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PHYTOMASS RESERVES IN THE ALPINE TUNDRA OF
THE NORTHERN URALS AND THEIR VARIATION
DURING SUCCESSION

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The phytomass reserves were studied in five alpine-tundra plant communities belonging to different elements of the succession series. It was established that there was a tendency toward changes in phytomass reserves (subdivided into live and dead), the ratio of the aerial and subterranean components, and reserve structure (primarily that of the live forms) during succession.

The International Biological Program, which has entered its final, synthetic stage, has promoted the expansion of research on the biological productivity of plant communities in different geographic regions and altitude zones. The alpine tundra characteristic of the upper Urals is an interesting subject of studies of this sort. The composition, structure, distribution patterns, and successional-variation tendencies of the flora of the Ural alpine tundra have been rather thoroughly elucidated (Gorchakovskii, 1966). It was established that, as the blocks of massive-crystalline rock are pulverized, the relief becomes smoother, melkozem is deposited, the water supply is stabilized, and a more highly developed soil is formed in high alpine areas, there is a gradual transformation of the flora from primary labile moss-lichen communities on rocky slopes to climax communities of the herb-moss tundra. However, the succession stages in alpine tundras were previously analyzed only on the basis of habitat transformation, floristic composition, and plant-community level structure. The changes in the productivity of alpine-tundra communities during succession remained unclear. In this connection, we attempted to trace the changes in the phytomass reserves in communities of the Ural alpine tundra during succession.

TABLE 1. Characteristics of Alpine Tundras Studied (Projective coverage, species composition of main components, and abundance)

Level	Association				
	primary moss-lichen communities on rocky slopes	dryad (rock)	blueberry-crowberry (shrub-moss)	dwarf birch-Hylocomium (shrub-moss)	sedge-Rhacomitrium-Hylocomium (herb-moss)
Shrub	—	—	5%; sol.— <i>Salix reticulata</i> , <i>S. glauca</i> , <i>S. arctica</i>	60%; cop. ₂ —cop. ₃ — <i>Betula nana</i> , sp.— <i>Salix reticulata</i>	10%; sp.— <i>Salix reticulata</i> , <i>Betula nana</i>
Herb-shrub	—	40%; cop. ₂ — <i>Dryas octopetala</i> , cop. ₁ — <i>Festuca supina</i> , sp.— <i>Vaccinium uliginosum</i> , <i>V. vitis-idaea</i>	60%; cop. ₁ —cop. ₂ — <i>Vaccinium uliginosum</i> , <i>Empetrum hermaphroditum</i> , cop. ₁ — <i>Dryas octopetala</i> , sp.— <i>Carex hyperborea</i> , <i>Polygonum bistorta</i> , <i>Anemone biarmiensis</i>	45%; cop. ₁ —cop. ₂ — <i>Vaccinium vitis-idaea</i> , sp.— <i>V. uliginosum</i> , <i>Dryas octopetala</i> , <i>Empetrum hermaphroditum</i> , <i>Carex hyperborea</i> , <i>C. vaginata</i> , <i>C. capillaris</i> , <i>Polygonum viviparum</i>	85%; cop. ₂ — <i>Carex hyperborea</i> , sp.— <i>C. vaginata</i> , <i>C. sabyensis</i> , <i>Thalictrum alpinum</i> , <i>Myosotis asiatica</i> , <i>Lagotis uralensis</i> , <i>Polygonum bistorta</i> , <i>Valeriana capitata</i>
Moss-lichen	10%; cop. ₁ —cop. ₂ — <i>Rhacomitrium lanuginosum</i> , <i>Umbilicaria pennsylvanica</i> , cop. ₁ —sp.— <i>Rhizocarpon geographicum</i> , <i>Haematoma ventosum</i> , <i>Lecidea flavocoeerulecens</i>	45%; cop. ₁ —cop. ₂ — <i>Cladonia alpestris</i> , <i>C. situatica</i> , sp.— <i>Cetraria islandica</i> , <i>C. nivalis</i> , <i>Thamnolia vermicularis</i> , <i>Dicranum congestum</i> , <i>Alectoria ochroleuca</i>	70%; cop. ₂ — <i>Hylocomium splendens</i> , sp.—cop. ₁ — <i>Pleurozium schreberi</i> , <i>Dicranum congestum</i> , sp.— <i>Cladonia alpestris</i> , <i>Cetraria laevigata</i> , <i>Thuidium abietinum</i>	95%; cop. ₂ —cop. ₃ — <i>Hylocomium splendens</i> , sp.—cop. ₁ — <i>Pleurozium schreberi</i> , <i>Dicranum congestum</i> , sp.— <i>Polytrichum strictum</i>	90%; cop. ₂ —cop. ₃ — <i>Hylocomium splendens</i> , cop. ₁ — <i>Rhacomitrium lanuginosum</i> , sp.— <i>Aulacomnium turgidum</i> , <i>Dicranum congestum</i> , <i>Pleurozium schreberi</i>

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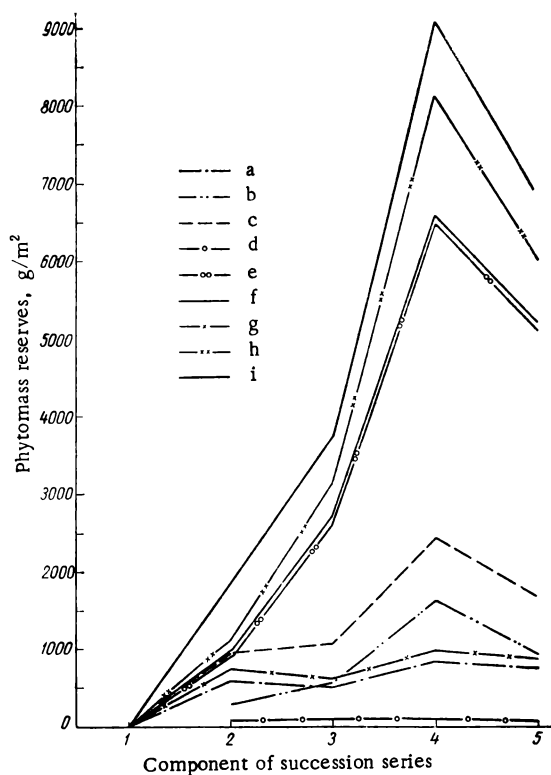


Fig. 1

Fig. 1. Change in phytomass reserves (g/m^2) during succession of alpine-tundra flora (from studies made in 1972). 1) Primary moss-lichen communities on rocky slopes; 2) dryad tundra; 3) blueberry-crowberry tundra; 4) dwarf birch-Hylocomium tundra; 5) sedge-Racomitrium-Hylocomium tundra. Live phytomass reserves: a) aerial; b) subterranean; c) total. Dead phytomass reserves: d) aerial; e) subterranean; f) total. Total phytomass reserves: g) aerial; h) subterranean; i) total.



Fig. 2

Fig. 2. Structure of aerial biomass during different stages of succession in alpine tundra (from studies made in 1972). 1-5) The same as in Fig. 1. Life forms: a) lichens; b) mosses; c) low shrubs; d) shrubs; e) herbs.

MATERIALS AND METHOD

Field investigations were conducted over two growing seasons, 1971 and 1972. The area of our investigations was Konzhakovskii Kamen', a typical mountain massif of the Northern Urals, where all basic stages in the succession of the alpine-tundra flora were well represented. Our subjects were five alpine-tundra communities (at an altitude of 950-1050 m above sea level) belonging to the same ecogenetic series and reflecting the stages in the succession of the alpine-tundra flora (Table 1). Primary sampling plots with an area of 100 m^2 each were laid out in each type of tundra.

In order to determine the aerial phytomass reserve, plots with sizes of 20×20 , 25×25 , or 50×50 cm were laid out in the main sampling plots on a random basis. The size of these smaller plots was selected in accordance with the size of the plant aerial organs: for the primary moss-lichen communities on rocky slopes, where relatively small lichen thalli and moss mats predominated, a size of 20×20 cm was employed; for most of the alpine-tundra associations (except the shrub-moss associations), we selected a plot size of 25×25 cm; for the shrub-moss tundra with large dwarf birch shoots, a size of 50×50 cm was used. The number of sample plots on each main plot was chosen in such fashion that the statistical error in determining the phytomass reserves did not exceed 10-15%. A total of 340 sample plots with a total area of 22.3 m^2 was laid out for determination of the aerial phytomass reserve.

At the height of the growing season, when the aerial phytomass reserves were close to maximal, the aerial organs of the plants were cut (at the boundary between the green and brown portions for the mosses) and divided into basic life forms (lichens, mosses, shrubs, low shrubs, and herbs); they were

TABLE 2. Phytomass Reserves in Alpine Tundras (from results of studies over two growing seasons)

Type of tundra	year of study	Phytomass, g/m ²								
		aerial			subterranean			total reserve		
		live (mass of flowering plants in paren.)	dead	total	live	dead	total	live	dead	total
Primary moss-lichen communities on rock slopes	1971	15	—	15	—	4	4	15	4	19
	1972	14	—	14	—	3	3	14	3	17
Dryad (rock)	1971	497(142)	74	571	171	414	585	668	488	1156
	1972	612(131)	113	725	278	838	1116	890	951	1841
Blueberry-crowberry (low shrub-moss)	1971	586(218)	123	709	665	2156	2821	1251	2279	3530
	1972	512(187)	130	642	534	2629	3163	1046	2759	3805
Dwarf birch-Hylocomium (shrub-moss)	1971	907(506)	90	997	1340	5365	6705	2247	5455	7702
	1972	851(514)	138	989	1623	6498	8121	2474	6636	9110
Sedge-Rhacomitrium -Hylocomium (herb -moss)	1971	707(255)	90	797	1023	5128	6151	1730	5218	6948
	1972	726(248)	87	813	920	5154	6074	1646	5241	6887

dried to the air-dry state and weighed. The aerial phytomass was divided into live and dead. All dead plant material fell into the latter category, including both that still attached to the foliage and that which had dropped and was on the surface of the moss or in its green layer. The green parts of the mosses were considered to be a component of the live phytomass.

In order to determine the subterranean phytomass reserves, we took soil monoliths of the same size as the plots used to evaluate the aerial phytomass. The depth of the monoliths corresponded to the maximum depth of root penetration. The number of plots was selected in such fashion that the statistical error did not exceed 15-20%. We laid out 300 sample plots with a total area of 16.7 m² for determination of the subterranean phytomass. The litter and the brown parts of the mosses were first collected from the surface of each plot. The monolith was then dug and the underground portions of the stems, rhizomes, and large roots were separated and washed free of soil particles. The remainder of the subterranean phytomass was separated from the soil by washing in sieves with a mesh diameter of 0.25 mm. The subterranean organs of the flowering plants were separated into live and dead on the basis of color and consistency. The subterranean phytomass reserve was determined separately for the air-dry live and dead components. The litter and the brown portion of the mosses were included in the dead phytomass, in conformity with the recommendations made by Aleksandrova et al. (1958). The small semidecomposed plant particles retained by the sieve were also included in the dead matter.

Procedures for determining the dead phytomass reserve (both aboveground and subterranean) and criteria for distinguishing it are still poor. There are many difficulties in dividing the branches, rhizomes, and roots of flowering plants and mosses into live and dead portions. Some dead matter may be lost during washing. However, if researchers state that they are using the procedure we have adopted for separation of live and dead phytomass, the results they obtain can be utilized for comparison and generalization.

RESULTS AND DISCUSSION

The phytomass reserves (classified as live and dead, aerial and subterranean) in different components of the tundra-community succession series are given in Table 2 and Fig. 1.

Analysis of these data showed that the aerial phytomass reserves increased during succession, from 15 (14) g/m² in the primary moss-lichen communities * to 907 (851) g/m² in the shrub-moss tundra; the biomass reserves decreased to 707 (726) g/m² on moving to the herb-moss tundra. The dead aerial phytomass reserve remained roughly constant in most elements of the succession series (from the second to the fifth).

*Here and in the text that follows, the figures in parentheses for the phytomass reserve represent the second year of our investigations.

TABLE 3. Ratio of Aerial and Subterranean Phytomass in Alpine Tundra (from results of investigations conducted over two growing seasons)

Type of tundra	Year of study	Ratio of aerial and subterranean phytomass		
		live only	dead only	total
Primary moss—lichen communities on rocky slopes	1971	—	—	1:0,3
	1972	—	—	1:0,2
Dryad (rock)	1971	1:0,3	1:5,6	1:1
	1972	1:0,4	1:17,5	1:1,5
Blueberry—crowberry (low shrub—moss)	1971	1:1,1	1:20,2	1:4
	1972	1:1	1:24,1	1:4,9
Dwarf birch—Hylocomium (shrub—moss)	1971	1:1,5	1:59,6	1:6,7
	1972	1:1,9	1:47,1	1:8,2
Sedge—Rachomitrium—Hylocomium (herb—moss)	1971	1:1,4	1:57	1:7,7
	1972	1:1,3	1:59,2	1:7,5

A similar pattern was observed for the change in subterranean biomass: as succession proceeded, the reserve increased from 171 (278) g/m² in the rocky tundra to 1340 (1623) g/m² in the shrub—moss tundra and dropped to 1023 (920) g/m² in the herb—moss tundra.

The increase in the dead phytomass reserve was due almost wholly to the subterranean component. There was an increase in soil peat content.

The curve representing the change in dead phytomass reserve during the course of succession resembled that for the changes in aerial and subterranean live phytomass, but the reserves of dead material were considerably greater than those of live material and the difference between the former curve and the latter two increased continuously as succession progressed. This was apparently due to the fact that, on moving from each succession stage to the next, the annual aerial-biomass production increased and the rate of plant-material decomposition remained essentially unchanged. This led to a continuous increase in the dead phytomass reserve.

On the whole, there was a tendency toward an increase in the reserves of live and dead phytomass (both aerial and subterranean) from the primary moss—lichen communities to the shrub—moss tundra and a slight decrease on moving to the herb—moss community. The decrease in the reserve of live aerial and subterranean phytomass on moving from the shrub—moss tundra to the herb—moss tundra was due to the fact that the dominant shrubs with long-lived, woody stems that did not die back to the ground and long-lived woody roots were replaced by herbaceous plants with aerial organs that died at the end of the growing season.

The structure of the aerial biomass in the communities investigated (as distributed over the principal life forms) is shown in Fig. 2. As can be seen, the dominant component of the aerial biomass in the primary moss—lichen communities studied was the mosses, with the lichens constituting a considerably smaller proportion. The lichens had the advantage in the rocky tundra, followed by flowering plants, which were represented primarily by low shrubs, and mosses. The mosses dominated with respect to biomass in the low shrub—moss tundra, second place being occupied by flowering plants (also primarily low shrubs), and third place by lichens. Flowering plants were clearly dominant in the shrub—moss tundra (primarily shrubs, represented by dwarf birch), followed by mosses and lichens. On moving to the herb—moss tundra, mosses again began to dominate the aerial biomass, with flowering plants (mostly herbs) lagging considerably behind and the role of the lichens being slight.

It follows from the data given above that the aerial biomass in most of the tundra types considered above was dominated by mosses, which gave way to lichens only in the rocky tundra and to flowering plants only in the shrub—moss tundra.

The aerial phytomass (total live and dead) exceeded the subterranean phytomass by a factor of 3-5 in the primary moss—lichen communities on rocky slopes (Table 3). In the rocky tundra, the aerial phytomass was approximately equal to the subterranean phytomass or about one-third less. In subsequent elements of the succession series, the ratio of aerial and subterranean biomass ranged from 1:4 or 1:5 in the low shrub—moss tundra to 1:7 or 1:8 in the shrub—moss and herb—moss tundra. The increased role of the subterranean phytomass in the more productive stages of the succession was due primarily to the dead component. When only the live phytomass was compared, the ratio of its aerial and subterranean

components was 1:0.3 (0.4) in the rocky tundra, 1:1 in the low shrub—moss tundra, 1:1.5 (1.9) in the shrub—moss tundra, and 1:1.4 (1.3) in the herb—moss tundra. As can be seen, the relative role of the live subterranean phytomass increased during succession until the shrub—moss stage was reached and then decreased somewhat in the herb—shrub stage. In the fifth element of the succession series, the previously dominant shrubs were replaced by herbaceous perennials and this was accompanied by a decrease in the relative role of the live subterranean phytomass.

It is of interest to compare the results obtained with data on the productivity of alpine tundras in other regions of the USSR. Chepurko's data (1966, 1971) on Khibina can be used for this purpose. The primary moss—lichen communities studied in the Urals (rocky slopes) have environmental conditions similar to those of the lichen tundra described by Chepurko, which were located on high-altitude (1000–1200 m above sea level) plateaux; however, the Urals communities were characterized by a greater proportion of mosses. The aerial phytomass reserve in the Ural tundras of this type was somewhat lower than that of the Khibina communities (15 and 24 g/m² respectively). Our low shrub—moss alpine tundra had a component composition to some extent similar to that of the Khibina dwarf arctic birch—crowberry tundra but differed from it in having a greater proportion of mosses and hence a greater aerial-phytomass reserve (586 (512) g/m², as against 475 g/m²). The subterranean biomass reserve was lower in the Ural low-shrub tundra than in the corresponding Khibina tundra, the respective figures being 665 (534) and 1228 g/m². The relative role of the subterranean phytomass was thus greater in the Khibina dwarf arctic birch tundra than in the Urals. A somewhat greater aerial phytomass and a considerably smaller subterranean phytomass also characterized the Ural herb—moss tundra in comparison with the Khibina bilberry—motley grass tundra [the aerial biomass reserves were 707 (726) and 535 g/m² respectively, while the subterranean reserves were 1023 (920) and 2165 g/m² respectively].

CONCLUSIONS

1. During the succession of the alpine—tundra flora, there is a tendency toward an increase in subterranean and aerial biomass reserves from the primary moss—lichen communities to the shrub—moss communities; a slight decrease in biomass reserve occurs on moving to the climax communities of the herb—moss tundra (as a result of replacement of the previously dominant shrubs by herbs).

2. Succession was accompanied by gradual accumulation of dead subterranean phytomass, whose reserves were 4–5 times those of the live phytomass during the most productive stages. This indicates retarded decomposition of plant material in alpine tundras.

3. The replacement of the dominants during the course of succession entails a change in biomass structure (the ratio of basic life forms). During most elements of the succession series (with the exception of the second), however, the mosses remained a very important component of the biomass, being dominant in the third and fifth stages. The role of flowering plants (first low shrubs and then shrubs) in the consumption of the aerial biomass gradually increased as succession progressed from the first to the fourth stage. These plants reached an absolute maximum and were dominant over other components in the shrub—moss tundra, where shrubs played the main role in biomass accumulation. On moving to the herb—moss tundra, where the previously dominant shrubs were replaced by herbs, the absolute and relative role of the flowering-plant component was reduced.

4. The biomass in the primary moss—lichen communities on rocky slopes was represented solely by the aerial component. During subsequent stages of the succession series, there was a gradual increase in the relative role of the subterranean biomass (with a slight decrease during the fifth stage). The aerial biomass was considerably larger than the subterranean biomass in the rocky tundra, both components were equally represented in the low shrub—moss tundra, and the subterranean biomass was approximately 1.5 times the aerial biomass in the shrub—moss and herb—moss tundras.

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