrażone w g/l m² i w procentach, zestawiono w tabeli I. Ujmują one stany masy zielonej i martwej roślin naczyniowych, mchów oraz całej biomas nadziemnej. Przebieg zmian biomas wydzielonych kategorii obrazuje figura 1.

Zmiany stanów biomas zielonej wykazują prawidłowy obraz, zgodny z rozwojem roślinności w ciągu roku. Od wiosny do lipca następuje dość szybki wzrost biomas zielonej; od sierpnia do października obserwujemy masowe zamieranie roślin. Przeciętny udział masy zielonej roślin zielnych stanowi niewielką część ogólnej biomas badanej runi łąkowej: około 15% (od 3,5 do 27,1%).

Odwrotnie niż stany biomas zielonych kształtują się stany biomas martwej (fig. 2, 3). Ogólnie biorąc, wahania masy martwej w ciągu roku są daleko niższe niż wahania masy zielonej. Zapas masy martwej jest zawsze stosunkowo duży i wynosi przeciętnie 35–40%.

Udział mchów w biomasie runi łąkowej jest również znaczny i wynosi od 35 do 57%. Stany biomas ogólnej wahają się w ciągu roku nieznacznie: od 660 do 861 g/m² w 1964 oraz od 632 do 760 g/m² w 1965 roku; średnio – 749 i 722 g/m².

Zdecydowaną przewagę ilościową osiągają w badanej runi łąkowej *Carex fusca*, *C. panicea* oraz *Deschampsia caespitosa* i *Festuca rubra*. Na ogólną ilość 46 gatunków roślin zielnych, stanowiących roślinność badanej łąki, przypada na wspomniane cztery gatunki przeciętnie aż 65% masy zielonej. Analiza gatunkowa wykazała również, że pojedyncze gatunki osiągają swe szczytowe stany w dość zbliżonym okresie, głównie w lipcu i na początku sierpnia (tab. II). Zestawiając je z obserwacjami fenologicznymi można ustalić, że stany maksymalne zbiegają się z fenofazą kwitnienia i owocowania.

Pomiary stanów masy martwej i żywej roślin zielnych obrazują stosunkowo ściśle wzajemne, naturalne stosunki wzrostu i zamierania roślinności – jej cykl rozwojowy w sezonie wegetacyjnym.

Porównanie tempa rozkładu materiału martwego z serii prób i siatek plastikowych dowodzi, że współczynnik zanikania był, średnio biorąc, w pierwszym przypadku ponad czterokrotnie wyższy niż współczynnik wyliczony z danych dostarczonych przez drugą metodę (siatki plastikowe).

Na podstawie danych o stanach biomas można postawić pytanie: w jakim stosunku przedstawiają się stany biomas do produkcji, czyli, jak na podstawie zmieniających się stanów biomas obliczyć produkcję?

Najprostszym sposobem oceny produkcji byłoby przyjęcie założenia, że maksymalny stan biomasy równa się produkcji. Założenie takie jest jednak obarczone wieloma błędami. Szczytowy stan masy ogólnej ma niewiele wspólnego z oceną aktualnej produkcji tegorocznej, chociażby dlatego, że oprócz masy zielonej z danego roku wchodzi w jej skład zeszłoroczne biomasy zielone, a przede wszystkim części martwe nawet z kilku lat ubiegłych. Maksymalne stany biomasy ogólnej wynosiły w badanym przypadku 861,2 (1964) i 760,0 g/m² (1965) i przypadały na grudzień, kwiecień lub czerwiec. Daleko dokładniejsze i bardziej zbliżone do produkcji netto są wartości szczytowe stanu biomasy zielonej. Sprawa ta komplikuje się jednak o tyle, że wzrost i zamieranie roślin zachodzą okresami równocześnie, że nie są to procesy wykluczające się całkowicie w czasie. Oprócz tego nie uwzględniamy również błędów wynikających z tego, że różne gatunki mogą w różnym czasie osiągać stany swych szczytowych biomas oraz że osobniki danej populacji też niejednocześnie osiągają swe maksyma biomas. Z tych względów ocena taka może odzwierciedlać jedynie wartość przybliżoną do rzeczywistej produkcji. W wyniku tej oceny otrzymano 163,3 g/m² w 1964 roku oraz 193,6 g/m² w roku następnym. Innym jeszcze sposobem oceny produkcji jest sumowanie szczytowych biomas poszczególnych gatunków. Postępując w ten sposób otrzymujemy 205 g/m² w pierwszym roku badań oraz 230 g/m² w roku następnym. Wartości te są większe od maksymalnych stanów biomasy zielonej o 22,0 i 25,5%.

Sposób oceny produkcji w oparciu o sumę przyrostów masy zielonej zaproponowali Wiegert i Evans (1964). Opiera się on na kilku podstawowych parametrach: znajomości tempa rozkładu materiału martwego (współczynnik zanikania — r_i) oraz znajomości zmiany stanów biomas żywych i martwych w badanym okresie. Ocenę produkcji, obliczoną w powyższy sposób (por. wzór (7)), przedstawia tabela III. Wartość produkcji wyniosła za pierwszy rok 300,7, za drugi — 345,2 g/m².

Autorzy ci zaproponowali również wyliczenie produkcji w oparciu o ilość martwego materiału roślinnego oraz o jego zanik w ciągu roku. W ekosystemach zrównoważonych ilość ta powinna być równa ilości materiału wyprodukowanego w tym okresie. Ocena ta przyniosła również inne wyniki niż ocena poprzednia. Zestawienie wartości produkcji uzyskanych powyższymi sposobami zawiera tabela VII. Wyniki te nie są bynajmniej zgodne i, co więcej, trudno jest przesądzić, który z nich jest najwłaściwszy. Wydaje się, że należy dążyć do oceny produkcji na podstawie bezpośredniej analizy przyrostów masy zielonej, a nie na podstawie pośredniej oceny przyrostów obliczonych ze zmian średnich stanów biomasy zielonej lub martwej.

Należy zauważyć, że przy ocenie produkcji pierwotnej metodą żniwną, nie uwzględniliśmy przynajmniej dwóch wartości: respiracji, tzn. energii wydatkowanej przez roślinność na własne utrzymanie, oraz strat biomasy roślinnej wynikających z różnorodnego oddziaływania zwierząt. Będzie to więc produkcja pierwotna netto pomniejszona o wartość strat spowodowanych przez roślinożerców, lub szerzej — heterotrofów.

Zestawienie sumaryczne wyników produkcji netto trzech zasadniczych kategorii: części nadziemnych roślin naczyniowych, ich części podziemnych (korzeni) oraz produkcji mchów (tab. VII) wykazuje, że ogólna produkcja pierwotna netto badanej łąki wyniosła 746,7 w 1964 i 768,19 g/m² w 1965 roku. Przyjmując, że wartość kaloryczna jednego grama suchej masy roślinnej równa się około 4,35 gcal (Golley 1961, Wiegert i Evans 1964), można obliczyć, iż produkcja wynosi w odpowiednich latach 3,248 i 3,348 kcal/m².

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