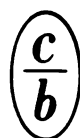


Vol. 6, No. 3, May-June, 1975

SJECAN 6(3) 191-294 (1975)

THE SOVIET JOURNAL OF
ECOLOGY
ЭКОЛОГИЯ/ÉKOLOGIYA

TRANSLATED FROM RUSSIAN



CONSULTANTS BUREAU, NEW YORK

PRIMARY PRODUCTIVITY OF SEVERAL MEADOW
COMMUNITIES IN THE SOUTHERN URALS

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UDC 581.553;581.526.4

An improved paired plot method was used in three mountain-spring meadow associations to determine over two seasons the standing phytomass (divided into above and below ground, alive and dead), the seasonal and annual fluctuations, the variation in net primary production and deposition, and the general pattern of biological circulation.

Temperate meadows are one of the most interesting and suitable objects for the study of the productivity of terrestrial biogeocenoses (ecosystems). This is partly because of their great agricultural significance and partly because of a number of special features of meadow biogeocenoses (particularly the short cycle of growth, death, and deposition of aboveground plant material), which simplify the task of analyzing the pattern of biological circulation.

This article considers the main features of the primary productivity of mountain-spring meadow communities in the lower levels of the southern Urals. Results were mainly obtained in two years' field work carried out by sections of the International Biological Program in the territory of the V. I. Lenin Il'menskii Reserve (Chelyabinskaya region). This area is dominated by montane southern taiga pine forest with some larch and birch, and includes in places some preforest-steppe birch-larch-pine forests complexed with stepped, grassy meadow on the southern slopes. The aim of the study was to examine the seasonal and annual changes in standing phytomass, the dynamics of net primary production and deposition, and the main features of biological circulation.

SITES AND METHODS OF INVESTIGATION

Three communities were chosen for study: Alchemilla-Ranunculus, mixed herbaceous-Alchemilla, and mixed herbaceous-Calamagrostis meadows (Table 1). These are mountain-spring meadows found in gullies and depressions in the relief, with a dispersed outflow of groundwater at the lower surface. As

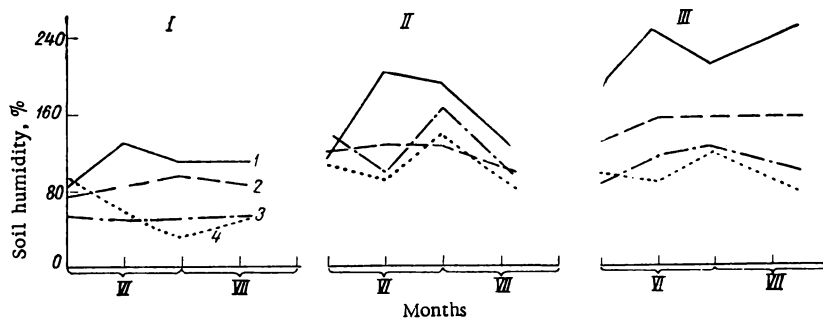


Fig. 1. Dynamics of soil moisture. Associations: I) Alchemilla-Ranunculus, II) mixed herbaceous-Alchemilla, III) mixed herbaceous-Calamagrostis. Relative humidity of soil horizons: 1) 0-5 cm, 2) 5-10 cm, 3) 10-20 cm, 4) 20-30 cm.

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Translated from *Ékologiya*, No. 3, pp. 5-17, May-June 1975. Original article submitted January 13, 1975.

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TABLE 1. Brief Characterization of Meadow Communities Studied

Site No.	Association	Position in relief	Microrelief	Surroundings	Moisture	Soil	Vegetation	
							total No. of spp.	projective cover, height, main species and their abundance
1	Alchemilla-Ranunculus meadow	Very steep northeast slope	Slightly hillocky	Mixed pine-birch forest with Sorbus aucuparia and Tilia cordata	Moderate uniform	Turfy-meadow, light loamy	58	75-85%; $h_1=50-60$ cm; cop. ₂ - cop. ₃ - <i>Ranunculus polyanthemus</i> , cop. ₂ - <i>Alchemilla atrifolia</i> , cop. ₁ - <i>Polygonum bistorta</i> , sp. - <i>Fritularius europaeus</i> , <i>Galium boreale</i> , <i>Potentilla erecta</i> , <i>Geum rivale</i> , <i>Geranium pratense</i> , <i>Lysimachia vulgaris</i> , <i>Sanguisorba officinalis</i> , <i>Pulmonaria mollissima</i> , <i>Betonica officinalis</i> , <i>Carex canescens</i> , <i>Phlomis tuberosa</i>
2	Mixed herbaceous-Alchemilla meadow	Slightly inclined southeast slope	Hillocky	Mixed herb meadow and pine-birch forest, river on east	Fairly abundant uneven, standing water in surface horizons (clay at 14 cm)	Turfy-meadow, medium loamy, gleyed	57	80-90%; $h_1=60-70$ cm; cop. ₂ - cop. ₃ - <i>Alchemilla atrifolia</i> , cop. ₁ - <i>Filipendula ulmaria</i> , <i>Geranium pratense</i> , sp. - <i>Bupleurum aureum</i> , <i>Betonica officinalis</i> , <i>Potentilla erecta</i> , <i>Cirsium heterophyllum</i> , <i>Polygonum bistorta</i> , <i>Lathyrus pisiformis</i> , <i>Poa palustris</i>
3	Mixed herbaceous-Calamagrostis meadow	Slightly inclined southeast slope	Hillocky	Pine-birch forest, Prunus padus, and willow along river valley to southeast	Abundant, uniform	Turfy-meadow, heavy loamy with some superficial gleying	52	80-95%; $h_1=60-80$ cm; cop. ₂ - cop. ₃ - <i>Calamagrostis arundinacea</i> , cop. ₁ - <i>Filipendula ulmaria</i> , <i>Alchemilla atrifolia</i> , <i>Polygonum bistorta</i> , sp. - <i>Sanguisorba officinalis</i> , <i>Geranium pratense</i> , <i>Pulmonaria mollissima</i> , <i>Cirsium heterophyllum</i> , <i>Potentilla erecta</i>

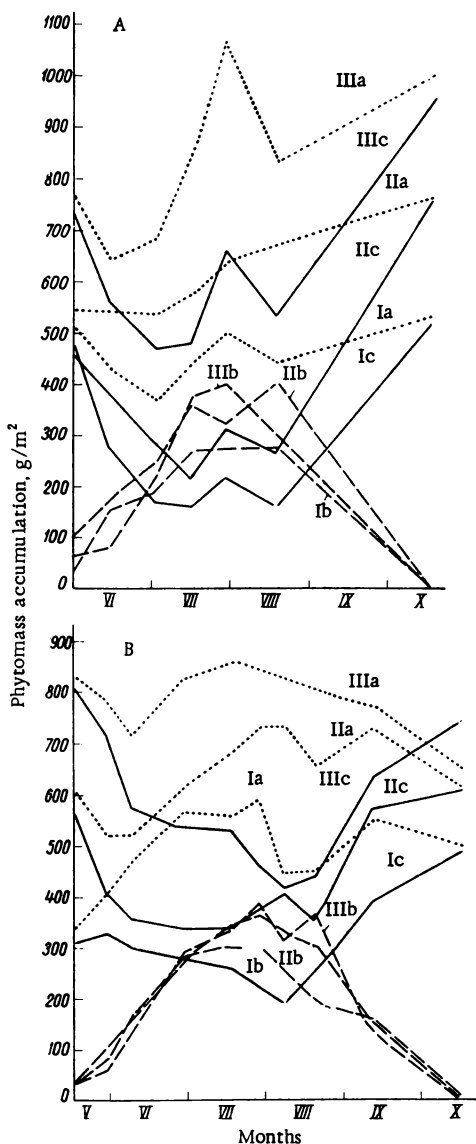


Fig. 2. Dynamics of accumulation of aboveground phytomass in meadow communities in the 1972 (A) and 1973 (B) growth seasons. Associations: I) Alchemilla-Ranunculus, II) mixed herbaceous-Alchemilla, III) mixed herbaceous-Calamagrostis; a) total phytomass accumulation, b) living material, c) dead material (dead leaves and litter).

has the living plants cut at time t_0 . Plot 2 has the living plants cut at time t_1 , and the dead leaves and litter collected. New plots are set out through the season to repeat these observations. The dead mass g collected on plot 2 at time t_1 is the sum of the accumulated dead material w_0 at time t_0 plus the material falling (h) over the period $t_1 - t_0$ minus the mass of material decomposed over this period, i.e., $g = w_0 + h - (w_0 - w_1)$. It follows from this that $w_1 = g - h$. Although this modification of the method removes assumption (4), it introduces a new assumption (5) that the removal of litter and dead leaves does not affect the deposition of dead material. Net primary production is determined as $y = h + (b_1 - b_0)$, where h = deposition over given interval, b_0 and b_1 = accumulation of biomass at the beginning and end of the time interval, respectively.

noted by E. V. Dorogostaiskaya (1961), the humidity caused by this water is often enough to prevent the growth of woody vegetation. However, these meadows bear the mark of human interference (clearing of scrub, felling of trees, mowing). Sample areas were laid out in the southern part of the Il'menskii Reserve, 5 km from Lake Miassovo, near the Nyashevka river which runs into the lake. All the associations studied were suitably moisture-dependent: They lay in valleys at the foot of mountain slopes, close to the river. The mechanical composition of the soil varied from light loamy in the first association to heavy loamy in the third; soil moisture increased from the first association to the third (Fig. 1); the second and third associations showed gleying of the soil; standing water was more prominent in the second association, in which the clay horizon lay at 14 cm. Moss cover was almost absent in all associations.

The study of the primary productivity of the meadows (aboveground parts of communities) was based on the modified paired-plot method of Wiegert and Evans (1964). Evaluation of net primary production and the rate of decomposition of plant material in each community is based on a pair of identical plots. The living material is cut at time t_0 on the first plot, leaving the dead material, while the living plants are left on the second plot, and only the dead material collected (w_0). After an appropriate interval, at time t_1 , the dead plant material is collected on plot 1 (w_1), but no observations are made on plot 2. Another pair of plots is set out at time t_1 and the same operations carried out as at time t_0 . This is repeated throughout the growing season. The rate of decomposition is estimated from the ratio between the weight of dead material w_0 at time t_0 and the weight of dead material w_1 at t_1 . The value w_0 is determined on plot 2 at time t_0 . The value for net primary production can be calculated given the data on decomposition rates. The following assumptions are made in this calculation: 1) Decomposition rate is identical in paired plots, 2) the mass of dead material and the composition of its components are identical in the paired plots, and 3) no dead material has been added to plot 1 over time interval t_0 to t_1 . A further assumption (4) is necessary, although the originators of the method did not make it clear: The removal of vegetation does not affect the rate of decomposition of dead material.

Lomnicki et al. (1968) modified Wiegert and Evans' method to remove the necessity for this fourth assumption. This was achieved by determining w_1 in a different way. Plot 1 is used throughout; live material is left on it at time t_0 and dead material collected; at time t_1 and all subsequent times, fallen material is determined. Its parallel plot 1a

TABLE 2. Accumulation of Phytomass in Meadow Communities, g Air-Dry Matter per m²

Association	Year of observations	Aboveground parts			Below-ground parts			Total accumulation (above and below)			Ratio of above-ground phytomass to below-ground
		living	dead	total	living	dead	total	living	dead	total	
Alchemilla-Ranunculus meadow	1972	281	220	501	1677	883	2560	1958	1103	3061	1:5
	1973	301	262	563	1005	503	1508	1306	765	2071	1:3
	2-year mean	291	241	532	1341	693	2034	1632	934	2566	1:4
Mixed herbaceous-Alchemilla meadow	1972	403	270	673	1288	643	1931	1691	913	2604	1:3
	1973	366	367	733	901	450	1351	1267	817	2084	1:2
	2-year mean	384	318	703	1094	546	1641	1479	865	2344	1:2,5
Mixed herbaceous-Calamagrostis meadow	1972	400	660	1060	1624	812	2436	2024	1472	3496	1:2
	1973	386	460	846	910	455	1365	1296	915	2211	1:2
	2-year mean	393	560	953	1267	633	1900	1660	1193	2853	1:2

In order to remove the possible aftereffects of the collection of dead plant material of subsequent deposition, we have modified Lomnicki's method slightly by not using constant sample plots for the observations on deposition.

Our experimental scheme was as follows. At time t_0 , dead plant material (dead leaves and litter) was carefully collected from the first plot, leaving the living plants. The second plot was left with living plants and the dead material. At time t_1 , living plants were cut at soil level on the first plot, and the dead plant material accumulated over the period collected. The total dead material was collected from the second plot, leaving the living plants. A new plot was then set out for subsequent observation. This sequence was then repeated throughout the whole growing season.

The biomass consumed by heterotrophic organisms was not considered in our calculations.

The advantage of the paired plot method in our modification, compared with the others, lies in the possibility of determining not only the net primary production, but also the dynamics of accumulation of aboveground biomass, loss by death, and decomposition of dead material.

TABLE 3. Main Indices of the Rate of Biological Circulation in Meadow Communities

Association	Period of observations	Net primary production, g/m ² per year	Deposition, g/m ² per year	Litter deposition coefficient	Decomposition rate, %			Mass of decomposed plant material calculated by formula (3), g/m ² per year
					by experiment (end of growth season)	by formula (1)	by formula (2)	
Alchemilla-Ranunculus meadow	V/1972—	574	524	1	26	52	68	679
	V/1973	643	592	0,8	27	64	68	628
	V/1974 2-year mean	608	558	0,9	26,5	58	68	653
Mixed herbaceous-Alchemilla meadow	V/1972—	799	779	1	36	63	67	825
	V/1973	702	670	0,9	37	62	63	681
	V/1974 2-year mean	750	724	0,9	36,5	62,5	65	753
Mixed herbaceous-Calamagrostis meadow	V/1972—	654	625	1,6	18	46	47	638
	V/1973	846	787	1	21	52	53	796
	V/1974 2-year mean	750	706	1,3	19,5	49	50	717

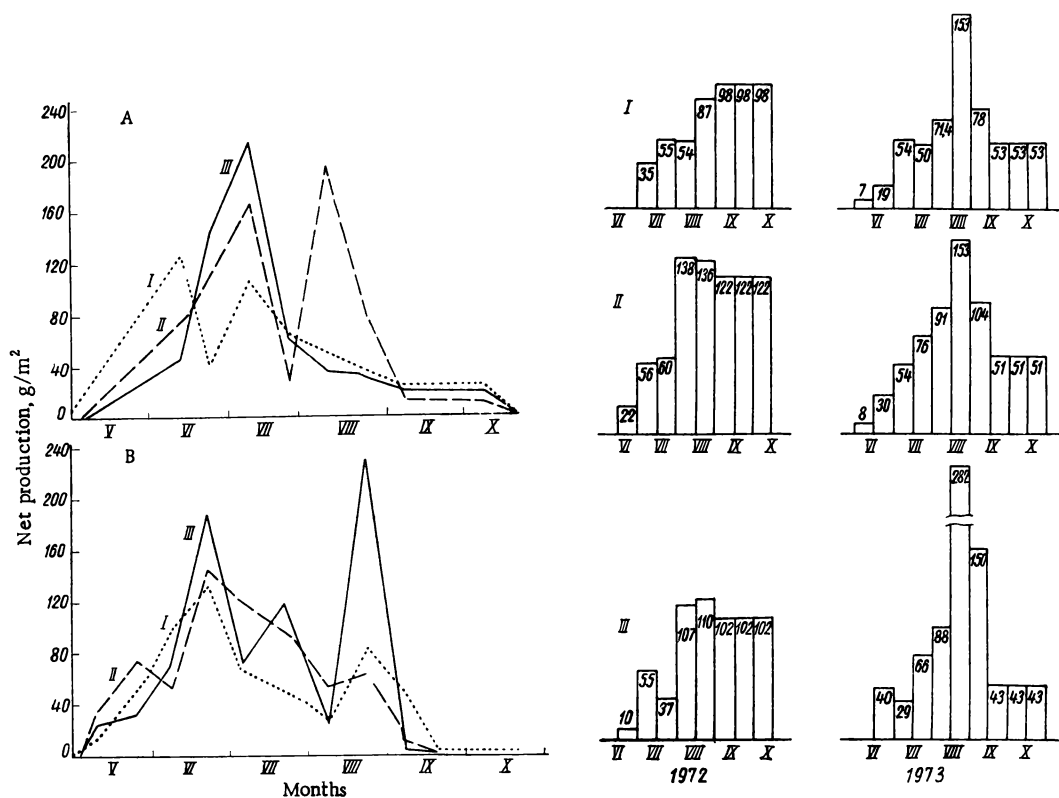


Fig. 3. Change in net primary production through the growth season of 1972 (A) and 1973 (B). I, II, III) As in Fig. 2.

Fig. 4. Dynamics of death of aboveground biomass (g/m^2 per 15 days) in two growth seasons. I, II, III) As in Fig. 2.

The size, shape, and number of plots used for determining the accumulation of aboveground phytomass were based on the recommendations of authors who have studied meadow communities in other areas (Jankowska, 1967; Van Dyne et al., 1964; Dymina, 1971). One main plot 10×10 m was laid out in each of the three meadow associations. Phytomass was collected from May to November at regular intervals (mostly 15 days) from circular recording plots ($1/16 \text{ m}^2$), selected at random within the main sample plots. The collected phytomass (living, sorted by species, and dead) was air-dried and weighed.

It was shown experimentally that determination of the aboveground phytomass with a statistical error less than 15% required 12 to 30 recording plots to be set up in each association.

The accumulation of below-ground phytomass was determined at the period of maximum development of the vegetation by the "core" method (Shalyt, 1960). Ten 25×25 cm cores were taken each year for each sample plot, to give biomass determinations with a statistical error less than 10%. The depth of the cores corresponded to the maximum root depth. Washing was carried out in a rotating drum placed in tapwater. A sieve with 1 mm^2 mesh was fitted to the end of the drum. The washed samples of below-ground phytomass (not sorted into living and dead) were air-dried and weighed. Further calculations requiring a separation of the below-ground phytomass into living and dead material were based on the approximate assumption that about a third of the roots and rootstocks die every year (Rodin and Bazilevich, 1965).

TABLE 4. Calorific Value of Individual Phytomass Components (cal per g absolute dry weight)

Association	Aboveground biomass		Below-ground biomass
	living	dead leaves and litter	
Alchemilla-Ranunculus meadow	4258	4309	4119
Mixed herbaceous-Alchemilla meadow	4299	4420	4372
Mixed herbaceous-Calamagrostis meadow	4395	4279	4410

TABLE 5. Energy Stored in Meadow Communities (mean values for two years), kcal per m²

Association	Aboveground parts			Below-ground parts (living and dead)	Total (above and below ground)
	living	dead	total		
Alchemilla-Ranunculus meadow	1240	1040	2280	8380	10,660
Mixed herbaceous-Alchemilla meadow	1650	1400	3050	7170	10,220
Mixed herbaceous-Calamagrostis meadow	1730	2390	4120	8380	12,500

The rate of decomposition of plant material r was determined experimentally and by calculation. In the experiments, samples of plant material (mixture of species, 5 g air-dry weight) were placed in nylon bags on the surface of the soil between the stems of the plants. The change in weight of the samples was determined at the end of the growth season (from May to September).

The rate of decomposition was calculated from the formula (Jenny et al., 1949)

$$r = \frac{h}{h + w_0} \quad (1)$$

and by our improved formula

$$r = \frac{w_0 - g + h}{w_0 + h}, \quad (2)$$

where h = deposition over the year, w_0 = dead plant mass (dead leaves and litter) at the beginning of the period of observations, g = the same at the end of the period of observations. The litter-deposition coefficient k was calculated by the formula $k = g/h$, where g = dead plant mass at the end of the growth period. The amount of plant material decomposed in a year (d) was calculated by the formula

$$d = h + (w_0 - g). \quad (3)$$

Phenological observations were carried out by the method of I. N. Beideman (1954) for 5-7 days over the whole plant community in each main sample plot. Soil humidity was determined by standard methods (Rode, 1960) at four times during the growth season. Soil samples for humidity determination were collected at five points in each sample plot, at depths of 0-5, 5-10, 10-20, and 20-30 cm. The calorific value of the plant material was determined in the laboratory using a calorimeter.

During the productivity studies on meadow communities, aboveground phytomass was collected from a total of 69 m², deposition from 45 m², and underground phytomass from 3.7 m². Decomposition rates in the meadows were estimated from 30 nylon bags, containing a total weight of plant material of 150 g.

RESULTS AND DISCUSSION

A general picture of the accumulation of plant material in the meadow communities studied at the time of maximum development of vegetation (end of July-August) is given in Table 2. It can be seen that the accumulation of living aboveground phytomass was relatively small in the first association (291 g/m² on average for two years), rather higher in the second (384 g/m²), and greatest in the third (393 g/m²). The associations studied differed even more in the amount of dead aboveground phytomass (dead leaves and litter): The second community had more than the first, and the third more than either of the others. The accumulation of large amounts of dead leaves and litter in the third community must be due to the slow decomposition of the tough *Calamagrostis* leaves. The same ratio was seen in comparing the total accumulations of aboveground phytomass (living and dead).

Although the *Alchemilla-Ranunculus* community fell short of the others in accumulation of above-ground biomass, it exceeded them in below-ground accumulation (1341 g/m² on average). Second place in the below-ground accumulation was taken by the mixed herbaceous-*Calamagrostis* association, and third place by the mixed herbaceous-*Alchemilla* association. The greater development of below-ground biomass in the *Alchemilla-Ranunculus* association is probably due to the special ecological regime of the site (low relative humidity of the soil, Fig. 1).

The total biomass accumulation (above and below ground) was greatest for the third association (1660 g/m²), slightly less for the first (1632 g/m²), and lowest for the second (1479 g/m²). The same pattern was apparent for the total accumulation of all phytomass (living and dead, above and below ground).

The mean ratio of above-ground phytomass to below-ground in the three communities studied (1:4, 1:2.5, and 1:2, respectively) reflects their relative positions on an ecological gradient of increasing soil humidity (the below-ground part of the phytocenose is more developed in the sites less well provided with water, and least developed in the best provided sites).

The results of the two-year observations showed that phytomass accumulation (aboveground and particularly below-ground) showed considerable fluctuation from one year to the next. The 1972 growth season was relatively hot and dry (mean July temperature 16.4°C, 179 mm precipitation from May to August inclusive), while 1973 was cooler and wetter (mean July temperature 14.7°, 242 mm precipitation from May to August). The sample plots showed greater biomass accumulation (above and below ground) in 1972 than in 1973. This shows that the main factor controlling annual fluctuation in biomass accumulation at the different sites is change in the temperature regime (biomass accumulation greater in hot summers). Differences in rainfall were only of secondary importance, in view of the presence of groundwater relatively near the surface in all the communities studied.

The growth season began slightly earlier (28-30 April) in the Alchemilla-Ranunculus association, owing to the drier soil, than in the other associations (3-8 May). The season terminated at almost exactly the same time for all associations, with the arrival of heavy frosts (in the second half of September or first half of October).

The seasonal changes in aboveground phytomass (divided into living and dead) are shown in Fig. 2. The accumulation of living aboveground plant material reached a maximum in the second half of the growth season (second half of July and first two decades of August). The accumulation of dead plant material (dead leaves and litter) reached a minimum at about the same time. This was clearly because of the high rate of decomposition of dead phytomass during the hottest period of the summer.

The change in accumulation of living plant material through the season had the form of a unimodal curve (with the maximum at the middle of the period). The curve for dead material showed two peaks (usually with a maximum at the end of the period, and a smaller one in the spring). The greater amount of accumulated dead material in the fall compared with the spring was due to the continuation of decomposition processes after the end of the growth period (late fall, winter, early spring).

There was almost always a tendency for an increase in the total aboveground phytomass (living and dead) towards the end of the season. The total accumulation of living and dead phytomass was not subject to such a large seasonal fluctuation as the accumulation of the individual components, since the sharp changes in the living and dead phytomasses tended to cancel each other out.

The maximum values for aboveground phytomass coincided with maximum flowering of the main components of the vegetation. In the Alchemilla-Ranunculus association, which was composed mainly of plants flowering in the early summer (Ranunculus auricomus etc.) and midsummer (Alchemilla atrifolia, Trollius europaeus, etc.), biomass accumulated relatively fast at the beginning of the growth season (till the middle of July), and there was then hardly any further growth. The mixed herbaceous-Alchemilla and mixed herbaceous-Calamagrostis associations had plants flowering mainly in the mid and late summer (Bupleurum aureum, Calamagrostis arundinacea, Filipendula ulmaria, etc.), and usually showed a slower increase in biomass at the beginning of the season, then an increase in growth rate continuing after mid-July, and maximum biomass accumulation was reached significantly (July 30-31 for the third association and July 30-August 21 for the second).

All the meadow associations studied had their dominant species (the four species dominant or sub-dominant in each association) contributing a large part of the total aboveground biomass. In 1972, the contribution of the dominant species to the aboveground biomass varied from 46 to 61% for the first community, 71-87% for the second, and 54-89% for the third. The seasonal dynamics of change in biomass for the dominant species followed the same pattern as the total biomass.

The net primary production figures for the year can be seen from the data in Table 3. The Alchemilla-Ranunculus association was characterized by a fairly low annual net primary production (608 g/m² on average for the two years), while the others had a higher figure (750 g/m² on average).

The change in net primary production through the growth season (at 15-day intervals) in the three communities is shown in Fig. 3. It can be seen that the period of active biomass increase began in the middle of May and finished in the first decade of September.

The 1972 observations showed that the Alchemilla-Ranunculus association had relatively little oscillation in the rate of net production during the active growth period. Two peaks in net production were seen (in the first half of June and in the middle of July). The mixed herbaceous-Alchemilla association showed slightly greater variation in the rate of net production. There were two peaks in net production at later dates than for the Alchemilla-Ranunculus association (a first lesser peak in the middle of July and a second, greater peak in the middle of August). The mixed herbaceous-Calamagrostis association showed the greatest variation in rate of net production, but had only one peak in the course of the season (middle of July).

The 1973 observations showed a rather more stable rate of net production in the first two associations than in the third. The first association again had two peaks in net production: the first in the second half of June as in 1972, and the second, significantly later, in the middle of August. The second association showed three peaks in net production: a first minor peak at the end of May, a second stronger peak in the middle of July, and a third peak in the middle of August. The third association also had three peaks: a strong peak in the middle of June, a weak peak in the middle of July, and a very strong peak in the middle of August.

The absolute maximum in net production was seen in the mixed herbaceous-Calamagrostis association (middle of August, 1973, 230 g/m² in 15 days), and the absolute minimum during the period of active growth in the Alchemilla-Ranunculus association (first half of August 1973, 26 g/m² in 15 days).

The oscillations in net production rate were apparent not only within one growth season, but also between different seasons. In 1972, all three associations had their greatest net production in July (in total 483 g/m² in 15 days). Peaks at other dates (June, August) were smaller and noted only for some associations.

In 1973, however, the greatest net production by all three associations was seen in June (total of 468 g/m² in 15 days). This was also the time of highest growth rate in the season for two of the associations. The mean temperature in this month was 16°, and the rainfall 72 mm. July (with a mean temperature of 14.7° and rainfall of 50 mm) showed a depression in net production: A slight growth peak was noted only for the wettest of the three associations (mixed herbaceous-Calamagrostis) which still had considerable reserves of water in the root layer (5-10 cm) at this stage (Fig. 1). The first and second associations showed a smaller peak in the middle of August, while the third had its main peak at this time.

The seasonal variations in net primary production in different years did not coincide in time, owing to variations in the heat and moisture regime. Comparison of the dynamics of biomass increase with meteorological data for 1972 and 1973 showed that maximum increase coincided with the hottest periods of the summer, and the lowest with the coolest. Seasonal variation in rainfall had a less significant effect on net production. This must evidently be because the meadow communities studied do not suffer from lack of water during short dry periods, owing to an adequate supply of spring water.

The rate of biological circulation in the communities is shown in Table 3. There was a clear correlation between the values for annual deposition and annual net primary production, the observed deviations being nonsignificant.

Analysis of a diagram of the seasonal deposition dynamics (at 15-day intervals) in the three meadow communities showed significant differences in this index in different years (Fig. 4). In 1972, only the second association had maximum deposition in August, the others having their maximum at a later time (September, first half of October). In 1973, all associations gave maximum deposition in the second half of August, with a much lower figure for the later months. These differences were due to the different meteorological patterns of the two years: The 1972 summer was hot and dry (mean July and August temperatures 16.4 and 16.3°, respectively, rainfall from May to August 179 mm). The 1973 summer was cooler and wetter (mean temperatures in July and August 14.7 and 14.4°, rainfall during growth period 241 mm). The main factor controlling the seasonal dynamics of deposition was the temperature regime: The hot summer of 1972 shifted intensive deposition to the end of the growth season (September, first half of October), while the cooler summer of 1973 gave maximum deposition in the second half of August. Differences in rainfall were apparently less important, since any lack of atmospheric water was compensated by ground-water.

Comparison of the results on biological circulation within the communities studied showed that decomposition of plant material was relatively slow in the third association and rather faster in the first and second. Experiments with nylon bags gave a comparative view of decomposition rates, but tended to underestimate the true rate of decomposition, as has been noted by other authors.

The litter deposition coefficient can be used to compare the different associations for their rate of decomposition of plant material. According to the formula of Jenny et al. (1949), the amount of plant material decomposing in a year should equal the amount of material deposited. However, observation shows that the amount of material deposited does not necessarily coincide with the amount of material decomposed in any one year, owing to varying meteorological conditions. Calculations by our formulas (2) and (3) (see "Methods" and Table 3) gave a more objective view of decomposition rate and of the amount of material decomposed in a year.

The calorific value of the various phytomass components varied from 4.1 to 4.4 kcal per g absolute dry weight (Table 4). There were no significant differences between the calorific values of different components. Below-ground biomass had in several cases a higher calorific value than aboveground biomass, and aboveground dead biomass (dead leaves and litter) often had a higher value than living biomass. According to the results in Table 5, the largest reserves of energy were in the below-ground parts of the communities studied. The mixed herbaceous-Calamagrostis community had both the highest total energy capacity and the highest energy capacity of above-ground living and dead material.

CONCLUSIONS

1. The three mountain-spring meadow communities studied (Alchemilla-Ranunculus, mixed herbaceous-Alchemilla, mixed herbaceous-Calamagrostis) gave values of 291, 384, and 393 g/m² accumulation of living aboveground phytomass. The third association exceeded the others in total phytomass accumulation (below- and aboveground), and in accumulation of dead aboveground phytomass (dead leaves and litter).

2. The accumulation of living aboveground phytomass reached a maximum in the second half of the growth season; the accumulation of dead plant material (dead leaves and litter) reached a minimum at the same time. The fall accumulation of dead plant material was greater than the amount in spring, showing that decomposition continued after the end of the growth season.

3. The highest values for aboveground living biomass through the growth season coincided with the period of maximum flowering of the main components of the vegetation (mid-July in the Alchemilla-Ranunculus association, end of July and August in the other two).

4. The second and third associations showed high values for annual net primary production (about 750 g/m² on average) compared with the first (608 g/m² on average). There were significant fluctuations in the net production rate both within growth seasons and between them. Maximum growth rates coincided with the hottest times of the summer, and lowest growth rates with the coolest periods.

5. Biological circulation in the associations studied was balanced: The differences between the values for deposition, net primary production, and amount of decomposing plant material in the different associations were relatively small.

6. The meadow communities, with groundwater standing at relatively little depth, had temperature at the most important factor controlling annual and seasonal variation in phytomass accumulation, net primary production, and deposition. Differences in rainfall were only of secondary importance, since the groundwater tended to level them out. Deposition tended to shift to the end of the season in hot years.

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