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DYNAMICS OF ABOVEGROUND PHYTOMASS, NITROGEN, AND ASH ELEMENTS IN A LONG-TERM EXPERIMENT OF PEDOGENESIS

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Abstract. Aboveground phytomass of grass-herbaceous vegetation was studied beginning from the 21st year of an experiment established in 1963 and initiated in 1964. Three levels of annual and diurnal productivity were ascertained. The highest occurred four years after the improvement of sown sward with cultural grasses, the lowest during the last quinquennium with continuous summer draughts. Spontaneous vegetation revealed relatively stable productivity although it was also characterized by different levels. Phytoproductivity and the composition of phytomass were dependent on weather relationships characterized by climatograms constructed after H. Walter (1955. Die Klimagramma als Mittel zur Beurteilung der Klimaverhältnisse für ökologische, vegetationkundliche und landwirtschaftliche Zwecke. Ber. d. Deutsch. bot. Gesellschaft, 68, 7-10, 331-344.). Owing to highly changeable weather, advective in origin, with frequent seasonal radiation, both annual and diurnal production as well as ash and nitrogen, participating in plant-soil interactions, revealed fluctuations in their outcome regularities. Beginning from the severe summer draught of 1988 and especially that of 1992, the intensity of phytocoenotic processes started to decrease. Instead of the spring-summer season, first late summer and thereafter midsummer became important in the production of organic matter and absorption of nutrients in it. Continuous radiation during the second half of the vegetation period resulted in a decrease in production phenomena at the outset of the next season. Inhibited production efficiency in spring led to the replacement of grasses by root weeds and green mosses as well as to a manifold decrease in total phytoproductivity and biological absorption of nutrients. Cycling intensity was low in 42-60% and high in 30-40% of the years, although the share of summer seasons in the distribution of the proportion of production and its constituents increased. As a result of the removal of the yield, 109, 24, 5, and 22 g kg⁻¹ of ash, nitrogen, phosphorus, and potassium, respectively, were eliminated. Nearly the same amounts of constituents per dry phytomass were returned with yield to stimulate accumulative processes in soil development.

Key words: primary production, climatogram, weather/production relationships, turnover of ash and NPK.

Plant organic matter and its humification products represent the main sources of the initiation and development of pedogenesis. The higher the production capacity, the greater are the amounts of organic agents and energy used for the intensification of pedogenesis as well as for the turnover of substances in plantsoil systems (Bazilevich, 1979; Kylli, 1981). On the basis of fundamental research into the pattern of photosynthetic and respirational processes, Tooming (1984) suggested that maximum plant productivity is characteristic of any vegetation level (leaves, plant, community, coenosis) in any given ecological situation. This means that phytocoenotic adaptation is directed towards ensuring maximum productivity that is possible under certain environmental conditions. This results in increasing intensity of soil processes because combinations of vegetation and soils represent an inseparable whole in nature, the productive phenomena of the former leading to a rise and progress of the latter and vice versa (Reintam, 1988). Production and pedogenetic activities themselves form part of an interdependent integral complex of ecosystems, which is characterized by a common energy flow, mutual turnover of substances and energy, as well as by synchronous cyclicity of different accumulative and transformative processes. They are wavy in origin, every new wave being expressed as a new level achieved (Pärna, 1978).

Although the total amount of organic carbon in a one-metre section of World soils is about threefold bigger (Bohn, 1976) than that in World biomass (Bazilevich, 1979), 3×10^{12} and 0.974×10^{12} Mg, respectively, the renewal of soil supplies is everywhere and always caused by the progress and dynamics of vegetation. To study contemporary processes in a certain situation, the method of experimental modelling was introduced (Bryant & Arnold, 1994; Hoosbeek & Bryant, 1994). Attention has been focused mostly on the quantification of soil formation over short time and/or development of soil horizons and properties (Graham et al., 1995; Creemens, 1995). Only a few investigations have dealt with synchronous results of production and pedogenetic processes (Sau, 1979, 1983).

Our long-term experiment, established in 1963 for studying pedogenesis on reddish-brown calcareous till, has lasted already 34 years. Changes in the organic agents of pedogenesis and in mineral soil constituents as well as some properties have been determined. The results have been published by decades (Reintam & Pogorelova, 1987; Reintam, 1982, 1995, 1997). Summarized amounts of organic residues, subjected to transformation phenomena, have also been presented. However, the annual and diurnal dynamics of aboveground phytomass and its constituents against the background of concrete climatic parameters have not yet been discussed. The aim of this paper is to fill this gap and to deal with changes in the accumulation and turnover of plant organic matter, nitrogen, and some ash elements during the last 14 years. Although the material and some of the methods of this study have been described earlier (Reintam, 1995, 1997), it appears indispensable to briefly repeat them here.

MATERIAL AND METHODS

Foundation of the experiment, layout, and variants

The experiment was founded at Eerika, Tartu County, Estonia (58°22′ N, 26°36′ E) in autumn 1963. An *Albi-Eutric Luvisol* profile on reddish-brown calcareous till was excavated to a depth of 2 m in an area of 9 m². The formed pit was divided into four equal parts (2.25 m² each), isolated from every side by saturated felt, and filled with unchanged reddish-brown calcareous till dug from a depth of 1.5–3 m in the neighbouring cellar pit of a lysimeter building. The initial bulk density (1.71 Mg m⁻³) of the transferred till was preserved by the volume.

The actual experiment was initiated in spring 1964 after natural winter subsidence and formation of sown agricultural herbaceous vegetation. Four variants, differing in their organic sources of pedogenesis, were the following:

- (1) G-G-G+: 1964-73 white clover and grasses without harvesting, 1974-83 grasses and herbs without harvesting, 1984-97 grasses and herbs weighed and returned; all formed grass-herbaceous biomass represented the source of pedogenesis.
- (2) L-G-G-: 1964-73 hop lucerne without harvesting, 1974-83 spontaneous grasses and herbs without harvesting, 1984-97 vegetation weighed and eliminated; against the background of previous complete accumulation of organic residues, elimination prevailed during the last 14 years.
- (3) B-G-BG+: 1964-73 summer barley without harvesting, 1974-83 spontaneous grasses and herbs without harvesting, 1984-87 barley weighed, grains eliminated, straw and spontaneous hop lucerne and weeds returned, 1988-97 spontaneous hop lucerne, grasses and herbs weighed and returned; against the background of annual vegetation, perennial herbage with intermittent accumulation and elimination of residues.
- (4) 0-G-G+: 1964-73 without vegetation, 1974-83 spontaneous herbs and grasses without harvesting, 1984-97 vegetation weighed and returned; against the background of continuous absence of organic agents complete accumulation of formed spontaneous biomass to the advantage of pedogenesis.

As during the second decade spontaneous grass-herbaceous vegetation occurred in case of all variants with papilionaceans and some sown grasses ousted from the sward, a mixture of meadow-grass, red fescue, timothy, ryegrass, and white clover, recommended by Sau (1983) for long-term pasture, was sown in variants 1 and 2 in 1984 to restore their initial sward. No fertilizers or herbicides were used.

Sampling

From 1984 (beginning of the third decade) the dynamics of the formation of aboveground phytomass was determined 3–4 times during each season: in late May/early June, in late June/early July, in August/early September, and in October/early November. In half of the years investigated the growth of aboveground phytomass was inhibited by obvious moisture deficiency after the third cutting, and the last sampling became impossible. Vegetation was cut from the entire area of variants, weighed and sampled for the determination of dry matter (in three replications) and for laboratory analyses. Raw phytomass was cut up and returned or removed according to the above scheme.

Analyses and calculations

Analytical procedures were carried out in the laboratories of the Institute of Soil Science and Agrochemistry, Estonian Agricultural University, by research assistant Raja Kährik. Tatyana Pogorelova-Sokolova, a PhD student, participated in this work in 1984–85. For the determination of dry matter, weighed raw samples of aboveground phytomass were dried at 105 °C in three replications and weighed again after cooling. On the basis of the obtained data total raw phytomass was recalculated as dry phytomass and expressed in g m⁻² of dry matter.

Milled dry material was used both for dry combustion and wet digestion techniques. Total ash was ascertained by the method of dry combustion at 600 °C. Nitrogen, phosphorus, and potassium were determined, respectively, by the method of wet digestion with concentrated sulphuric acid after Kjeldahl, photocolorimetrically with ammonium vanadate, and with the help of flame photometry (Rodin et al., 1968). Supplies of ash and the elements determined were calculated on the basis of particular phytomass and the percentage of measured constituents. Total supplies were found as sums of seasonal measurements. The duration of seasons (in days between two dates of measurement) was used for the calculation of diurnal changes in the characteristics studied. Traditional statistical analysis was employed for the determination of standard deviation and confidence level at 95% significance.

Walter's (1955) method was applied for the construction of climatograms. The idea of this method consists in the simultaneous graphic representation of air temperature (t, °C) and precipitation on two scales: in the first case 20 and in the other case 30 mm of precipitation corresponds to 10 °C. Precipitation curves above the temperature curve indicate sufficient moisture for normal development of vegetation. Precipitation curves below the temperature curve show moisture deficiency and draughts within the vegetation period. According to Walter, especially severe draughts are characteristic of the second (10 °C = 30 mm)

scale of temperature/precipitation relationship. Walter called climate (weather) "advective" in case precipitation curves were located above the temperature curve, and "radiational" and/or "advective with radiational elements" in case precipitation curves were located partly below the temperature curve. Data for monthly air temperature and precipitation were received from the Eerika Meteorological Station at the Faculty of Agronomy, Estonian Agricultural University, situated some hundred metres southwest of the site of our experiment.

RESULTS AND DISCUSSION

Weather situation and phytomass dynamics

Although the average of 15 years reveals advectivity of weather at Eerika, in fact there were only two (1985 and 1991) advective years (Fig. 1a–c). One or several radiation spaces in time were characteristic of all the other years. Weak air draughts occurring only in spring (1984, 1990, 1993) could have been compensated with the maintenance of available moisture status under the sward. Actually this was evidently realized in 1984 (Table 1) when April and May were warm and moisture assimilation was favoured. In spite of the similar starting situation, the process was obviously inhibited in cool springs of 1990 and 1993 (Fig. 1b), and only in midsummer did conditions for production improve. During these years, characterized by spring radiation, the vegetation period lasted until late autumn, although a decrease in annual production was observed at the end of the decade. Almost the same course of events was observed during 1987, 1989, and 1994 with weak summer radiation (Fig. 1a–b, Table 1). The seasonally wavy level of production seemed to be correlated with climatic fluctuations during these years.

Alternating weak and severe draughts in the summer of 1983, which closed the second decade of spontaneous vegetation, had no impact on the phytoproductivity of the following spring. In spite of the warm and draughty spring of 1986, the fairly good yield was obviously formed on account of soil moisture, as a result of which desuctive drying-up had to take place already by late June. Therefore, the following precipitation could neither restore available soil moisture (Fig. 1a) nor guarantee sufficient production (Table 1). Vegetation stopped practically already in early August, although air temperature and moisture relationship would still have allowed it. The situation was well reestablished by the year 1987 which was, in spite of two weak attributes of radiation (Fig. 1a), the most productive and had the longest period of vegetation (Table 1). The next (1988) year seemed to be decisive in the following formation of the amounts and dynamics of aboveground herbaceous phytomass. An obvious decrease in the organic agents of pedogenesis has been discussed already earlier (Reintam, 1995). A clear tendency towards a decrease in



t°C, air temperature; precip. mm/2, precipitation per 10 °C = 20 mm; precip. mm/3, precipitation per 10 °C = 30 mm.





Aboveground phytomass (g m⁻² of dry matter)

Table 1 continued

$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	B-G-BG+ 124 41	0-G-G-
6 July 39 33 30 31 Aug 56 26 36 Total 141 186 177 1993 20 May 36 95 60 29 June 40 70 52 20 Aug 52 105 80 27 Sep 38 18 11 Total 166 288 203 1994 31 May 53 79 57 30 June 30 54 51 26 Aug 57 88 65 24 Oct 59 25 9 Total 199 246 182		100
31 Aug 56 26 36 Total 141 186 177 1993 20 May 36 95 60 29 June 40 70 52 20 Aug 52 105 80 27 Sep 38 18 11 Total 166 288 203 1994 31 May 53 79 57 30 June 30 54 51 26 Aug 57 88 65 24 Oct 59 25 9 Total 199 246 182	41	183
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$		47
1993 20 May 36 95 60 29 June 40 70 52 20 Aug 52 105 80 27 Sep 38 18 11 Total 166 288 203 1994 31 May 53 79 57 30 June 30 54 51 26 Aug 57 88 65 24 Oct 59 25 9 Total 199 246 182	32	54
1993 20 May 36 95 60 29 June 40 70 52 20 Aug 52 105 80 27 Sep 38 18 11 Total 166 288 203 1994 31 May 53 79 57 30 June 30 54 51 26 Aug 57 88 65 24 Oct 59 25 9 Total 199 246 182	197	284
29 June 40 70 32 20 Aug 52 105 80 27 Sep 38 18 11 Total 166 288 203 1994 31 May 53 79 57 30 June 30 54 51 26 Aug 57 88 65 24 Oct 59 25 9 Total 199 246 182	105	130
20 Aug 52 105 80 27 Sep 38 18 11 Total 166 288 203 1994 31 May 53 79 57 30 June 30 54 51 26 Aug 57 88 65 24 Oct 59 25 9 Total 199 246 182	53	28
27 Sep 38 18 11 Total 166 288 203 1994 31 May 53 79 57 30 June 30 54 51 26 Aug 57 88 65 24 Oct 59 25 9 Total 199 246 182	90	108
Total 166 288 203 1994 31 May 53 79 57 30 June 30 54 51 26 Aug 57 88 65 24 Oct 59 25 9 Total 199 246 182	7	21
1994 31 May 53 79 57 30 June 30 54 51 26 Aug 57 88 65 24 Oct 59 25 9 Total 199 246 182	255	317
30 June 30 54 51 26 Aug 57 88 65 24 Oct 59 25 9 Total 199 246 182	74	102
26 Aug 57 88 65 24 Oct 59 25 9 Total 199 246 182	62	81
24 Oct 59 25 9 Total 199 246 182	76	91
Total 199 246 182	13	21
	225	295
1995 2 June 53 96 57	80	105
28 June 26 65 56	84	88
14 Sep 78 76 60	92	122
Total 157 237 173	256	315
1996 23 May 39 51 28	46	69
10 July 48 86 75	87	141
10 Sep 62 67 44	57	89
Total 149 204 147	190	299
1997 29 May 41 44 24	43	83
2 July 34 95 64	89	130
21 Aug 50 68 50	64	108
Total 125 207 138	196	321

* Barley vegetation lasted 93, 101, 90, and 106 days in 1984, 1985, 1986, and 1987, respectively.

phytoproduction as well as to the replacement of grasses by herbs (dandelion, yarrow, speedwell, etc.) and even mosses (*Rhytidiadelphus squarrosus*), beginning from the draughty year of 1988, has been mentioned too.

Except for variant O-G-G+, the total level as well seasonal dynamics of production did not improve sufficiently during either weakly draughty 1989–90 or even completely advective 1991 (Fig. 1b, Table 1). A very severe continuous draught occurred in 1992 and recurred in 1994–97. Except 1994, vegetation stopped in August/early September, while both seasonal and total production

were several times lower compared to those of 1984–87 (Table 1). A particularly marked decrease in productivity was observed in the conditions of systematic elimination of aboveground phytomass (L-G-G-). At the same time, a relatively stable situation was characteristic of the spontaneous succession of vegetation (O-G-G+), although the efficiency of natural adaptation and maximum productivity (Tooming, 1984) here were also 1.5–2.2 times higher at the beginning of the second decade of plant cover compared to that after recurrent severe draughts caused by continuous radiation.

Considering total annual and average diurnal phytomass, three levels of productivity could be distinguished after calculating both the vegetation period and the yield (Table 2). The production level of 1974–83, calculated on the basis of annual dead grass (Reintam & Pogorelova, 1987), was quite similar to the level of 1988–91. Owing to the variability of annual and monthly precipitation (Fig. 1a–c), the diurnal productivity by seasons showed great variation as well (Fig. 2). Predominant reciprocal interdependences between productivity

Table 2

Year	No of days	Total annual phytomass, g m ⁻²				Diurnal accumulation, g m ⁻² d ⁻¹				
		<i>G–G–G</i> +	LGG	- <i>B</i> - <i>G</i> - <i>BG</i> +	0GG+	<i>G</i> – <i>G</i> – <i>G</i> +	LGG	B-G-BG+	0-G-G+	
1974-	164*	364	342	332	404	2.2	2.1	2.0	2.5	
1983	212**					1.7	1.6	1.6	1.9	
1984	212	543	437	255	568	2.6	2.1	2.7***	2.7	
1985	124	563	486	257	548	4.5	3.9	2.5***	4.4	
1986	103	388	356	282	379	3.8	3.5	3.1***	3.7	
1987	204	589	626	227	683	2.9	3.1	2.1***	3.4	
1988	134	323	413	338	336	2.4	3.1	2.5	2.5	
1989	181	358	334	392	480	2.0	1.8	2.2	2.7	
1990	198	349	323	424	381	1.8	1.6	2.1	1.9	
1991	196	333	321	372	409	1.7	1.6	1.9	2.1	
1992	141	186	177	197	284	1.3	1.3	1.4	2.0	
1993	166	288	203	255	317	1.7	1.2	1.5	1.9	
1994	199	246	182	225	295	1.2	0.9	1.1	1.5	
1995	157	237	173	256	315	1.5	1.1	1.6	2.0	
1996	149	204	147	190	299	1.4	1.0	1.3	2.0	
1997	125	207	138	196	321	1.7	1.1	1.6	2.6	
1984-87*	161	521	476	255	545	3.2	3.0	1.8	3.4	
1988-91*	177	341	348	382	402	1.9	2.0	2.2	2.3	
1992-97*	156	228	170	220	305	1.5	1.1	1.4	2.0	

Total aboveground phytomass and average diurnal accumulation

* Average annual and/or diurnal.

** Possible maximum number of days.

*** Barley vegetation lasted 93, 101, 90, and 106 days in 1984, 1985, 1986, and 1987, respectively.



Fig. 2. Diurnal accumulation of above ground phytomass, g $m^{-2}\,d^{-1}.$

A, from the beginning of vegetation until late May/early June; B, from late May/early June until late June/early July; C, from late June/early July until August/early September; D, from August/early September until October/early November.

and climatic relationships seem to be fundamental there. Severe draughts in the second half of the vegetation period influenced production efficiency at the outset of the next year. Therefore, beginning from the year 1989, which followed the draughty year of 1988, a general decrease in diurnal accumulation of aboveground phytomass has taken place. Moss cover developed particularly intensively after 1992, which has caused a manifold decrease in annual and average diurnal herbaceous mass compared to previous periods (Table 2). Against the background of more or less homogeneous summer temperature (monthly deviation only 1.3-1.7 °C from June to August, and 1.9-2 °C in May and in September-October), monthly differences in precipitation were up to 20-fold in June and August and 6-7-fold in July and September-October. Therefore unstable production was characteristic of all seasons, being on average a little higher in early summer (Fig. 2, B) when only 1988 and 1992 were arid, and a prevalently advective regime occurred. Owing to the warm and moist springs in 1984-88 (Fig. 1a) notable seasonal and diurnal increments of phytomass were attained in May (Table 1, Fig. 2, A). Except for draughty 1988, total annual phytomass was the highest in these years due to spring accumulation (Table 2).

Irrespective of absolute annual and diurnal production, the seasonal distribution of aboveground phytomass (% of annual) demonstrated strong dependence upon weather relationships (Figs. 1 and 3). A decrease in productivity in spring was evident after draughty 1988 and particularly after 1995. The main production in these years was formed in midsummer, obviously because of soil moisture whose evaporation was prevented by *Rhytidiadelphus* and which was not used by spring vegetation suffering for the weather radiativity of the previous year. The largest portion of spring phytomass was characteristic of draught years with low absolute productivity. The longer was the vegetation period, the larger was the share of productivity falling on late summer and autumn.

The impact of seasonal changes in weather relationships on the botanical composition of herbaceous vegetation and phytoproductivity as its quantitative outcome has been revealed by the theory and practice of grassland husbandry (Klapp, 1956; Toomre, 1965; Sau, 1965, 1983). Frequent temporary moisture deficiency has always resulted in the replacement of ground grasses by root weeds and other more adaptable herbs, while aboveground productivity decreased many times. Besides weather dynamics, the impact of cutting has been considered important in bringing along changes in phytocoenotic successions and productivity (Kukk & Kull, 1997). Although three trial variants were characterized by a closed turnover of substances, the eventual deficiency of available nutrients could induce degradation of cultural grass sward, as it appeared in case of pastures under arid conditions (Toomre, 1965; Sau, 1983). Therefore, beginning from years with continuous radiation (1988, 1992), the variant of primary succession $(\partial-G-G+)$ proved more efficient than any other.



Fig. 3. Seasonal distribution of aboveground phytomass, % of annual.

1, from the beginning of vegetation until late May/early June; 2, from late May/early June until late June/early July; 3, from late June/early July until August/early September; 4, from August/early September until October/early November.

Phytomass composition and turnover of substances

In general, the total ashness increased towards autumn and it was higher in the two last (B-G-BG+ and 0-G-G+) variants characterized by primary succession (Table 3). At the same time the spring and spring-summer aspects of these variants were enriched with sappy herbs owing to which the ashness of the first two variants (G-G-G+ and L-G-G-) was about 10-20% higher. Greater

Table 3

Average ash and NPK content (x) and its confidence limits at 95% significance (s) in the aboveground phytomass of perennial herbs, %

Variant	Season	Ash		Nitrogen		Phosphorus		Potassium	
	o, 1970), and could be in	x	S	x	S	x	S	х	S
G = G = G +	Until late May/early June	9.3	2.0	2.17	0.28	0.39	0.04	2.12	0.38
	Late May/early June until late June/early July	9.2	0.9	2.10	0.28	0.44	0.07	2.56	0.33
	Late June/early July until August/early September	10.2	1.1	2.06	0.28	0.42	0.04	2.18	0.32
	August/early September until October/November	10.9	3.2	2.80	0.35	0.48	0.04	2.15	0.38
L-G-G-	Until late May/early June	9.2	2.7	2.29	0.34	0.43	0.08	2.08	0.37
systems annual	Late May/early June until late June/early July	9.1	1.1	2.15	0.45	0.49	0.15	2.55	0.36
	Late June/early July until August/early September	10.0	1.0	2.23	0.28	0.44	0.04	2.27	0.36
	August/early September until October/November	11.8	4.8	2.77	0.40	0.50	0.05	2.08	0.30
B-G-BG+	Until late May/early June	7.6	0.7	2.10	0.15	0.38	0.04	2.45	0.16
	Late May/early June until late June/early July	9.3	1.4	2.18	0.25	0.42	0.03	2.46	0.18
	Late June/early July until August/early September	9.2	0.9	2.18	0.20	0.41	0.04	2.23	0.25
	August/early September until October/November	10.8	4.7	2.62	0.50	0.42	0.05	2.02	0.46
0-G-G+	Until late May/early June	8.7	1.6	2.04	0.29	0.44	0.05	2.44	0.23
	Late May/early June until late June/early July	8.7	0.8	2.00	0.25	0.47	0.07	2.45	0.30
	Late June/early July until August/early September	10.0	1.1	2.01	0.25	0.47	0.07	2.29	0.25
	August/early September until October/November	10.7	1.8	2.68	0.43	0.46	0.04	2.07	0.56

variation of ashness there was caused by some extremely high (14–23%) features in the autumn of 1984 and 1989, but also in the spring (14–24%) of 1984 and 1987. An extremely low ashness (5.8–6.8%) occurred in springs (1994, 1996, 1997) following moist autumn and winter. Summer phytomass was characterized by quite uniform ashness in all variants. Barley grains contained 2.2–3.5% of ash, while the ashness of barley straw depended upon the mixture of spontaneous hop lucerne: 5.6–6.3% in 1984–85, 7.6–8.0% in 1986–87. Owing to this, the area under barley was spontaneously overgrown with lucerne and grasses.

Nitrogen and phosphorus also showed a tendency to increase towards autumn, although differences were smaller than in case of ash. Standard deviation was bigger in autumn compared to the other seasons (Table 3). In phosphorus there were no considerable differences between the variants. A slight variant-related and seasonal enrichment with nitrogen seemed to be due to hop lucerne and white clover up to 1987. Spontaneous herb vegetation (O-G-G+) was comparatively poor in nitrogen, and only in autumn an increase had taken place. In general, this phenomenon is irregular (Arvisto, 1970), and could be interpreted only as a prolonged synthesis of albumens by grasses with relatively warm and damp weather. Contrary to other features, potassium increased and/or was stable from spring to summer and decreased until late autumn. Such a dynamics was similar to that of carbohydrates (Arvisto, 1970) and can be due to the seasonal absorption of potassium for biosynthesis as well as due to its metabolic release and cyclings. Barley grains were slightly richer in phosphorus (0.4-0.8%) than grasses (0.38–0.5%) and straw (0.2–0.5%). Barley was poor in potassium: <1%in grains and <2% in straw.

Nitrogen and ash elements that have been circulating in plant-soil systems and/or have been removed with yields revealed a temporary decrease in annual amounts in 1986 and a continuous decrease from 1988 onwards, both calculated on the basis of the same data for seasonal phytomass content (Figs. 4 and 5). With a few rare exceptions, the dynamics of substances demonstrated an identical reflected image on both sides of the zero line, with annual differences in variants being greater for potassium and smaller for total ash. As a result of the removal of the yield (*L*-*G*-*G*-), 468.6, 101.6, 20.9, and 96.6 g m⁻² of ash, nitrogen, phosphorus, and potassium, respectively, were eliminated from the site during 14 years. Such an impoverishment of the site resulted in a decrease in the soil sources and pedogenetic intensity (Reintam, 1995, 1997). The rate of removal with the aboveground yield amounted to about 109, 24, 5, and 22 g kg⁻¹ (kg Mg⁻¹) of ash, nitrogen, phosphorus, and potassium, and potassium, respectively. Such a situation in agricultural practice can lead to an impoverishment of soil even under perennial herbaceous sward, not to speak of cereal monoculture.

Against the background of yield return, nearly the same amounts of elements participated in biogeochemical turnover (Table 4). Only spontaneous lucerne, grasses, and herbs contained about 25% less ash in annual cycling after four years of barley (B-G-BG+) compared to herbaceous vegetation in the two other



Fig. 4. Amount of ash and nitrogen in the aboveground phytomass, $g m^{-2}$.

variants with a permanent perennial cover. This seemed to be mainly due to the lower ashness of the yield in spring and late summer (Table 3). Low intensity of the cycling of substances (amounts less than annual average) was characteristic of 43-60% of the years; a medium intensity around the average value was revealed in 14–36% of the cases (Table 4). The rate of biological absorption and restoration by aboveground phytomass of perennial herbaceous vegetation was $95-105 \text{ g kg}^{-1}$ of ash and $20-22 \text{ g kg}^{-1}$ of nitrogen.

The seasonal distribution of ash and nitrogen was dynamic depending on the composition of sward and on weather relationships (Figs. 6 and 7). After the improvement of sward in 1984, the increase in spring absorption of mineral



Fig. 5. Amount of phosphorus and potassium in the aboveground phytomass, g m⁻²

nutrients lasted until 1987. Then more than 50% of them was removed (L-G-G-) or 40–60% returned by the yield (G-G-G+). Increased removal of main biogens (NPK) continued one more year, but against the background of phytomass return, a clear increase occurred in their summer absorption. Except for the extremely arid year of 1992, predominant ash and nitrogen accumulation was first transferred to late summer–early autumn and then (from draughty 1994 and/or 1995) to midsummer when vegetation that had suffered for former draughts recovered a little. Also, the dynamics of the seasonal distribution of nitrogen as well as phosphorus can be accounted for by the predominant summer synthesis of albumens and nucleoproteins by grasses and herbs (Arvisto, 1970).

Variant	Constituent	Total amount, g m ⁻²	Annual average, g m ⁻²	Number of years with the following cycling intensity			
				high	medium	low	
<i>G–G–G</i> +	Ash	503.8	36.0	4	4	6	
	Nitrogen	101.8	7.3	4	4	6	
	Phosphorus	22.0	1.6	6	1	7	
	Potassium	105.2	7.5	6	2	6	
<i>B–G–BG</i> +	Ash	283.8	28.4	4	0	6	
	Nitrogen	63.9	6.4	4	0	6	
	Phosphorus	12.4	1.2	3	1	6	
	Potassium	68.7	6.9	4	0	6	
0-G-G+	Ash	534.9	38.2	5	3	6	
	Nitrogen	114.1	8.2	4	2	8	
	Phosphorus	26.4	. 1.9	3	5	6	
	Potassium	129.7	9.3	4	4	6	

Characterization of substances cycling in perennial grasses and herbs

About two thirds of ash and nitrogen also accumulated in the spring phytomass of spontaneously formed vegetation in draughty 1992. A few years after barley the increased ash, nitrogen, and phosphorus contents in August phytomass were obviously caused by the larger share of spontaneous hop lucerne there. In connection with the dynamics of both quantitative and qualitative characteristics (Tables 1-3, Figs. 2, 3) basic biological absorption during the last quinquennium has been transferred to midsummer. Almost the same was characteristic of the seasonal distribution of substances in the fourth variant, where annual differences were markedly smaller and the portions of both spring and late summer accumulations slightly more homogeneous. This can also be interpreted as an example of interregulated adaptation in the progress of primary succession (Tooming, 1984). Systematic consumption of ash elements, among them main biogens, on account of soil sources mobilized as a result of weathering and pedogenetic activities, can keep them in action against the background of the returning regime with simultaneous relative enrichment of the thin uppermost solum. However, downward migration of some portion of nitrogen and ash elements cannot be excluded because of an increase in their summer and autumn accumulation and a decrease in their spring accumulation in phytomass.







Fig. 7. Seasonal distribution of nitrogen (% of annual amount) in the aboveground phytomass. Seasons 1–4 see Fig. 3.

The productivity level and dynamics of sown and spontaneous perennial herbaceous vegetation depended to a great extent on weather advectivity and/or presence and frequency of radiation attributes, forming specific temperature/moisture relationships and the moisture availability status. Weak spring draughts in cool weather were sufficient to exert a negative impact on productivity and its further dynamics, while early radiation affected production to a lesser extent in seasons following warm but draughty spring. Weak summer radiation led to a slight seasonal decrease in productivity whereas fluctuations in annual weather resulted in the waviness of the seasonal efficiency of production. Severe summer draughts affected not only the productivity of the current year and the length of the vegetation period, but also the situation of the following years. Radiativity in the second half of the vegetation period had a negative impact on the production at the outset of the following year. Beginning from the particularly draughty years of 1988 and 1992, characterized by continuous summer radiation, a drastic decrease in productivity continued. Simultaneously, there occurred a decrease in the spring proportion of production and an increase in the late summer and afterwards also in the midsummer proportion of production. Considering total annual and average diurnal phytomass, the highest level of efficiency was characteristic of the first quadrennium after sward improvement and the lowest, of the arid last quinquennium. Possible changes in weather towards increasing advectivity can restore coenotic cycles with higher productivity, although most papilionaceans and grasses would have been replaced by root weeds and green mosses. Annual and seasonal changes in the composition of swards seemed to be worthy of special observation. Spontaneous vegetation revealed quite good adaptation in case of any weather situation, while the greatest decrease in productivity occurred under systematic removal of the aboveground yield.

An increase in ashness as well as in the content of nitrogen and phosphorus, and a decrease in potassium towards autumn were characteristic of aboveground herbaceous phytomass. Owing to some extreme values in different years, heterogeneity of composition occurred in spring and autumn, relative homogeneity being characteristic of summer. At the same time, the amounts of phytomass constituents participating in ecosystem processes and/or being eliminated with the yield had been previously dependent on the amount of organic matter. Therefore the basic dynamics of phytoproductivity was reflected in the dynamic turnover of substances. Around the zero line there appeared a mirror reflection of substances returned into the system and removed from it. Due to frequent radiations and severe draughts, up to 60% of the years were characterized by a low-intensity turnover of substances. High intensity was characteristic of about 30-40% of the years. With the aboveground yield 109, 24, 5, and 22 g kg⁻¹ (kg Mg⁻¹) of ash, nitrogen, phosphorus, and potassium,

respectively, were eliminated. Such a situation corresponds to modern agriculture where in the absence of fertilization (without ecological regulation of biogeochemical cyclings) progressive impoverishment of the solum can take place even in fallowed fields with perennial grass-herbaceous vegetation. Similar amounts of substances returned into circulation appeared to prevent soil exhaustion but could not ensure either preservation of sown sward or initial production efficiency. Only primary succession in the form of spontaneous progress of the herb cover seemed to confirm also interregulated adaptation and preservation of chemical constituents. Relative enrichment of thin topsoil on the account of reddish-brown till transforming into soil took place, although some downward migration of nitrogen, potassium, and perhaps aluminium and silica could not be excluded.

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REFERENCES

- Arvisto, E. 1970. Content, supply, and net primary production of biochemical constituents in the phytomass of spruce stands on brown forest soils. In *Estonian Contributions to the International Biological Programme, I* (Frey, T., Laasimer, L. & Reintam, L., eds.). Tartu, 49–70.
- Bazilevich, N. I. 1979. Productivity and biochemistry of recent biosphere and functional models of ecosystems. *Pochvovedenie (Soviet Soil Science)*, 2, 5–21.
- Bohn, H. 1976. Estimate of organic carbon in World soils. Soil Sci. Soc. Am. J., 40, 3, 468-470.
- Bryant, R. B. & Arnold, R. W. 1994. *Quantitative Modeling of Soil Forming Processes*. SSSA Spec. Publ. No 39. ASA, CSSA, SSSA. Madison, WI, 185.
- Creemens, D. L. 1995. Pedogenesis of Cotiga Mound, a 2100-year-old woodland mound in Southwest West Virginia. Soil Sci. Soc. Am. J., 59, 5, 1377-1388.
- Graham, R. C., Ervin, J. O. & Wood, H. B. 1995. Aggregate stability under oak and pine after four decades of soil development. *Soil Sci. Soc. Am. J.*, **59**, 6, 1740–1744.
- Hoosbeek, M. R. & Bryant, R. B. 1994. Pedodynamics: an approach to study and quantify soil forming process. In *Trans. of 15th World Congr. of Soil Science*. Vol. 6a: Comm. V: Symposia, 164–178. Acapulco, Mexico.
- Klapp, E. 1956. Wiesen und Weiden. Behandlung, Verbesserung und Nutzung von Grünlandflächen. Dritte Auflage. Paul Parey Verlag, Berlin-Hamburg.
- Kukk, T. & Kull, K. 1997. Puisniidud. Estonia Maritima. Publication of the West-Estonian Archipelago Biosphere Reserve No 2.

Kylli, R. K. 1981. On the biologic production of forest and agricultural biogeocoenosis types as related to soil properties. *Pochvovedenie (Soviet Soil Science)*, 10, 5–10.

Pärna, N. 1978. Rütm, elu ja looming. Loomingu Raamatukogu, 50/51, 90.

- Reintam, L. 1982. Changes in the balance of substances within the pedogenesis under the herbaceous vegetation. In Trans. of Estonian Agricultural Academy, 143. Soil Properties and Biological Productivity. Tartu, 3–18.
- Reintam, L. 1988. Interrelations between vegetation and soils and environmental control. In Protection of the Plant Kingdom in the Estonian SSR (Laasimer, L.-M., ed.). Valgus, Tallinn, 59-64.
- Reintam, L. 1995. Temporal and spatial changes in organic agents in the progress of primary pedogenesis during thirty years. *Proc. Estonian Acad. Sci. Ecol.*, **5**, 3/4, 61–76.
- Reintam, L. 1997. Pedogenetic changes in the quantity and distribution of textural and chemical soil constituents during thirty years. Proc. Estonian Acad. Sci. Biol. Ecol., 46, 3, 174–190.
- Reintam, L. J. & Pogorelova, T. A. 1987. Initial soil formation on red-brown calcareous moraine under herbaceous vegetation. Soviet Soil Science, 19, 2, 1–13.
- Rodin, L. E., Remezov, N. P. & Bazilevich, N. I. 1968. Methodical Instructions for the Study of Dynamics and Biological Turnover in Phytocoenosis (in Russian). Nauka, Moscow.
- Sau, A. 1965. Madalasaagiliste kultuurkarjamaade parandamine. Eesti Raamat, Tallinn.
- Sau, A. 1979. The intensity of the humus-accumulative process on reddish brown calcareous moraine. In Soils and Their Biological Production (Oja, A., ed.). Tartu, 17–18, 207.
- Sau, A. 1983. The intensity of soil formation process under the influence of perennial herbage. In Trans. of Estonian Agricultural Academy, 140. Theoretical Problems of the Intensification of Grassland Husbandry. Tartu, 27-46.
- Tooming, H. 1984. *Ecological Principles of Maximum Crops Productivity* (in Russian). Hydromet Publishers, Leningrad.
- Toomre, R. 1965. Pikaajalised kultuurkarjamaad ja nende kasutamise teaduslikud alused. Valgus, Tallinn.
- Walter, H. 1955. Die Klimagramma als Mittel zur Beurteilung der Klimaverhältnisse für ökologische, vegetationkundliche und landwirtschaftliche Zwecke. Ber. d. Deutsch. bot. Gesellschaft, 68, 7–10, 331–344.

MAAPEALSE FÜTOMASSI, LÄMMASTIKU JA TUHAELEMENTIDE DÜNAAMIKA MULLATEKKEPROTSESSI PÜSIKATSES

Loit REINTAM

Uuriti rohttaimede maapealse massi ja selle koostise dünaamikat 1963. aastal rajatud ning 1964. aastal käivitatud mullatekkeprotsessi püsikatses selle 21. kestusaastast alates. 14 aasta jooksul ilmnes aastases ja ööpäevases produktiivsuses kolm taset: kõrgeim neljal aastal vahetult pärast kultuurkõrreliste kamara parandamist ning madalaim viimasel viiel kestvate põudadega aastal. Kuigi loodusliku suktsessiooni teel spontaanselt moodustunud taimestu produktiivsuse ja fütomassi koostise võrdlemiseks kasutati Walteri (1955) meetodil koostatud kliimagramme peegeldamaks produktsiooniprotsessi fluktuaalsust seoses ilmastiku sesoonsuse ja muutlikkusega. Aastate keskmisena advektiivset ilmastikku iseloomustas aastati ajaliselt vahelduv ja sage radiatsioonilisus, mis põhjustaski mitmekordseid erinevusi fütomassi ja selle koostise dünaamikas. Alates kestvatest põudadest 1988. ja eriti 1992. aastal vähenes produktiivsus ja aineringes osalenud ainete hulk järsult. Kestev radiatsioonilisus vegetatsiooniperioodi teisel poolel mõjus negatiivselt ka järgmise aasta kevadsuvel arenevate protsesside intensiivsusele. Pärsitud produktsiooniprotsess kevadel tingis muutusi rohukamara koostises ja samblarinde moodustumise, mis omakorda vähendas maapealset saagikust ja bioloogilise neelamise mahtu. Ilmastikust tingituna oli aineringete intensiivsus madal 42-60%, kõrge aga 30-40% aastatest. Järjest vähenes kevadise ja suurenes suviste perioodide osatähtsus aastaproduktsioonis ning aineringe mahus. Taim-muld-süsteemist eemaldati maapealse fütomassiga vastavalt 109, 24, 5 ja 22 g kg⁻¹ (kg Mg⁻¹) tuhaelemente, lämmastikku, fosforit ja kaaliumi. Seega võib isegi mitmeaastastel söötidel saagi koristamine mulda oluliselt vaesustada. Maapealse massi tagastamisel mulda jääb ligikaudu samasugune kogus aineid bioloogilisse ringesse ning osaleb akumulatiivses mullatekkeprotsessis.