ECOSYSTEMS OF THE WORLD

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POLAR AND ALPINE TUNDRA

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PREFACE

Polar and alpine tundra have many similarities, but also differences; particularly towards the equator, high mountains show strong differences from polar regions. Therefore, workers in tropical mountains normally do not treat the highest elevated areas studied as tundra. Towards and in the subpolar regions there are generally more similarities between alpine belts and real polar tundra, although permafrost may often be missing in the mountains even there. However, these similarities justify the presentation of polar and alpine tundra in one volume of this series.

The chapters of the volume are mainly arranged geographically, starting with some general introductory chapters, followed by the alpine tundra of various regions, and ending with chapters on the polar regions.

There have been problems to find authors for some alpine areas, particularly smaller mountains. Generally, this reflects the fact that only little ecological work has been carried out in the area. It is also obvious from the chapters written, that in some areas more knowledge has been available on the ecology of plants than on other organisms.

The Arctic tundra of the world is divided between only few countries. Two of the chapters - those covering North America and Russia - are therefore particularly long.

Work on this volume started many years ago. Some of the authors were able to complete their assignments relatively fast; others took considerably longer. Apologies were therefore offered to the former group, who saw their writing go out of date, which, in some cases, necessitated considerable re-writing, when the volume as a whole was ready for press. As editor, I want to thank the various authors for their willingness to contribute, their patience, cooperation and acceptance of suggestions by the editor.

I also want to thank Prof. **D.W.** Goodall, Editor-in-Chief of the series, for all his help both in professional matters and in linguistic corrections.

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Chapter 16

ARCTIC ECOSYSTEMS IN RUSSIA

Yu.I. CHERNOV and N.V. MATVEYEVA

INTRODUCTION

Biological research in the Eurasian Arctic started at the beginning of the last century. Right from the dawn of investigations on nature in northern Europe and Siberia, there were attempts at some ecological generalizations to embrace and analyze the natural phenomena of life in the tundra. Schrenk (1848, 1854), for instance, gave many interesting and deep thoughts on the life of tundra plants and animals, and interesting ecological studies were made by Baer (1838), who visited Novaya Zemlya in 1837. The famous work of Middendorf (1869), which played a very large role in investigations on nature in arctic Siberia, should be considered as the starting point of scientific ecology in the Arctic.

At the end of the 19th and the beginning of the 20th centuries, interest in studying the organic world of the extreme North was dramatically increased. At that time, numerous expeditions were undertaken with special purposes: zoological, botanical, and entomological. Rich collections were built up which served as a basis of knowledge of the arctic flora and fauna; for example, in Russia, the collections of Jacobson in 1896 on Novaya Zemlya, and entomological and botanical materials from the expedition of the Kuznetsov brothers to the polar Ural and the Yugorskiy peninsula (Yugorskiy Poluostrov) in 1909. Vast materials on many groups of plants and animals were obtained by the Russian Polar Expedition headed by Toll in 1900-1903 on Taymyr and in some other regions of arctic Siberia. One of the participants of this expedition, Birulya (1907), studied many aspects of the biology of arctic birds and biocenotic relations. A veterinarian and traveller, Kertselli, collected a thoroughly documented herbarium of the flora of Bol'shezemel'skaya Tundra which formed the basis of the collection of the Botanical Institute of the Academy of Science for the northeast of Europe. In his book, Kertselli (1911) gives much interesting ecological information.

In the first decade of this century, the literature devoted to the plant and animal kingdoms of Eurasian tundras had become rather extensive. Common features in the composition and distribution of many taxa, particularly birds, mammals, insects, and vascular plants, were outlined (see reviews by Gorodkov, 1938; Aleksandrova, 1956; Rebristaya, 1977; Chernov, 1978b). For instance, in 1904 a detailed summary by Schalow on birds of the Arctic was published. Other issues of the *Fauna Arctica* published in Jena sum up the results from studies on various groups of animals at high latitudes. There, also, were published the first data on the microflora of the Arctic (Severin, 1909; Isachenko, 1914) and results are given from intensive studies of cryptogamic plants of the tundra zone (Elenkin, 1909; Brotherus, 1910).

Of great significance for the development of biological investigations in the Arctic were the numerous expeditions undertaken in the 1920s to Novaya Zemlya, which soon became in some way a standard of arctic nature. In that period, one Norwegian and several Soviet expeditions worked there, and great numbers of botanical and zoological papers were published. An especially important role was played by a series of papers by Tolmachev (1930, 1931) in which he gave an analysis of the composition of flora on Novaya Zemlya and, using this region as an example, raised the problem of floristic origins in the Arctic.

Yet, even now the qualitative composition of the arctic flora and fauna is far from being completely established. The vascular plant flora has been most thoroughly studied, as is reflected in the 10-volume edition of the *Arctic Flora of the USSR.* Important contributions to the study of the flora of arctic Eurasia were made by the founder of that series, Tolmachev, and some of his successors from the school created by him (Yurtsev, 1966, 1974; Petrovskyi, 1973, 1985; Rebristaya, 1977; Yurtsev et al., 1978; Tolmachev, 1986). At present, the composition of the vascular plant flora is one of the most advanced lines of biological investigation at high latitudes.

In general, the taxonomy and the zonal and regional distribution of mosses and lichens, the most important cenosis-formers in the Arctic, have also been clarified. A basic handbook of arctic mosses was published in 1961 (Abramova et al., 1961), and a number of recent papers are devoted to mosses and liverworts from different regions of the Russian Arctic (Blagodatskikh, 1973; Zhukova, 1973, 1978, 1986; Afonina, 1978; Blagodatskikh et al., 1979a,b; Kannukene and Matveyeva, 1986; and others). Studies of the arctic lichenoflora have also greatly progressed due to the investigations carried out at the Taymyr and Yamal peninsulas and Chukotka (Piin and Trass, 1971; Martin and Piin, 1978; Piin, 1979a,b, 1984; M.P. Andreyev, 1983,1984a,b; and others).

Soil algae, as well, play a very important role in terrestrial communities of tundras and especially of polar deserts. Therefore, data on these organisms are necessary in connection with the biocenology of the tundra, particularly in studies on trophic relationships. Intensive studies of soil algae in the Eurasian arctic landscapes were started as recently as the end of the 1950s (Dorogostaiskaya, 1959; Novichkova-Ivanova, 1963; Dorogostaiskaya and Sdobnikova, 1973; Getsen, 1985; and others). In all these works, much attention was given not only to the composition of the algal flora, but also to problems of ecology.

The development of studies of the mycoflora of Eurasian tundras was comparatively slow (Lind, 1927, 1934; Lebedeva, 1928; Vasilkov, 1967, 1969; Stepanova and Tomilin, 1971, 1978; Tomilin, 1971; Bab'eva and I. Chernov, 1982; I. Chernov, 1985). So far, only the broad features of the taxonomic composition of this very important group of organisms have been established. Some distinctive peculiarities of fungal biology and life cycles in arctic conditions have been pointed out. Yet, tundra mycology in Russia is still at its initial stage of development, though investigations on tundra fungi may be of great general significance. In particular, analyses of the tundra yeast flora have proved the necessity of revising many traditional ideas on the taxonomy of unicellular fungi (I. Chernov and Bab'eva, 1988).

Information on the soil microflora of the Russian arctic landscapes is also at an initial stage, with earlier work having been limited to some episodic works by Isachenko and Simakova (1934), Kriss (1947, 1952), and Sushkina (1960). At the end of the 1960s, Parinkina started her investigations on Taymyr. Owing to her systematic work, studies on the composition of the microflora and on the bacterial ecology of tundra soils have made noticeable progress (Parinkina, 1971, 1973, 1979a-c, 1986). However, there have so far been no successful attempts to carry out a detailed analysis of procaryotic communities at a species level.

For a long time tundras have attracted the attention of ornithologists. Numerous publications have been devoted to the avifauna of tundras and polar deserts of Eurasia, including vast summaries of both a general character (Pleske, 1928; Danilov, 1966; Uspenskyi, 1969) and a regional one (Krechmar, 1966; Portenko, 1972, 1973; Krechmar et al., 1978; Danilov et al., 1984). Many publications have been devoted to separate groups of birds, to the regularities of their distribution, and to the history of avifauna formation (Tugarinov, 1929; Kishchinskyi, 1974). A number of works have been devoted to individual species, especially to those of economic importance or in need of protection. Many important ecological problems have been elucidated using bird examples. The birds are one of the main groups used in studying adaptive processes, communication and ecology, and biocenotic relations in the conditions of the Arctic.

Many basic summaries, both general (Shwarts, 1963) and regional (Yudin et al., 1976; Chernyavskyi, 1985), have been devoted to the mammals of Eurasian tundras. The fur-bearing tundra animals have been constant objects of various ecological investigations - into their autecology, ecophysiology, population ecology, and biocenology. In particular, lemmings are the classical object for studies on population cycles - a question of great general ecological significance (Chernyavskyi and Tkachev, 1982). A series of studies on fundamental regularities of adaptive processes under extreme conditions have been based on arctic mammals (Shwarts, 1963).

Since the middle of the last century, constant attention has been attracted to the insects of Eurasian tundras. Quite a number of publications have been devoted to them - for instance a monograph by Kuznetsov (1938), who attempted to analyze the general peculiarities of the formation and composition of the arctic fauna by using insects as an example. This monograph remains, in a way, unique. The great majority of publications on the entomofauna of the Eurasian Arctic deal with separate taxa and are, as a rule, of regional character.

Some groups of the arctic insect fauna have been thoroughly studied. For example, there are extensive and detailed data on craneflies (Tipulidae), which play a very important cenotic role in tundras (Lantsov and Chernov, 1987). Comparatively well studied are the arctic Heteroptera (Kirichenko, 1960; Vinokurov, 1979) and Coleoptera (Yakobson, 1905-1916; Korotyaev, 1980; Medvedev and Korotyaev, 1980; Kiselev, 1981). The most important group of the tundra entomofauna, the Collembola, are under intensive study (Hammer, 1953; Ananjeva et al., 1987). At the same time, many biocenologically important groups of the Eurasian arctic entomofauna have hardly been touched upon in taxonomic, faunistic, or ecological works. Such are, for example, the midges (Chironomidae), houseflies (Muscidae), a number of lepidopteran groups, ichneumon flies (Ichneumonidae, Braconidae), sawnies (Tenthredinidae), and some others. The poor knowledge of the fauna and taxonomy of tundra insects and the difficulties in identifying the species, especially in the larval stage, are a serious obstacle to the development of investigations of cenotic relations (the structure of communities). It is quite evident that special guides to insects of the arctic fauna are most necessary.

Other groups of invertebrates inhabiting high latitudes of Eurasia have also been studied only irregularly and inadequately. For example, until recently, ecologists were convinced that in Siberian tundras they were dealing with only one species of earthworm, *Eisenia nordenskioldi.* Caryological analysis, however, made it necessary to classify one of the Taymyr populations as another species (Perel et al., 1985). It is possible that *E. nordenskioldi* is a whole complex of species. Another group of terrestrial oligochaetes, the Enchytraeidae, has also been very poorly studied, despite their great ecological significance in trophic chains, in the processes of soil formation, and in interrelations with microflora. In essence, special investigations on the taxonomy of this group in Siberian tundras, where it is very rich and ecologically diverse, are confined to the works of Ceika (1910, 1912, 1914) carried out on material collected by the expedition of E.V. Toll, as well as a paper by Piper et al. (1982). At present, in identifying the enchytraeid species from Siberian tundras, one has to be guided by works on Scandinavia, where there are no landscapes analogous to the true zonal tundras of Siberia.

Out of the vast group of mites (Acari) which is well represented in the Arctic in Siberian tundras, the beetle mites (Oribatei) have mainly been studied. Several publications on different regions of the Arctic have been devoted to them, mainly in the American-Atlantic sector. There have been attempts at a general analysis of oribatid distribution in the arctic regions (Hammer, 1952). All the other taxa of mites, including the numerous gamasid mites (Gamasina), have so far been very poorly studied in tundras.

For a long time, material on spiders of the Eurasian Arctic was confined to data in old papers, mainly from the beginning of the 20th century, and to investigations in the Atlantic sector (Greenland, Spitsbergen). An especially great contribution to studies of the arctic arachnofauna was made by A. Holm, who, along with investigations on Atlantic and American material, worked up Siberian tundra collections from polar expeditions of the 19th century. In recent years, the taxonomy of the spider fauna of the arctic region in northeastern Europe and in Siberia has been more thoroughly studied. Together with the description of many new species and the preparation of regional lists, broad features of zonal distribution and genetic relations of the fauna have been established (Eskov, 1985, 1986).

As in other zones, the tundra possesses a great variety and large numbers of nematodes. Unfortunately, sufficient attention has not yet been given to this group. Apart from separate publications on the southern regions of subarctic Russia, the soil nematodes in Siberian tundras have so far been studied only on the Taymyr peninsula (Poluostrov Taymyr) (Kuzmim, 1973, 1978, 1986; Chernov et al., 1979). The other groups of soil microfauna of the high-latitude Arctic, Tardigrada and Protozoa, have practically not been studied at all.

Investigations of parasites are of great importance for the development of synecology of the tundra zone and many publications have been devoted to them. Nevertheless, the parasites will not be covered here as they are normally treated as a special field which is somewhat apart from the general ecology of terrestrial communities. We shall only mention a recent review of data on the disease agents for various mammals in the Far North by Dunaeva (1985), and a series of papers on the helminths of northeastern Asia (the symposium volume *Paraziticheskie organizmy Severo-Vostoka Azii)* edited by Kontrimavichus (1975).

Synecological investigations of Eurasian tundras started essentially in the 1930s, particularly by analyses of the structure of vegetation cover. These works were regarded as the scientific basis of northern reindeer breeding. Besides that, maps of vegetation and geobotanical subdivisions were used in the general planning of land exploitation and use of natural resources. In the 1930s, geobotanical exploration was widely carried out in various tundra regions of the Soviet Union: on the Yugorskiy peninsula (V.N. Andreyev, 1932, 1935), on the Yamal (Avramchik, 1937; Nikolaeva, 1941), on Taymyr (Vinogradova, 1937; Sambuk, 1937), on Novaya Zemlya (Zubkov, 1934, 1935), and in river basins, such as the Anabar (Sochava, 1934). Analyses were also made on the abiotic environment - the climate including cryogenic processes and their influence on soil and vegetation, as well as interrelations of processes of soil genesis and the structure of vegetation (Gorodkov, 1932; Liverovsky, 1934). These works formed the basis for newer scientific ecological studies of the tundra and gave impetus to the development of subsequent, more profound and complex, investigations of arctic communities and ecosystems. In the 1930s, the main features of structure, zonal distribution, and regional peculiarities of the vegetation cover of Eurasian tundras were elucidated, attempts were made to give a classification of communities (Sambuk, 1937), and general geobotanical outlines of the tundra zone were published (Gorodkov, 1935, 1938).

Before 1940, studies of regional faunas and autecology dominated in zoological research on the Russian tundra. Some species - for example, the polar fox *(Alopex lagopus)* and the willow ptarmigan *(Lagopus lagopus)* - were studied in connection with their economic use. A number of papers presented important data on the numbers of birds and mammals and their distribution among biotypes as well as their interrelations with the abiotic and biotic environment (e.g., Naumov, 1931; Sdobnikov, 1937). At the same time, Fridolin (1936) studied in detail the cenotic relations of the subarctic, the Khibiny mountains. This work played an important role in the development of biocenological investigations in the North.

During the Second World War, the exploration of tundras was slowed down, but a series of interesting ecological investigations were still conducted. Tikhomirov (1946), later a prominent tundra specialist, wrote a paper of particular interest on the meadow plant communities of the tundra zone during the blockade of Leningrad. In 1941-1943, extensive year-round investigations on the Yamal led to fundamental papers on the ecology of birds of prey (Osmolovskaya, 1948) and of voles (Microtinae) (Dunaeva, 1948). These papers were of great importance for the development of tundra biocenology. They showed for the first time the important dependence of population dynamics on trophic relations and the state of forage reserves under tundra conditions. Later on, many of their hypotheses were confirmed in other regions and on other objects.

A monograph by Grigor'ev (1956) has played a noteworthy role in tundra science. In this book, Grigor'ev, the head of a prominent school of geographers, analyzed the general regularities of interactions of the vegetation cover and the animal kingdom of the tundra with the physicogeographical environment. He outlined the principles and criteria of subdivision of the polar territories.

In the 1950s, a still greater interest in synecological problems and in complex analyses of the interrelations of organisms among themselves and with the abiotic environment arose among the Soviet explorers of the north. In these years, the last works of the outstanding tundra specialist Gorodkov were published. The traditions of tundra ecology were continued by his successors, Aleksandrova and Tikhomirov. The descriptions of plant cover in the subzone of arctic tundras (Gorodkov, 1952, 1956, 1958; Aleksandrova, 1956) are fundamental investigations elucidating the problems of phytocenology and the nomenclature and distribution of plant communities, as dependent on various biotic and abiotic factors. A number of interesting biocenological works were published by Tikhomirov on the structure of plant communities in relation to cryogenesis, on the cenotic role of mosses, and on the influence of animals on plant cover (Tikhomirov, 1952, 1957, 1959).

The increasing interest in biocenological problems was also reflected in the work of Soviet zoologists during the same period. The first data on composition, distribution, number, and biomass of invertebrates in tundra soils were then published (Kozlovskaya, 1955; Stebayev, 1959; Chernov, 1961). The distribution and dynamics of vertebrate populations were also studied (Sdobnikov, 1959). One of the most peculiar and significant biocenotic complexes of high latitudes, the seashore colonies of birds, were analyzed synecologically (Uspenskyi, 1956; Belopolskyi, 1957).

The increased interest in biocenological problems reduced the barrier between botanical and zoological investigations. Tikhomirov (1959, 1960) published a series of papers on the influence of animals on the plant cover of the tundra, while other botanists gave much attention to the ecology of plant-pollinating insects (Shamurin, 1956; Panfilov et al., 1960). And yet, it must be admitted that real synecological investigations in the Russian tundra remained very episodic during the 1950s, but became more regular in the 1960s. For example, papers were then published on the dependence of plant growth and organ forms on environmental conditions (Tikhomirov, 1963), on processes of plant pollination and their interrelations with insects (Shamurin, 1966a; Chernov, 1966), and on trophic relations in the tundra biocenoses (Chernov, 1967).

Great attention has been paid to various aspects of human impact on the organic world of the tundra (Chernov, 1965; Dorogostaiskaya, 1972). Long-standing field experiments have been carried out in southern tundras of northern Europe with the purpose of creating agrophytocenoses, stable grasslands for forage (Khantimer, 1974).

In connection with the International Biological Programme (I.B.P.), the work of biological stations was intensified in the 1960s and the early 1970s. The most extensive arctic-subarctic studies in the Russian I.B.P. were performed on the peninsulas Taymyr and Yamal, and in mountain and forest tundras of the Kola peninsula (Kol'skyi Poluostrov). Later, investigations were performed in the Bol'shezemel'skaya Tundra on the Yugorskyi peninsula, in the north of Yakutiya, and in northeastern Asia on Chukotka.

During the first years of I.B.P. work in the tundra zone, investigations of synecology, production, and energetics were limited. Information about the qualitative composition of communities was also very limited, and the autecological and ecophysiological data necessary for calculating the different quantitative summary indices, turnover of substances, flow of energy, etc. were lacking. Therefore, much attention was given to taxonomic inventories of plants, fungi, procaryotes, and animals. By the end of the 1960s, intensive studies of various problems of population ecology and biocenology started in Russia - for instance, studies on typology of communities, seasonal development, dynamics of numbers of animals and factors of their regulation, trophic and symbiotic relations, distribution of biomass and dynamics of primary production, etc. A group of specialists working at the station "Tareya" during the I.B.P. period, ending in the mid-1970s, continued similar work in other regions of the Taymyr peninsula. By the mid-1980s, nearly all subzones from polar deserts to southern tundras had been covered. The major investigations were carried out on the Cape Chelyuskin (Mys Chelyuskin) (polar deserts), on the shores of Maria Pronchishcheva Bay (Bukhta Marii Pronchishchevoy) and near the settlement Dikson (arctic tundras), on the shores at the mouth of the Rogozinka River (the border of typical and arctic tundras), in the neighborhood of the Tareya settlement (typical tundras), and near the Kresty settlement (southern tundras). In addition, investigations were carried out in the northernmost tracts of the Ary-Mas forest and near the Agapa settlement (the southern part of typical tundras). The results of these studies are published in numerous papers and monographs, presenting a large body of material on the organization of communities over the vast territory of Taymyr, which is, therefore, to be regarded as a key region in studies of tundra ecology.

Various problems of the biocenology of southern tundras and forest tundra were studied on the Yamal. Production and energetics were also studied in the tundras of northern Europe (Archegova, 1985; Getsen, 1985). In the past decade, synecological studies have also been extensively developed in northeastern Russia from Vrangel Island (Ostrov Vrangelya) to the mountain tundras of the Magadan region.

The descriptive period of tundra ecology has probably come to an end. From general overall evaluations, ecologists are now turning to special analyses of various synecological problems, such as the stability of communities and regulatory mechanisms of their dynamics, regularities of tro-

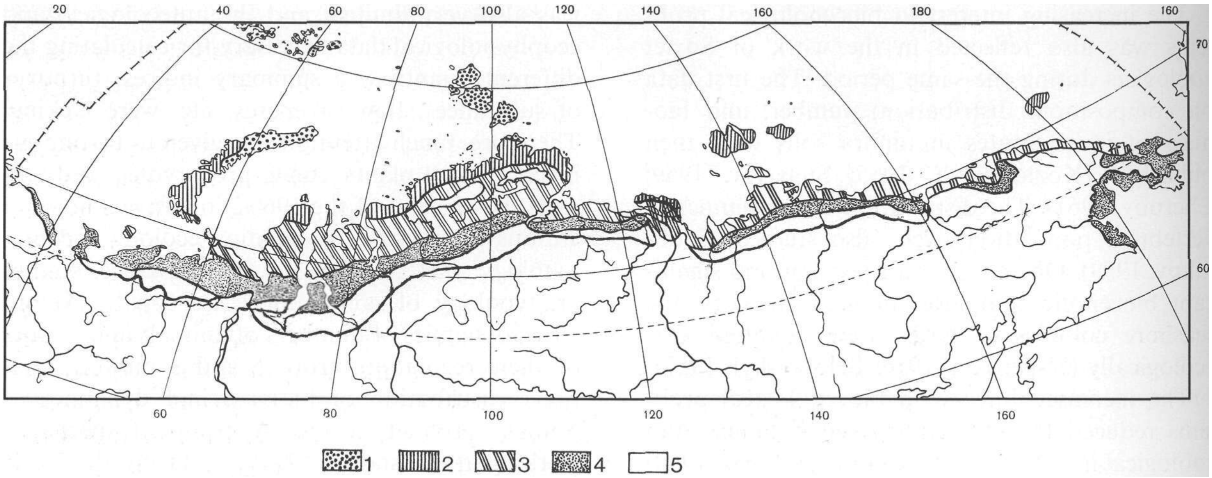

Fig. 16.1. The basic zonal landscapes of the Eurasian Arctic. 1, polar desert; 2, arctic tundra subzone; 3, typical tundra subzone; 4, southern (shrub and tussock) tundra subzone; 5, southern limit of the forest tundra.

phic and energetic processes, and cyclicity of the dynamics in biocenoses. Detailed mechanisms of biocenotic interrelations are also being studied; for example, relations in the complex of organisms causing the fixation of atmospheric nitrogen (Grunina and Getsen, 1984a,b) or in the "phytophage-plant" system (Bogacheva, 1982; Tishkov, 1985b), the role of trophic relations in the formation of a complex species structure in a community (Khlebosolov, 1986), and various forms of competitive and symbiotic relations (Litvin et al., 1985; Ovsyanikov and Menyushina, 1986). There have been some attempts at evaluating parameters of the productive process with regard to spatial and species structure of communities and to gradients of climatic and microclimatic conditions (Chernov et al., 1983; Nikonov, 1985; Vilchek, 1986). On the basis of accumulated data, experiments in the modelling of productive and energetic processes in tundra ecosystems have been undertaken (Bazilevich et al., 1986).

From the viewpoint of modern synecological concepts, however, the success of synthesizing all this information is still not sufficient with regard to the peculiarities in the dynamics of the arctic environment and the diversity of the internal organization of tundra ecosystems despite their external monotony (Chernov, 1985). So far, the production and energetic relations in the tundra, succession processes, the ways in which competition is manifested and its cenotic significance, and the regulatory role of biocenotic relations and their interrelation with abiotic factors, as well as other problems, are not quite clear. Some results on the primary production and nutrients in plants in Russian tundra are, however, given in Chapter 17 by Bazilevich and Tishkov and Chapter 18 by Bazilevich (this Volume).

The present account is not to be regarded as a comprehensive summary or synthesis of the data accumulated. This is only an attempt at discussing those aspects of organization of communities and ecosystems which, to our mind, seem to be the most important for the development of synecology of the tundra. We have chosen the problems for discussion without taking into account the degree of their development. We have proceeded from our own ideas on the significance of any given phenomenon in the general system of synecological analysis. Most attention has been given to the most characteristic tundra landscapes (arctic and typical tundra subzones, in our opinion) which in Eurasia are developed only in Russian territory. Much less attention has been given to landscapes transitional to the boreal forest belt.

LATITUDINAL DIVISION AND EXTENT OF POLAR AREAS

The width of the Eurasian tundra belt varies in different areas (see Fig. 16.1). On Taymyr, it extends 600-700 km from south to north. In the south, it borders the forest tundra and in the north the polar desert. However, in other places the continental arctic landscapes are sharply cut by the coastline. Thus, west of the Yugorskiy peninsula, only a narrow belt of the southern type of tundra

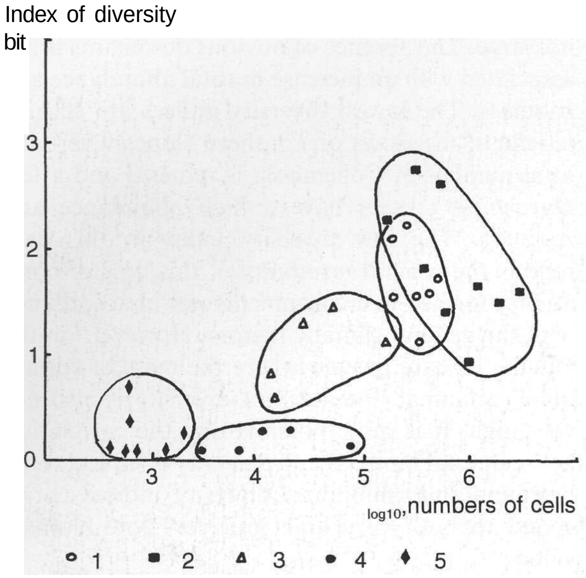

Fig. 16.32. Correlation of a diversity index and Iog$_{10}$ of number of yeast cells per gram soil in northwestern Taymyr. 1, green leaves; 2, dead dry unbroken leaves; 3, decomposing leaves; 4, humus; 5, soil. From I. Chernov (1985).

are too many species, it is highly probable that strong competition is regulating the species concentration in a biocenosis. That is why, at high species "saturation", the correlation between diversity and abundance should be negative, and when there are few species it is positive.

The data discussed in this section are not only of academic interest. Such peculiarities in the species structure of tundra communities, like superdominance, the small reserve of species for filling up the potential ecological niches, the weak possibility of vicariance, the formation of diverse cenotic complexes according to the recombination principle, and the low species representation of many important ecological "professions", all make special demands on the system which manages nature in the High Arctic. It is in the arctic biomes that the idea of the uniqueness of every species and of the disastrous consequences of the withdrawal of any of them from an ecosystem is most applicable.

It is more probable in arctic environments than anywhere else that a sharp reduction in the most active superdominant populations will inevitably cause intensive irreversible degradative processes in the ecosystems. A simplification in the species structure of arctic communities, a concentration of many important cenotic relations around very few species (often only one), and the weak "branching" of trophic chains, all result in an increased sensitivity to pollutants and their quick migration along trophic chains, and in the low ability of ecosystems to restore themselves.

The detailed study of different aspects of species structure in tundra communities is one of the current trends of tundra ecology. These investigations can be of more than local significance since the tundra may serve as a good model for the study of general features of the structure of communities formed in extreme environments.

HORIZONTAL STRUCTURE OF COMMUNITIES

Arctic communities have a complicated horizontal structure, although they are weakly diffejentiated vertically (Matveyeva, 1988b). A mosaic structure is normal in tundra communities and is caused by the following factors:

(1) Permafrost and active cryogenic processes in the soil layer, with thawing in summer, lead to the formation of patterned ground (Washburn, 1956) - that is, primary environmental heterogeneity with small size of each of the elements.

(2) Organisms of small and similar size are forced to share the same ecological niches within the limits of one or few layers, which are very close together because of the vertical reduction of the life sphere under the unfavorable climatic factors.

(3) The species have biological peculiarities connected with the extreme environment: a) a tendency to form dense mats and cushions - that is, a compact growth form; and b) slow growth.

Small size and slow growth are reasons why the organisms are unable to even out the heterogeneity of habitats, whose elements are larger than the size of individuals of all cryptogams and many vascular plants. The heterogeneity of the hydrothermal regime, which is due to patterned ground and nano- or microrelief, is reflected in the distribution of organisms and determines the cryogenic mosaics of plant cover. Compact growth of plants leads to phytogenic mosaics.

The main types of horizontal structure are rather few: (1) homogeneous; (2) sporadically spotted; (3) nodal; (4) regular cyclic; and (5) irregular mosaics (Fridland, 1972; Chernov, 1973a). All these structural types are most pronounced in[1] the vegetation cover, but they are followed by the distribution of animals and microorganisms (Chernov, 1978b; Parinkina, 1979c; I. Chernov, 1985) as

Fig. 16.33. *Eriophorum scheuchzeri* stand with homogeneous vegetation pattern in a river shallow, Kresty, Taymyr.

well as by elements of the soil cover structure (Ignatenko, 1971, 1973). In the tundra zone, the first three types are not so widely distributed.

Homogeneous type

This type of horizontal structure is not characteristic of true tundra communities on "plakor". It is typical for communities with primarily homogeneous environments. These are, first of all, communities developed in very wet habitats (mires, low silted river banks, salt marshes, pools, lakes), where cryogenic processes do not lead to the formation of patterned ground (Fig. 16.33). Environmental factors are smoothed down over the area in such biotopes, but they are unstable in time (fluctuations of degree and character of moistening and salting, over the years, or during the growing period and the day). Homogeneous herb stands of *Arctophila fulva, Carex stems, Dupontia fisheri, Eriophorum angustifolium, E. scheuchzeri, Hippuris vulgaris, Puccinellia phryganodes,* and *Ranunculus pallasii,* moss carpets of *Bryum tortifolium, Calliergon giganteum, C. richardsonii, C. sarmentosum,* and *Drepanodadus exannulatus,* or combinations of vascular plants and mosses *(Carex chordorrhiza, C. rariflora, C. stans, Cinclidium arcticum, C. latifolium, Drepanodadus intermedius, D. revolvens,* and *Meesia triquetrd)* are typical of such environments. The plant cover can be continuous or disrupted. With respect to succession, these communities are pioneers - either permanent pioneers or early stages of hydroseres whose development is prevented by external factors such as the rise and fall of the tide, floods, or lemming activity. Plants which form such communities are not inclined to compact growth; they are herbs and grasses with long rootstocks and mosses which do not form isolated cushions. In the saturated environments a general extreme character' caused by climate is added to the specific regimes found in hydromorphic biotopes: low soil fertility and temperature, minimal depth of soil thawing, and surplus of water. These communities are the poorest with regard to the number of species since so few can exist under such conditions. For reasons discussed above, the abundance of certain species becomes greater. Consequently, there are obvious dominants in these communities, and in the extreme cases there are pure monodominant stands. Analogous to such environments, in a way, is the surface of fresh landslides with moist and sometimes salty ground at the initial stages of succession. There the sparse or relatively closed plant cover has a homogeneous structure, usually consisting of the grasses *Alopecurus alpinus,*

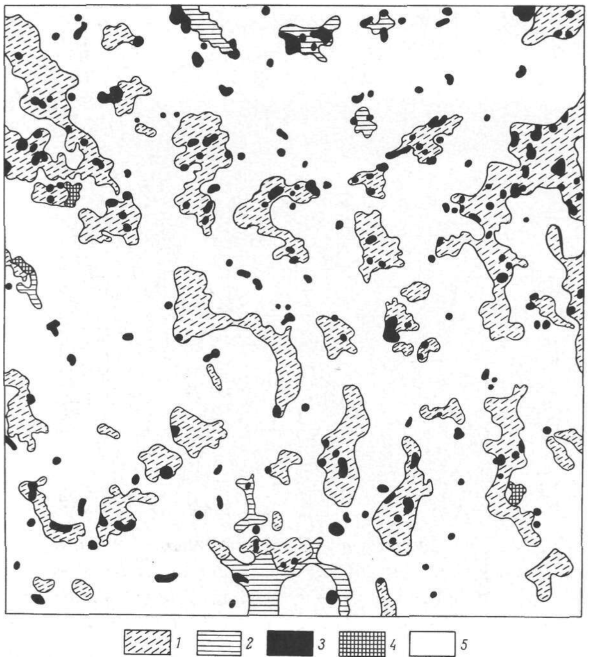

Fig. 16.34. Sporadically spotted type of horizontal structure in a *Dryas punctata* heath on a fell-field in Maria Pronchishcheva Bay, Taymyr. 1, *Dryas punctata; 2, Salix polaris;* 3, *Novosieversia glacialis; 4,* moss turf of *Dicranum elongatum* and *Polytrichum strictum;* 5, fell-fields with crustose lichens. Sample plot 10x10 m.

Arctagrostis latifolia, Deschampsia glauca, and *Poa alpigena.*

The very dense (> 80% cover) shrub thickets of the willows *(Salix lanata, S. pulchra)* and alder *(Alnaster fruticosus),* which do not frequently occur in the tundra zone, also have a homogeneous structure. Such stands contain a shrub layer and litter of dead leaves or a sparse layer of herbs. The environments have been made uniform by the vegetation which leads to phytogenic homogeneity. One can find small fragments of dense thickets only in the southern tundra subzone. They are normally short-lived because of the worsening hydrological regime, which leads to a degradation of vegetation, a dying of shrubs, and the appearance of gaps in the thickets.

Although the homogeneous type of horizontal structure is not characteristic of the tundra zone as a whole, communities with this kind of horizontal structure can occupy vast areas in regions where the "plakor" type of landscape is not well pronounced and where very wet depressions predominate.

Sporadically spotted type

This horizontal structure is typical of the initial stages of succession of both dry fell-fields, snowless in winter, and snow beds with plant species forming isolated cushions and mats. The main reason for this type is biotic: the potential ability of some species to form compact individuals or aggregations. This ability is seen to a great extent in the two contrasting environments mentioned. Species such as *Cerastium regelii, Dryas punctata, Saxifraga oppositifolia,* and *Stereocaulon alpinum,* which usually grow in the form of scrubby individuals (vascular plants) or as isolated stems (mosses) and podetia (lichens), form dense cushions, mats, or compact aggregations in the outlying parts of their ecological amplitude (Figs. 16.34, 16.35). In the tundra zone, this structural type is typical of "intrastenozonal" communities occupying very small areas (Chernov, 1975). In the polar deserts, however, where the majority of species (lichens: *Cetraria delisei, C. islandica* var. *polaris, Stereocaulon rivulorum, Thamnolia subuliformis',* mosses: *Ditrichum flexicaule, Orthothecium chryseum, Racomitrium lanuginosum* vascular plants: *Draba oblongata* and *Saxifraga oppositifolia)* form corn-

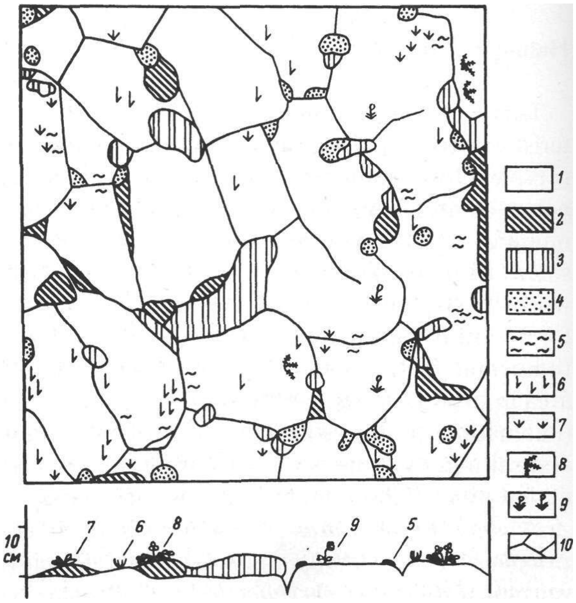

Fig. 16.35. Sporadically spotted type of horizontal structure and vertical profile in a moss-lichen polar desert at Cape Chelyuskin, Taymyr. 1, bare ground; 2, *Orthothecium chryseum;* 3, *Bryum tortifolium;* 4, *Stereocaulon rivulorum;* 5, *Thamnolia subuliformis;* 6, *Phippsia algida;* 7, *Cerastium regelii;* 8, *Saxifraga oppositifolia; 9, S. cernua;* 10, cracks with small stones. Sample plot 1 x 1 m.

pact, almost hemispherical cushions, many "zonal" communities have this type of horizontal structure. In succession, such communities are permanent pioneers, their internal development being prevented or permanently impeded under the influence of abiotic factors (physical damage or delay of growth). Usually, the mats and cushions are only some centimeters in diameter, and real soil does not develop under them. Under *Dryas* mats with an area of 1 m^2 and more, however, a peat layer appears above the stony ground untouched by soil formation. Therefore, the cause of sporadically spotted horizontal structure is biotic. It is a consequence of the compact growth of plants in the initial stages of succession.

Nodal type

This type does not occur in its pure form in the tundra, but may be recognized in parts of communities dominated by plant species that are important in changing the environment - so-called "edificators" (tall shrubs such as *Alnaster fruticosa, Betula exilis, B. nana,* and *B. middendorfii,* tussocks of *Eriophorum vaginatum,* cushions or mats of the dwarf-shrubs *Dryas octopetala, D. punctata, Salix nummularia,* and *S. rotundifolia,* and the herbs *Novosieversia glacialis, Oxytropis middendorfii, O. nigrescens, Silene acaulis,* and some *Potentilla* species). These plants change the environment locally through, for instance, the leaf litter under *Alnaster fruticosus,* the pockets of humus under *Novosieversia glacialis,* and the organic matter of decomposing plant remains in *Eriophorum* tussocks. They represent a "node", a concentration of organisms absent or infrequent outside the influence of the "edificator" (Polozova, 1970; Matveyeva and Chernov, 1977; Chastukhina, 1984). Concentric distribution of soil invertebrates can be observed around large single individuals of vascular plants. Their numbers and abundance decrease with their distance from the "edificator" (Chernov, 1973a). The density of the microbial population is also considerably greater within the sphere of influence of such plants than outside (Matveyeva et al., 1975; Parinkina, 1979a). The nodal type therefore is exclusively phytogenic. It is not very characteristic of tundra communities proper, although it manifests itself in *Eriophorum vaginatum* tussock communities and partly in *herb-Dryas* communities on slopes and in *Dryas* heaths on fell-fields. This weak representation of the nodal type is a consequence of the weak "edificator" power of tundra plants, including their small size.

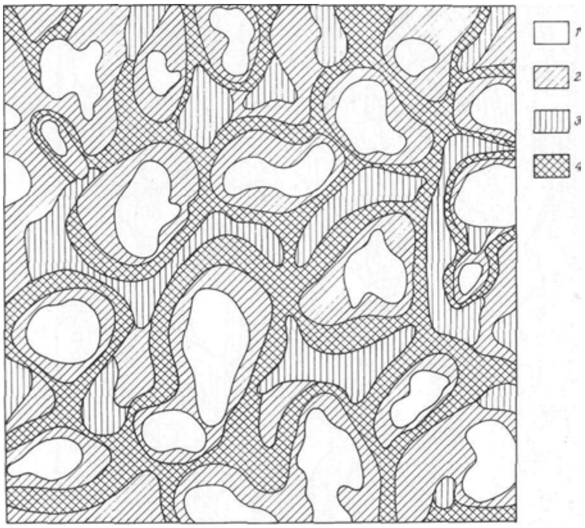

Fig. 16.36. Regular cyclic type of horizontal structure (first variant on a flat surface) in a frost-boil community at Kresty, Taymyr. 1, patches of bare ground in different successional stages; 2, *Hylocomium alaskanum* + *Aulacomnium turgidum* + *Carex ensifolia* ssp. *arctlsibirica* + *Dryas punctata;* 3, *Tomenthypnum nitens* + *Betula nana* + *Vaccinium uligonosum* var. *microphyllum;* 4, *Tomenthypnum nitens* + *Aulacomnium turgidum.* Sample plot 10 x 10 m.

Regular cyclic type

This horizontal structure is characteristic in both the tundra zone and the polar deserts. It is pronounced in the so-called polygonal and spotted (frost-boil) communities. A regular repetition of a certain set of nanorelief elements (usually 2-3) caused by cryogenic processes in soil (patterned ground: polygons, nets, strips, etc.; Washburn, 1956) forms the basis for this structural type. It has three variants.

In frost-boil tundras (in flat areas and on slopes up to 5°) a set of three elements is regularly repeated: namely, patches, rims, and troughs (Fig. 16.36). The number of such cycles per 100 m^2 increases northward: about 20 in the southern tundra subzone, from 30 to 60 in the typical tundra, and from 90 to 150 in the arctic tundra subzone. The vegetation cover on different elements of the cycle differs in many features. In the patches, vegetation is absent or sparse, consisting of small mosses (often many species), liverworts,

Fig. 16.37. Second variant of a regular cyclic structural type on a slope in the arctic tundra subzone in the mouth of the Uboinaya River, Taymyr. 1, bare ground with solitary vascular plants; 2, border of *Salix arctica* + herbs on the polygon surface; *3, Hylocomium alaskanum* + *Salix arctica* in troughs; 4, crustose lichens and small mosses. Sample plot 10 x 10 m.

crustaceous lichens, and solitary small vascular plants. The plant cover is closed on the rims and in the troughs because of a well-developed moss turf and a relatively high cover of herbs and dwarf-shrubs, but the number of species is normally low.

The same structural type is of a somewhat different pattern on slopes between 5° and 30°. All elements, especially troughs, are then oriented along the slope in the form of strips (Fig. 16.37). The species distribution and the vegetation structure of microcommunities are similar to those in the main variant mentioned above.

In the arctic tundra subzone and the polar desert, a simpler variant is found consisting of two elements: namely, continuous plant cover in a net-like pattern in the troughs and sparse plants on the polygon surfaces (Figs. 16.38, 16.39). This variant precedes the main 3-element type. At this stage, it is clear that the reason for the environmental heterogeneity is the cracking of the ground into regular (symmetrical) pentagons or hexagons with a diameter from 20 cm to 1 m. This variant can also be seen in the typical tundra subzone, but only on the higest elements of the relief (snowless in winter) and on loamy ground.

Each of the elements in the regular cyclic type has either an irregular mosaic (on rims and troughs) or a sporadically "spotted" structure (on patches in the polygon centers (Figs. 16.40, 16.41).

This type of structure is due to abiotic factors (primary cryogenic heterogeneity giving a regular pattern), which is intensified by plant components and reflected in the distribution of soil invertebrates (Chernov, 1978b) and microorganisms (Parinkina, 1971, 1986), as well as in the structure of the soil profile (Ignatenko, 1971; Fig. 16.42). As a whole, it precedes the terminal irregular mosaics with closed cover in northern regions, or it can be a consequence of a disturbance of the continuous cover under the influence of cryogenic processes in southern parts of the tundra zone. The special feature of this type of structure is that the terminal and pioneer stages of succession co-exist and alternate over some decimeters; that is, this is a single dynamic system, an internal cyclic series. Strong variations in the environment over a small area lead to high species diversity and richness. Thus, the "zonal" tundra communities of the Taymyr with a regular cyclic type of horizontal structure are the richest in species per unit area - and not only in the tundra zone. From 130 to 160 plant species (about 50-60 vascular plants, the same

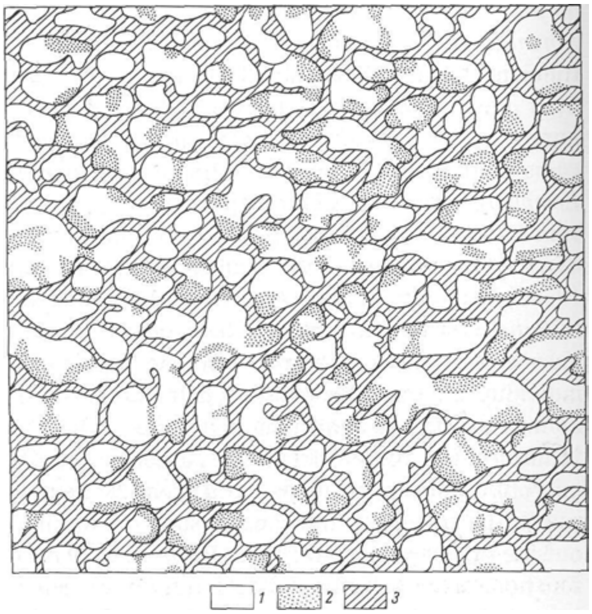

Fig. 16.38. Regular cyclic type of horizontal structure (third, two-element variant) in the arctic tundra subzone in Maria Pronchishcheva Bay, Taymyr. 1, bare ground; 2, solitary vascular plants and crustose lichens; 3, *Hylocomium alaskanum* + *Salix polaris.* Sample plot 10 x 10 m.

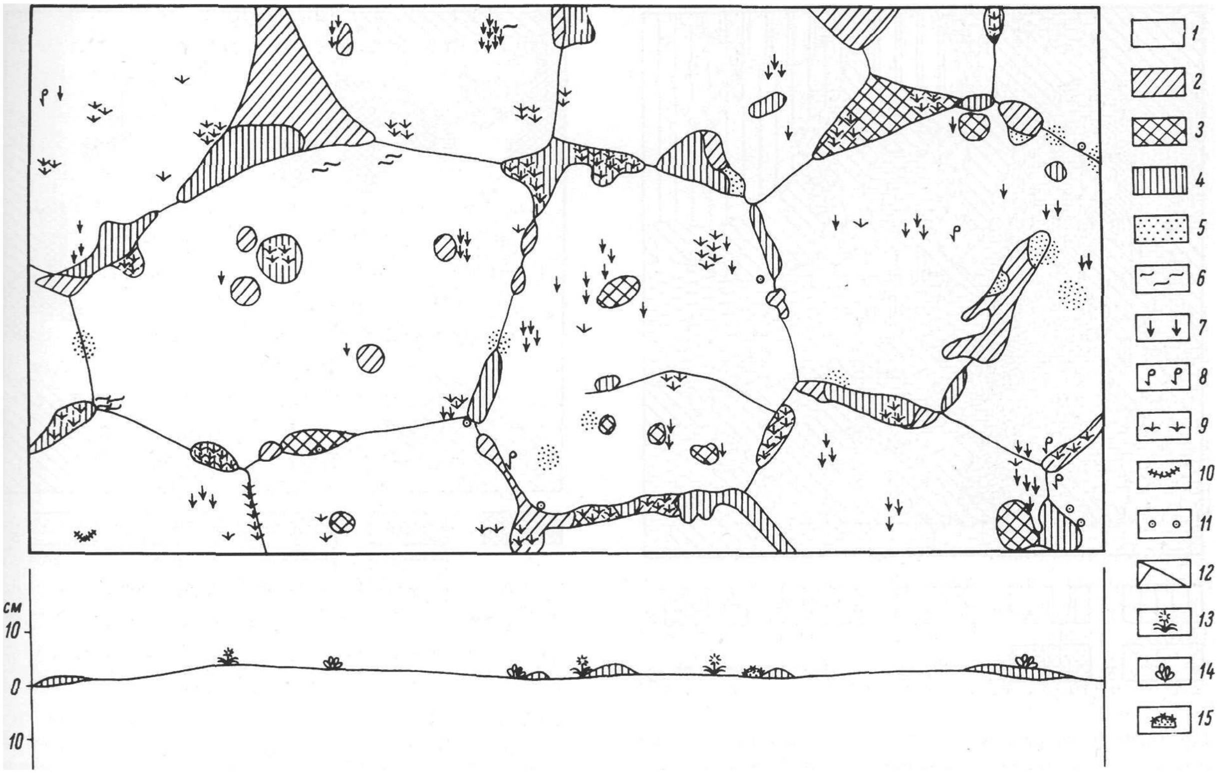

Fig. 16.39. The initial stage of the two-element variant of the regular cyclic structural type in the polar desert at Cape Chelyuskin, Taymyr. 1, bare ground with stones; 2, *Aulacomnium turgidum; 3, Bryum tortifolium; 4, Orthothecium chryseum; 5, Psoroma hypnorum; 6, Thamnolia subuliformis;* 7,13, *Phippsia algida;* 8, *Saxifraga cernua;* 9,14, *Cerastium regelii;* 10, *Stellaria edwardsii;* 11,15, *Draba oblongata;* 12, cracks. Sample plot 1 x 2 m.

number of lichens, and about 30-40 mosses) may be found in 100 m^2. Undoubtedly, such high species diversity is partly a result of the high number of small cryptogams. Mosses and lichens, however, are also components of many boreal forest and bog communities, but such high species diversity is not typical of them. Heterogeneity of this environment, its contrasts with frequent alternation of elements, general biota poverty, small size of organisms, possible weakened ability to compete, all these features together give a high alpha- diversity of tundra communities with regular cyclic horizontal structure. Nevertheless, the entire mechanism for increased species diversity is not yet clear.

The regular cyclic structure type is not only the most characteristic of tundra communities, but it is probably also specific for the high-latitude tundra zone, although some analogues can be found in extreme mountainous regions as well as in the arid zone. At any rate, it does not manifest itself there on such a scale as in the tundra zone.

Irregular mosaic type

This type is characteristic of true "zonal" tundra communities on "plakor" which are widely distributed and occupy vast areas in the middle and the southern part of the tundra zone. The primary environmental heterogeneity, which is due to cryogenic nanorelief with height differences between elements of about 10-20 cm, is irregular (Fig. 16.43). Species with this type of horizontal structure show the ability to form multistemmed dense individuals or compact growth (mosses, lichens), but there are no obvious dominants and "edificators" able to smooth out the environmental heterogeneity. The irregular mosaic structure is typical of communities with continuous cover, formed by plant patches of individuals of a single species alternating with aggregations of various species within the same life form, generally mosses (Petrovskyi, 1960). Moreover, some species of bryophytes show a tendency to grow on raised elements of the nanorelief *(Aulacomnium turgidum, Hylo-*

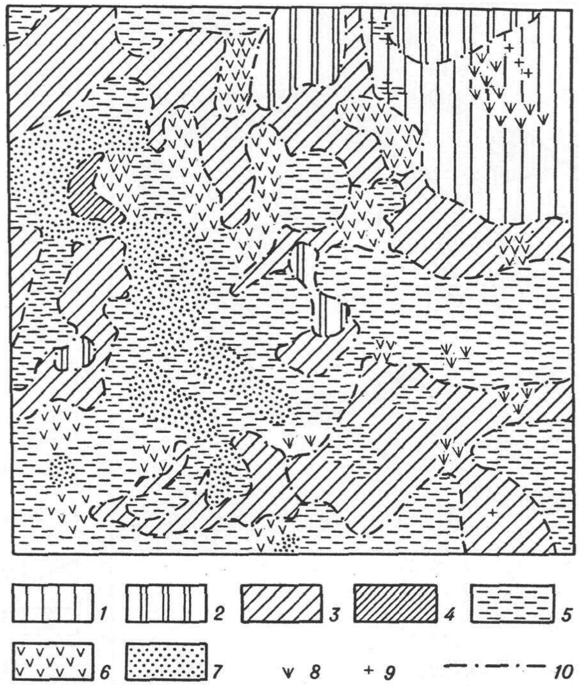

Fig. 16.40. Irregular mosaics in the trough and on the rim in a frost-boil Dryas-sedge-moss community at Tareya, Taymyr. 1, *Tomenthypnum nitens',* 2, *Aulacomnium turgidum;* 3, *Hylocomium alaskanum;* 4, *Racomitrium lanuginosum;* 5, *Dryas punctata;* 6, *Carex ensifolia* ssp. ***arctisibirica;*** *1,* foliose lichens *(Nephroma, Peltigera);* 8, *Salix polaris; 9, Polygonum (Bistorta) viviparum;* 10, boundaries between plant aggregations. Sample plot 50 x 50 cm.

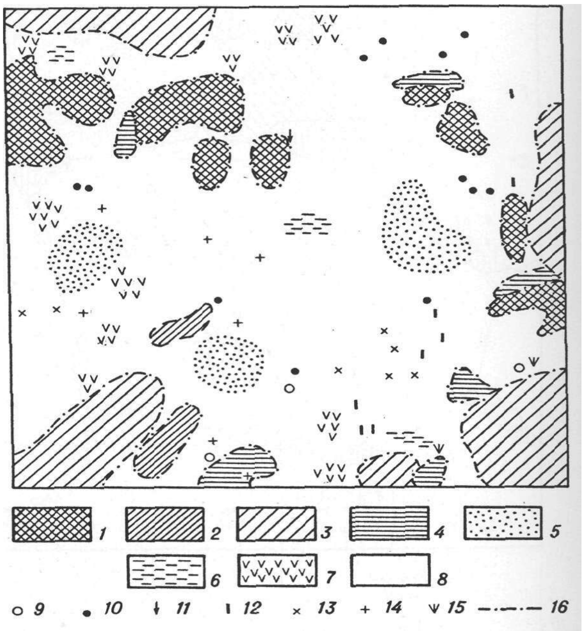

Fig. 16.41. Sporadically "spotted" structure in a frost-boil Dryas-sedge-moss community at Tareya, Taymyr. 1, *Dicranum spadiceum; 2, Hypnum bambergeri;* 3, *Hylocomium alaskanum;* 4, *Ditrichum flexicaule;* 5, crustose lichens *Toninia lobulata, Baeomyces carneus;* 6, *Dryas punctata; 7, Carex ensifolia* ssp. *arctisibirica;* 8, *Festuca brachyphylla; 9, Juncus biglumis; 10, Luzula nivalis;* 11, *Stellaria ciliatosepala;* 12, *Minuartia rubella;* 13, *Polygonum (Bistorta) viviparum;* 14, *Salix polaris;* 15, bare ground; 16, boundaries between plant aggregations. Sample plot 50 x 50 cm.

comium alaskanum, Racomitrium lanuginosum), while others grow in microdepressions *(Dicranum spadiceum, Ptilidium ciliare, Tomenthypnum nitens).* Some species form small compact hummocks *(Dicranum elongatum, Polytrichum strictum, Sphenolobus minutus).* The aggregation of foliose lichens *(Nephroma expallidum, Peltigera aphthosa, P. polydactyla, P. rufescens)* and dwarf-shrubs *(Dryas punctata, Vaccinium vitis-idaea* ssp. *minus)* are also elements of phytogenic mosaics. The elements of such mosaics are measured in centimeters, and the boundaries between them are vague. These plant mosaics are not reflected in the soil. The cryogenic mosaics, however, do affect the soil and will influence the distribution of soil invertebrates and microorganisms, although not so obviously as in the case of the regular cyclic structural type. Communities with an irregular mosaic structure and a closed cover are the most stable terminal stage of endogeneous succession on "plakor" in the tundra zone. They are absent in the polar deserts.

As a whole, tundra communities are characterized by a combination of several types of horizontal structures, one of them normally predominat-

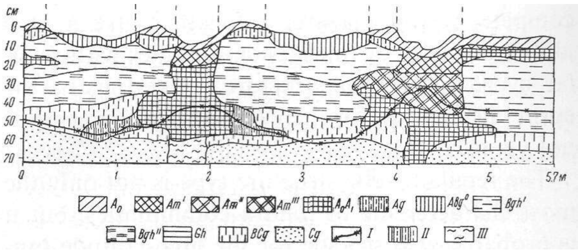

Fig. 16.42. Structure of a soil profile in a frost-boil *Dryas*-sedge-moss community in the typical tundra subzone at Tareya, Taymyr. Letter designations are soil horizons. I, permafrost level in August; II, humus streaks; III, ice wedge. From Ignatenko (1971).

Fig. 16.43. Irregular mosaic structural type in a *Dicranum elongatum-Betula nana-Carex ensifolia* ssp. *arctisibirica* hummocky community in the southern tundra subzone at Kresty, Taymyr. Vegetation on hummocks (1-5): 1, *Ptilidium ciliare* + *Dicranum* spp. + *Aulacomnium turgidum* + *Vaccinium vitis-idaea* ssp. *minus* + *Cassiope tetragona* + *Dryas punclata; 2, Ptilidium ciliare* + *Dicranum* spp. + *Aulacomnium turgidum* + *Betula nana* + *Salix reptans;* 3, *Ptilidium ciliare* + *Dicranum* spp. + *Aulacomnium turgidum* + *Vaccinium vitis-idaea* ssp. *minus* + *V. uliginosum* ssp. *microphyllum* + *Ledum decumbens* + *Betula nana;* 4, *Aulacomnium turgidum* + *Dicranum* spp. + *Ptilidium ciliare* + *Vaccinium uliginosum* spp. *microphyllum* + *Ledum decumbens* + *Betula nana* + *Carex ensifolia* ssp. *arctisibirica; 5, Dicranum elongatum* + *Sphenolobus minutus* + *Tritomaria quinquedentata.* Vegetation in troughs (6-10): 6, *Tomenthypnum nitens* + *Aulacomnium turgidum* + *Carex ensifolia* ssp. *arctisibirica; 1, Aulacomnium turgidum* + *Dicranum* spp. + *Betula nana;* 8, *Ptilidium ciliare* + *Dicranum* spp. + *Aulacomnium turgidum* + *Vaccinium uliginosum* ssp. *microphyllum* + *Ledum decumbens* + *Cassiope tetragona; 9, Ptilidium ciliare* + *Aulacomnium turgidum* + *Dicranum* spp. + *Carex ensifolia* ssp. *arctisibirica* + *Betula nana* + *Salix reptans;* 10, *Tomenthypnum nitens* + *Ptilidium ciliare.*

ing. Thus, the elements of nodal structure are combined with irregular mosaics (various communities with mosaics of mosses, dwarf-shrubs, and solitary tall shrubs or tussock communities of *Eriophorum vaginatum)* or with the sporadically spotted type in meadows on southern slopes. Regular cyclic and irregular mosaic types with nodal elements are characteristic of tundra communities proper which are most advanced in the succession and most stable. Homogeneous and sporadically spotted types are characteristic of "intrazonal" communities, mainly at early successional stages.

The elements of homogeneous, sporadically spotted, irregular mosaic, and nodal types are formed by individuals (heterogeneity of the first order). The regular cyclic type on the other hand shows a heterogeneity of the second order, with elements consisting of sinusia or microcommunities.

Mosaics of the cover of "zonal" communities on "plakor" cause problems in determination of homogeneous plots which could serve as the smallest units for the purpose of classification in order to establish syntaxa. In the Russian tundra literature, sites with a regular cyclic structure of vegetation cover are sometimes considered as complexes of phytocenoses (Norin, 1979) and their elements as phytocenoses. About 25 years of research in the

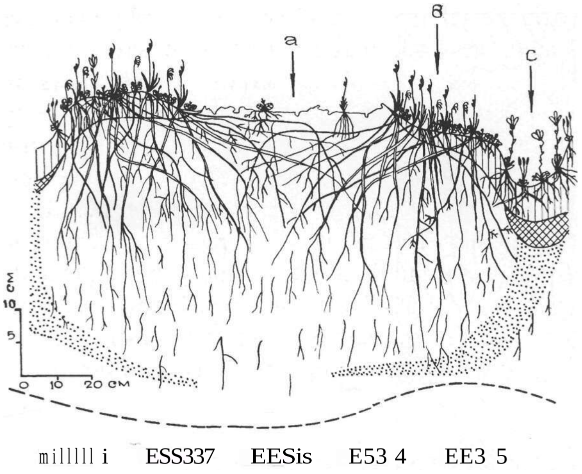

Fig. 16.44. Vertical section in a frost-boil -Dryas-sedge-rnoss community in the arctic tundra subzone at Dikson, Taymyr. a, patch of bare ground; b, rim; c, trough; 1, ***Hylocomium** alaskanum; 2,* dead part of moss turf; 3, peat; 4, surface of bare ground; 5, level of permafrost.

tundra zone, however, have led us to the conclusion that such sites with small horizontal structural elements of about 1 m^2, because of practical considerations (for mapping, classification) and by analogy with other zones, are better considered as phytocenoses, while mosaic elements are the internal structural parts. As seen in Figure 16.44, the size of individual vascular plants including their root system may well exceed the size of the mosaic elements. The size of the minimum area in such stands speaks in favor of our decision. All species which are frequent, relatively abundant, and constant, or are character and differential species, can usually be met on an area of 3 x 3 m. All elements of horizontal structure are normally repeated several times in this area, and thus all the essential properties of a phytocenosis are well developed. Only for the recording of solitary rare species of the first class of frequency and constancy in some community types is an area up to 100 m^2 necessary (Fig. 16.45). When describing communities with regular cyclic and irregular mosaic patterns, an area 5 x 5 m can be recommended for practical purposes. For homogeneous communities and for those with a sporadically spotted structure, 3 x 3 m or 2 x 2 m will be sufficient. These sizes are less than those commonly used for meadow and forest releves.

The types of horizontal structure described above (apart from the homogeneous type) are characteristic not only for the internal structure of a phytocenosis in the tundra zone, but for the pattern of vegetation cover as a whole, where the phytocenoses themselves are the elements. The irregular mosaics are typical for the distribution of plant communities on the interfluves and on sloping surfaces. The vegetation of polygonal mires (Fig. 16.46) and of *baidzharakh* are good examples of regular cyclic structure. A second variant of this type is represented by stripe-like communities stretched along the slope on concave and convex microrelief elements (Fig. 16.47) which vary in moisture. Flat-hummocky mires with peat or mineral hummocks dispersed on the ground of vast wet depressions have a sporadically spotted structure. The nodal pattern is typical of circular concentric ranges of communities (microbelts) around the lakes. An additional structural type of vegetation cover is represented by stripes of communities stretched across the slope which form ecological

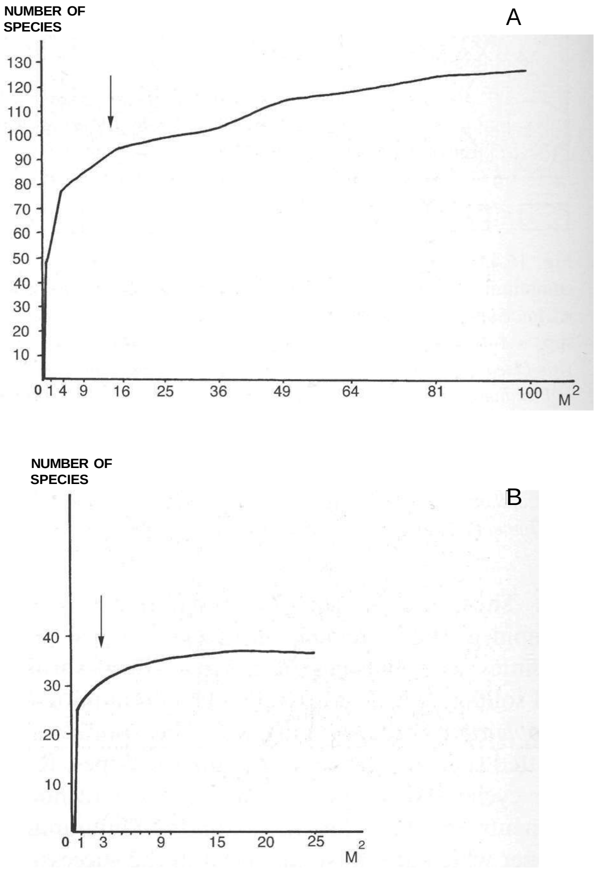

Fig. 16.45. Species number/area correlation in (A) a frost-boil .Dryos-sedge-moss community with regular cyclic structure and in (B) a *Carex stans-moss* mire with homogeneous structure in the typical tundra subzone in the mouth of Rogozinka River, Taymyr. Arrows show the position on the curves where species of the frequency classes II-V have been recorded.

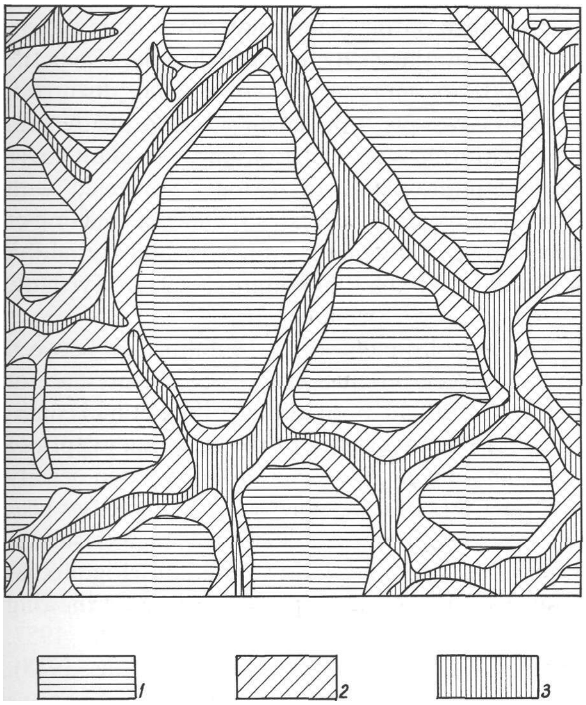

Fig. 16.46. Regular structural type of the vegetation cover in a polygonal mire at Tareya, Taymyr. 1, Saturated center of polygon with homogeneous plant cover; 2, rim with irregular mosaic structure; 3, saturated trough with homogeneous cover. Sample plot 60 x 60 m.

series following certain environmental factors, most often snow depth.

The special feature of the structure of vegetation cover in the tundra zone is its heterogeneity along with the relatively small size of the phytocenoses which, in turn, mainly have a mosaic pattern. Because of permafrost, all the usual forms of micro- and mesorelief and, consequently, the diversity of all types of intra-landscape vegetation pattern, are represented in a relatively small area. This results in small minimum areas of local flora and of the set of plant communities. All common types of communities are normally met repeatedly in an area of 5 x 5 km. In forest biomes, such an area can be occupied by a single tract of forest or bog with a poor and monotonous community.

DYNAMIC PROCESSES IN ARCTIC COMMUNITIES

One of the main features of arctic communities is the uniqueness of the succession processes. In the temperate zones of the globe, the natural development of an ecosystem unaffected by anthropogenic factors leads to a climax.

It is, however, problematic to apply the notion of climax to the "zonal" tundra communities. At the terminal stages of development of the living plant cover in High Arctic latitudes, there is no state of stable equilibrium. Changes in the environment resulting from the development of the living cover continue, and the thicker this layer becomes, the worse it is for plant life. The live plant cover, as its thickness increases, causes a deterioration of its environment and thereby creates the precondi-

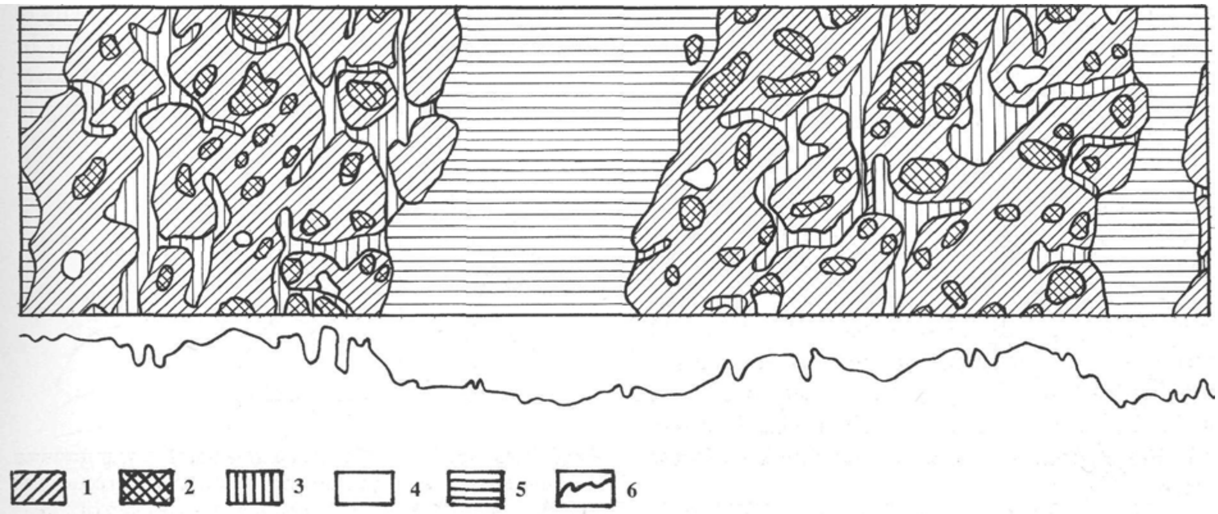

Fig. 16.47. Regular cyclic structure of the vegetation cover on a slope with repeated strips of concave and convex elements of microrelief at the middle current of Lenivaya River, Taymyr. 1-4, frost-boil community consisting of 1, rim; 2, overgrown patches of ground; 3, trough; 4, bare ground; 5, mire; 6, relief profile.

tion for its own destruction. This is especially typical for the arctic tundras and polar deserts. In the Arctic, the succession processes constantly come to an abrupt end. The state at the climax can be expressed schematically as

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The final stages of the development of the living cover in arctic conditions are different:

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The succession processes in the Arctic are characterized by low speed, shortening of sequences of succession changes, and diminution of the number of possible sequences. The main cause of reduced speed in succession processes lies in the unfavorable climatic conditions during the growing period (low temperatures, shortness of the frost-free period) and, as a consequence of this, reduction in growth and production in all groups of organisms (Chernov and Matveyeva, 1979; Chernov, 1985). The shortening of succession sequences is due to the predominance of disturbance of the living cover over the succession process. The reason for a limited number of possible succession sequences is the low diversity of flora and fauna. All the succession sequences tend to cease abruptly, but, depending on the strength of the factor which caused the destruction and the general scale of this phenomenon in space, the succession may start from the very beginning or from a more advanced stage. The process can take place over large territories - that is, the system may cover large system blocks - or they may proceed locally. Then the general functioning of the system is not disturbed.

Plant cover plays the leading role in the dynamics of natural systems. The changes in plant cover in the tundra zone are closely connected with dynamic cryogenic processes such as the melting of permafrost, solifluction, and frost-boil formation (Gorodkov, 1932; Tikhomirov, 1957; Tyrtikov, 1974).

The establishment of an equilibrium between soil and vegetation is prevented by the presence of permafrost. In an arctic climate, the optimal conditions for life are created at the maximum depth of seasonal thawing. However, an increase in density and thickness of vegetation turf also increases heat insulation properties, which will then result in worse thermal conditions in the soil (Fig. 16.48) and in a decrease of depth of its seasonal thawing (see Fig. 16.10 above) (Tikhomirov, 1957; Matveyeva, 1971; Tyrtikov, 1974; Lovelius, 1978). This is easily observed by comparison of various characteristics in communities differing in vegetation density.

The inverse relationship between the density of cover and the depth of thawing is especially clear in communities of frost-boil and polygonal tundras in the arctic tundra subzone. In frost-boil tundra, where the general cover is >80% and the surface is overgrown, the permafrost during almost the entire summer remains higher than in polygonal communities where 50% of the ground is bare. In polar deserts, communities with a total cover of 5-20% are optimal for the vital activity of all organisms. Clear signs of degradation can be observed in communities with higher plant cover (up to 60%) - for instance, soaking and dying of

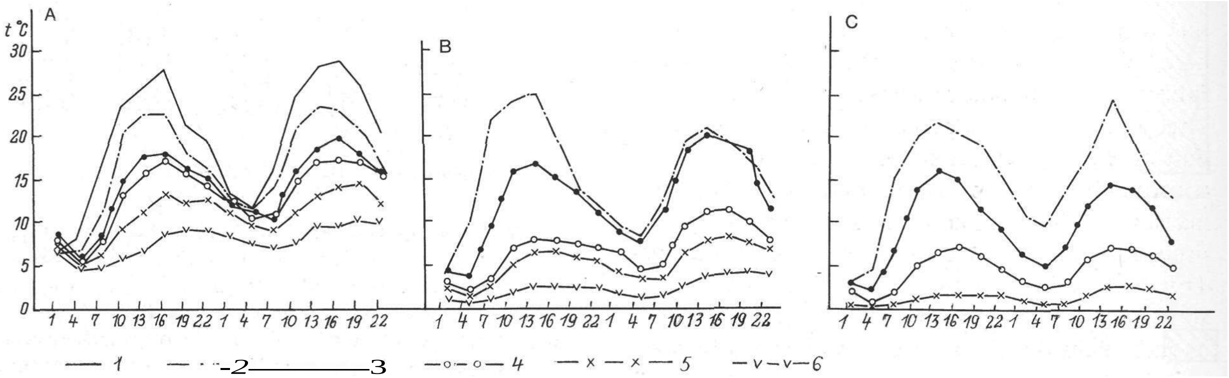

Fig. 16.48. Daily course of soil temperature in different elements of nanorelief in a frost-boil *Betula* «««a-sedge-moss community in the southern tundra subzone at Kresty, Taymyr, June 1976. A, patch of bare ground; B, rim; C, trough; 1, air; 2, soil or moss surface; 3, depth 2 cm; 4, depth 5 cm; 5, depth 10 cm; 6, depth 15 cm.

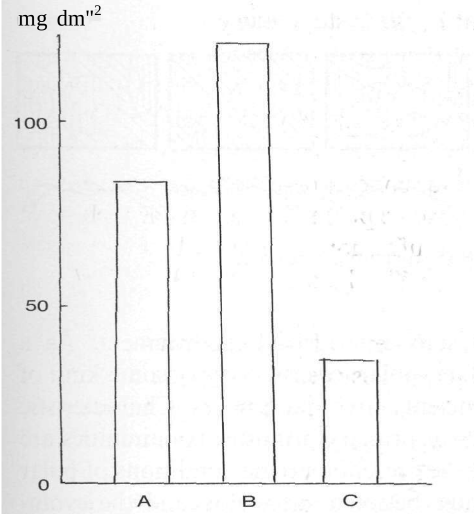

Fig. 16.49. Invertebrate mass (mg, fresh weight) under moss cushions in different polar desert communities with various density of plant cover at Cape Chelyuskin, Taymyr. A, 5% cover; B, 20% cover; C, 60% cover. From Chernov et al. (1979).

mosses and a decrease in production and biomass reserves in soil invertebrates (Fig. 16.49). This testifies to an imbalance between the cover and the climatic conditions (Matveyeva and Chernov, 1976; Chernov et al., 1979). Thus, the denser the cover, the worse the hydrothermal conditions in the soil, which in turn negatively influence the activity of microorganisms (Parinkina, 1971, 1973, 1979a-c, 1986) and of soil invertebrates (Fig. 16.50) (Chernov et al., 1971, 1973; Chernov, 1978b), inhibit the process of organic-matter decomposition, and thereby reduce the fertility of soil which is already very poor in nutrients. All this reduces the possibilities for growth and viability of plants and decreases their resistance to unfavorable environmental conditions. With a lowered plant activity, the cryogenic processes cause the turf to die off in patches, which lays the ground bare. This occurs even in the southern tundra subzone in communities with a dense plant cover. The process of bare-patch overgrowth parallels that of the appearance of new bare patches. Uncovering of the ground is the result not only of the inability of the plant cover to resist the cryogenic processes but also of erosion by wind and snow. The dense cover on the "plakor" of the tundra zone is an unstable phenomenon. The interruption in succession does not occur simultaneously over a large territory occupied by a given type of community. It is a local phenomenon. Thus, in spite of the permanence of these processes and their cyclicity (endogenic succession resulting in a continuous plant cover —> interruption of succession —> new development from the pioneer stage on bare ground), the general pattern of the cover remains invariable. The apparent stability of the cover is the reason why frost-boil, spotty, and even polygonal communities in the arctic tundra subzone are sometimes called climax communities (Gorodkov, 1956; Aleksandrova, 1959, 1970). This is correct only when terminal stages in the development of the plant cover may be identified in a given climate as climax stages, not taking into account such an essential feature as the state of equilibrium of productive and destructive processes. A dense plant cover can exist for a comparatively long time only in the southern tundra subzone and to some extent in the typical tundra subzone, but even there no complete balance of income and expenditure of organic matter is observed. In the arctic tundra subzone, the disequilibrium between plant cover and the environment is so strong that cover destruction often prevails over its recovery. In the typical tundra subzone, this is manifested in a high proportion of spotty tundras in "plakor" conditions (with partial overgrowth of the ground surface). In the arctic tundra subzone, communities with dense cover are absent on "plakor", while spotty and polygonal communities in which the bare ground has not been overgrown are predominant.

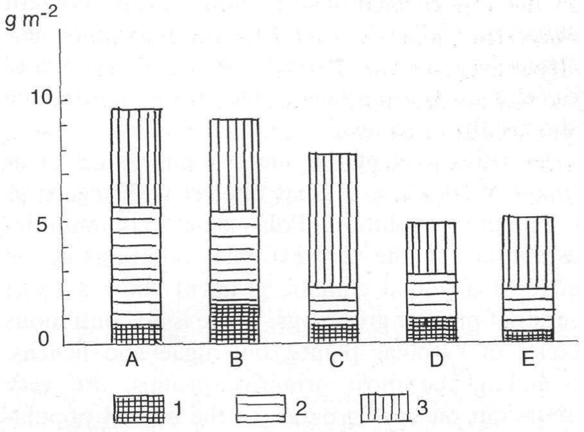

Fig. 16.50. Mass (g, fresh weight) of worms of different groups in elements of frost-boil communities with various density of plant cover in the typical tundra subzone at Tareya, Taymyr. A, patches of ground with crust of crustose lichens; B, patches being overgrown with small cushions of mosses and vascular plants; C, patches overgrown with continuous thin moss turf; D, rims with dwarf-shrubs, sedges, and mosses; E, troughs filled with mosses; 1, Nematoda; *2,* Enchytraeidae; 3, Lumbricidae *(Eisenia nordenskioldi).* From Y.I. Chernov et al. (1971).

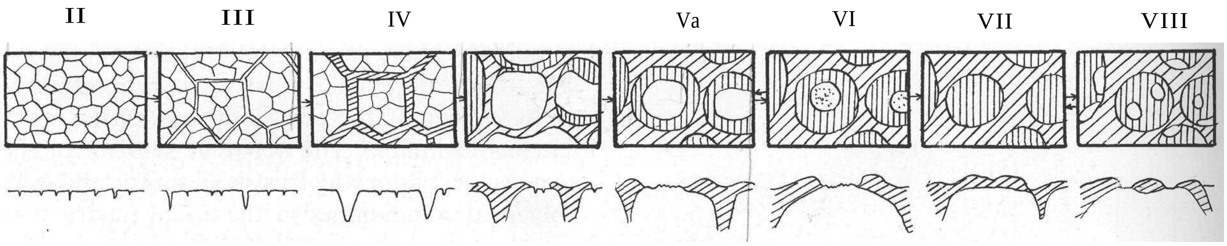

Fig. 16.51. Succession in the formation of "zonal" tundra communities in Arctic. For explanations, see text.

The plant cover in arctic landscapes is unstable and dynamic although physiognomically stable with the exception of catastrophic cases - for example, formation of landslides when the plant cover is fully destroyed over a large area, the soil is carried away, and the permafrost surface and the parent rock are uncovered. This is due to the low speed of succession processes, suppression of plant growth, low productivity, and small organism sizes.

Succession in the tundra is far slower than in temperate zones, which makes direct observation of the dynamics almost impossible. The most promising way to obtain an idea of the dynamic processes is by arranging existing communities into conventional "time sequences".

Successional changes in the plant cover on different substrates has been considered from this viewpoint. Latitudinal differences in the Arctic are much more strongly manifested than in the temperate zone. The course of succession in different subarctic and arctic subzones on analogous substrates may differ strongly in both speed and duration of the sequence (the further north, the shorter the sequence).

Investigations of the successional processes at high latitudes are of great interest with regard to community evolution. Polar desert communities established in the very extreme conditions at the edge of a global climatic gradient show a short series of pioneer groupings. There is no continuous cover of vascular plants, but algae and lichens, including the most primitive groups, are very abundant on bare ground. In the animal populations of such biotopes, water-based groups predominate. Consumers of algae, the midge larvae of the family Chironomidae, form the core of the trophic chains together with Enchytraeidae, Tardigrada, and hygro- and hydrophilous Collembola (Matveyeva and Chernov, 1976; Chernov et al., 1977). The historical development of polar desert communities is nothing but the transfer of water communities to a terrestrial environment. As a matter of fact, polar deserts portray some kind of image of ancient terrestrial cenoses. Characteristic peculiarities of primary primitive communities are imitated in the present extremei.conditioRS of polar deserts. Thus, between succession and the evolutionary origin of communities of high latitudes, approximately the same correlations can be traced as between ontogenesis and phylogenesis (a repetition of early stages of evolution in the early stages of individual development).

Formation of "zonal" communities

In arctic landscapes relatively undisturbed by man, primary successions, beginning with pioneer vegetation, can be observed in marine shallows, particularly in river estuaries, on fresh alluvial deposits of river valleys and diluvia in ravines, on bare surfaces on slopes, on patches free of snow during the winter, in rock streams resulting from the weathering of compact rock, and on landslide surfaces. Analyses of succession sequences from polar deserts down to southern tundras are of great importance for the establishment of the regularities in today's climatological conditions. Several stages (Fig. 16.51) can be observed in the

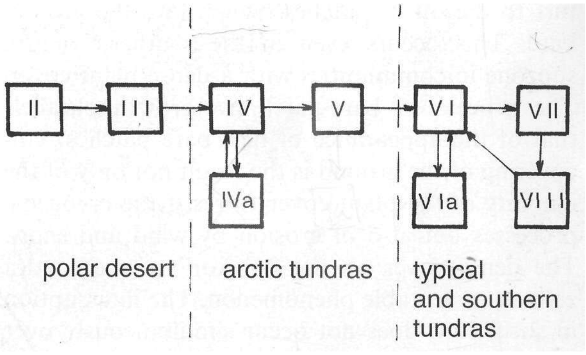

Fig. 16.52. Provisional scheme of successive stages in the formation of "zonal" tundra communities and their representations in different subzones. For explanations, see text.

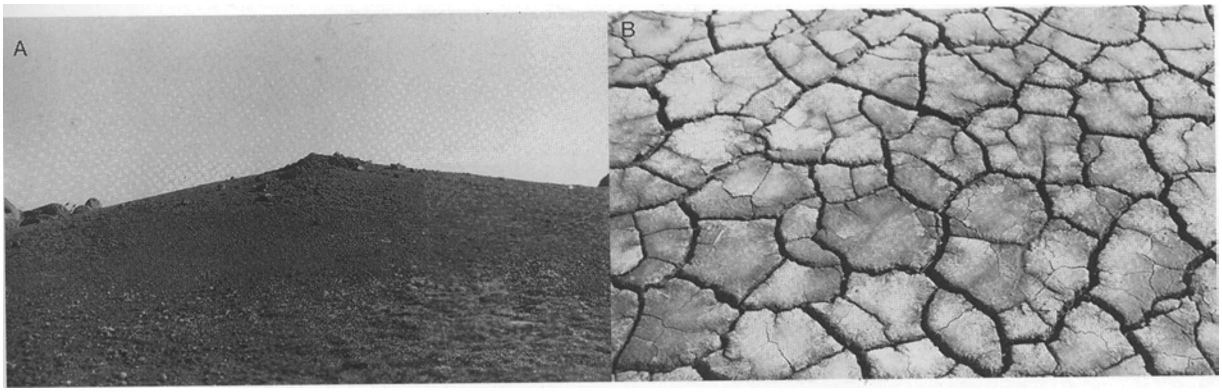

Fig. 16.53. Primary substrate as a result of (A) weathering (Dikson) and (B) water erosion (Rogozinka River, Taymyr).

formation of the plant cover on "plakor", from the establishment of the first plants to a close vegetation carpet. This is possible only in typical and southern tundras (Fig. 16.52).

The first stage

This stage consists of bare ground without macroscopic physiognomically noticeable organisms — surfaces that appear as a result of the retreat of the sea (such areas now exist in the Novosibirskiye archipelago on the Zemlya Bunge). They also appear because of the retreat of glaciers (on Severnaya Zemlya and on Zemlya Frantsa-Iosifa) or are formed as a result of a slipping and swelling up of the ground, snow action, and wind and water erosion (Fig. 16.53). In polar deserts such areas are extensive; in the tundra zone they are a local phenomenon.

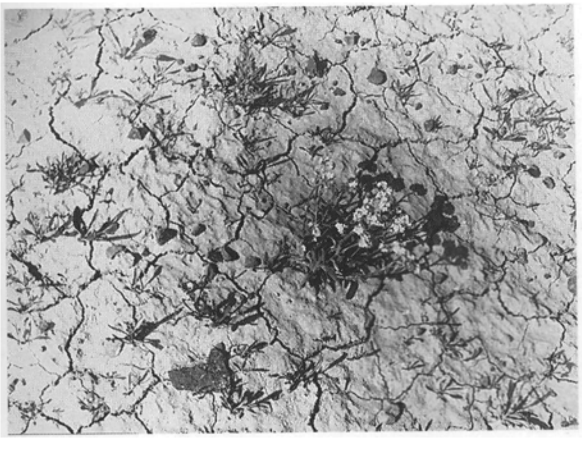

Fig. 16.54. Cracked surface of a solifluction slope with solitary vascular plants (the cracks become closed after rain) by the Rogozinka River, Taymyr.

The second stage (H in Fig. 16.51)

The ground surface becomes dry during the dry period of the summer, and a network of small cracks appears breaking into small pentagons and hexagons of 10-20 cm in diameter (Fig. 16.54). The cracks are up to 1 cm deep, but during rainfall and snow thawing they close up. Solitary flowering plants settle here, the species depending on the location. Usually they are arctic grasses such as *Alopecurus alpinus*, *Deschampsia borealis*, and *Puccinellia angustata* and forbs such as *Parrya nudicaulis*, *Saussurea tilesii*, and *Tripleurospermum phaeocephalum.* The distribution of plants is diffuse and not connected with the crack pattern. Plots at this stage of overgrowth are commonly seen in polar deserts and are episodic in arctic tundras (for example, on snow beds). They are extremely rare to the south.

The third stage (III in Fig. 16.51)

Some of the cracks are deepened and widened. They become permanent and do not close when the ground is wet - sometimes they are filled with cobbles. Very small pentagons or hexagons (from 0.6-0.8 to 1.0-2.0 cm in diameter) are formed (Fig. 16.55). Permanent cracks are populated by mosses and herbs. Some pioneer flowering plants appear - *Eritrichium villosum* and *Saxifraga hirculus* in the High Arctic and various species typical for eroded southern slopes (e.g., *Astragalus umbellatus, Valeriana capitata)* in the middle part of the tundra zone. The mosses are the same in all latitudes *(Drepanocladus uncinatus, Tortula ruralis).* They form a thin film or velvet up to 5 mm deep (usually 1-2 mm) on the walls of the cracks. The moss cover, though rather weak, already begins to form a substratum. This is a common state in polar

Fig. 16.55. Small polygon pattern of ground with permanent cracks at Cape Chelyuskin, Taymyr.

deserts and arctic tundras, while further south it is episodic (mainly on snowless protruding patches, on hilltops, on top of slopes, and especially on landslide surfaces).

The fourth stage (IV in Fig. 16.51)

The cracks are filled with vegetation (dead and living turf) and soil with a peat horizon is formed in them. The pioneer mosses give way to species which dominate in the cover at the terminal stage, in shallow and narrow cracks particularly *Hylocomium alaskanum.* Upon widening of the cracks, the turf in the central part sags with a simultaneous increase in the thickness of peat at the bottom of crack; the moisture rises and the temperature of the soil is reduced. Mesophilous bryophyte species are replaced in the tundra by the more hygrophilous *Ptilidium ciliare* and *Tomenthypnum nitens,* while in polar deserts the first to be established are *Aulacomnium turgidum* and . *Orthothecium chryseum* and then *Ditrichum flexicaule.* Along with herbs, the dwarf-shrub *Dryas punctata* starts to appear. With a simultaneous filling of the cracks, turf begins to "creep" onto the flat surface of the ground (its thickness in the center of the vegetation is up to 6-8 cm, on the edges 1-2 cm). The cracks disappear, the sharp angles are smoothed down and the nanorelief becomes even (the turf surface is at the level of bare ground). The pattern of the plant cover becomes net-like (Figs. 16.56-16.58). The proportion of bare ground is reduced (by no less than 50%). In polar deserts and in the northern part of arctic tundras, the succes-

Fig. 16.56. Net-like pattern of vegetation in the polar desert with mosses and lichens filling cracks at Cape Chelyuskin, Taymyr.

Fig. 16.57. Net-like pattern of vegetation in the arctic tundra subzone with mosses and herbs in cracks at Dikson, Taymyr.

sion is complete at this stage. Because of the action of cryogenic factors, a break takes place below the thick moss turf and a space is formed. The upper part hangs down and begins to dry up. The surface begins to be covered with solitary crustaceous lichens *(Caloplaca, Lopadium, Ochrolechia, Pachyospora, Pertusaria, Psoroma, Rinodina),* which later form a compact crust that completes the destruction of mosses. The dry material is blown away and the bare ground is uncovered. The turf similarly dies off on the edges of bare ground patches, where the succession is balanced by retrogression. A microsuccessional cycle is established (stage IVa in Fig. 16.52). Since the destruction and the re-establishment of turf occurs locally and not simultaneously, the polygonal tundras at this stage are perceived as stable. Besides the constant dying-off process of the turf, formation of a new patch of bare ground is also, possible in, the middle of a trough. In polar deserts, the turf often perishes as a result of water-soaking. Episodically, this can also be observed further to the south.

The fifth stage (V and Va in Fig. 16.51)

An elevated rim is formed around the patches of bare ground (Fig. 16.59) because of the thicker

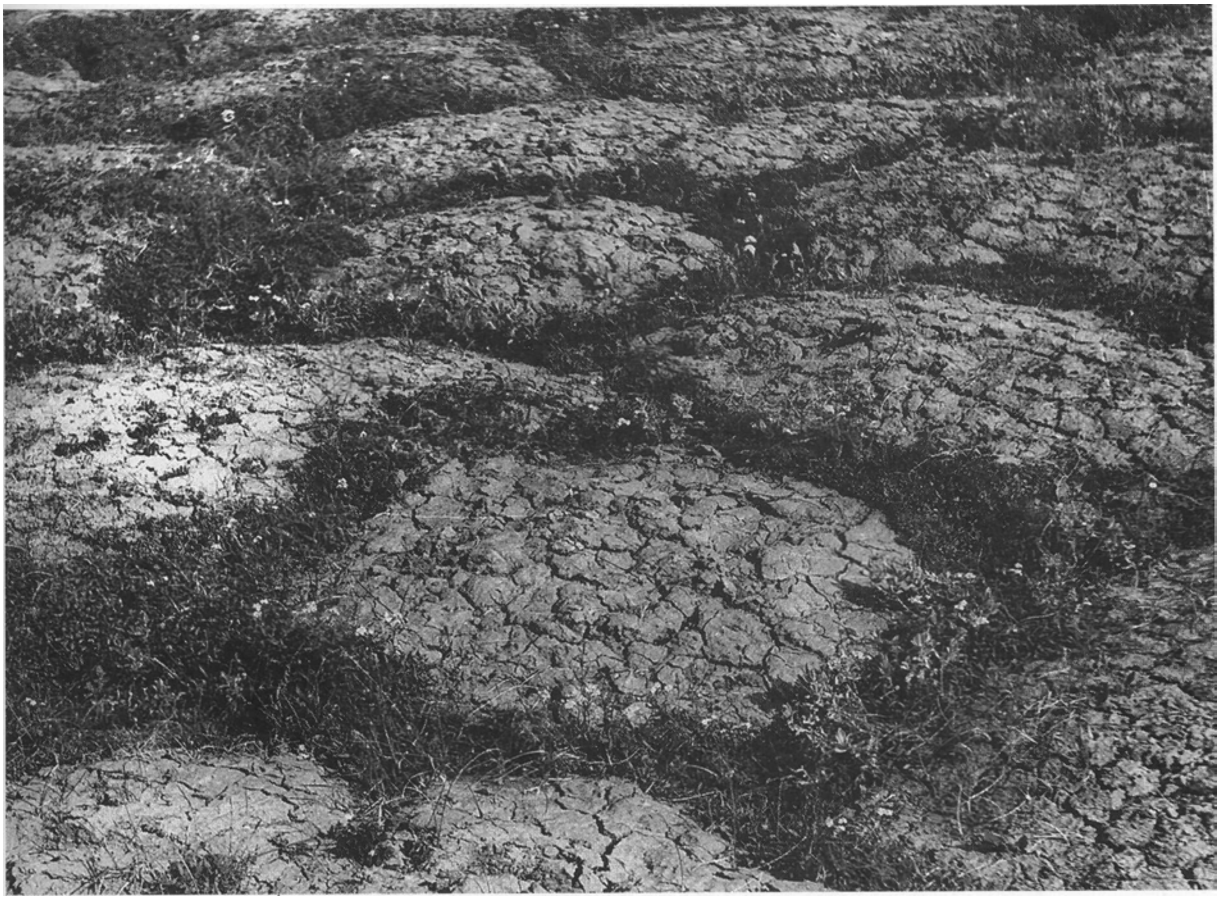

Fig. 16.58. Net-like pattern of vegetation cover in the typical tundra subzone with herbs in cracks at the mouth of the Rogozinka River, Taymyr.

Fig. 16.59. Rim around patch of bare ground in a frost-boil •community formed by mosses and *Carey, ensifolia* ssp. *arctisibirica* in the typical tundra subzone.

moss turf *(Aulacomnium turgidum, Dicranum elongatum, Hylocominum alaskanum, Racomitrium lanuginosum, Rhytidium rugosum)* and the growth of *Dryas punctata.* The sedge *Carex ensifolia* ssp. *arctisibirica* appears and becomes abundant; in southern tundra, the dwarf-shrubs *Vaccinium vitis-idaea* and *V. uliginosum* also occur.

Fruticose lichens *(Cladina arbuscula* ssp. *beringiana, C. rangiferina, Cladonia amaurocraea, C. macroceras, Cetraria cucullata, C. islandica* var. *polaris)* develop favorably in moss turf. The phytogenic nanorelief becomes differentiated: the lowest level is the surface of moss turf in a trough, the middle level is the bare ground, and the highest level is on the rims (10-15 cm higher). The hydrothermic conditions are worst in the troughs. Generally, the troughs are water-soaked and have a long-lasting snow cover and little thawing of the permafrost. This interferes with the normal functioning of decomposers, as a result of which the process of decay is inhibited. The thickness of the turf horizon increases and the conditions come close to those of mires. Mesophilous mosses are fully replaced by the more hygrophilous *Ptilidium ciliare* and *Tomenthypnum nitens.* Occasionally, hydrophilous mosses can also be found *(Drepanocladus intermedius, D. revolvens, Meesia triquetra, Scorpidium turgescens).* Flowering plants are sparse. Foliose lichens predominate *(Peltigera aphthosa, P. canina, P. polydactyla).* Areas of bare ground are reduced to 20%, but the remaining part is still not overgrown. Little aggregations of small-sized mosses *(Ditrichum flexicaule, Myurella julaced)* and crustaceous lichens *(Baeomyces carneus, Lecanora epibryon, Ochrolechia uppsaliensis, Pertusaria octomela, Rinodina roscida)* appear along small cracks as do *Thamnolia vermicularis* and solitary vascular plants. The cryogenic processes on the patches of bare ground are still so much stronger than the biogenic impact that the plants are constantly dying. This is the stage at which the plant cover shows the greatest contrast (stage Va on Fig. 16.51). Three elements can be clearly distinguished: patches of bare ground with solitary plants (i.e., the pioneer stage), rims with grass/dwarf-shrub/moss turfs (the te'rminal mesophilous stage), and small troughs with moss turfs (the terminal hygrophilous stage). The same kind of sharp differentiation is observed in the soil: quaternary marine deposits on the patches almost unaffected by soil formation; a tundra-gley soil on the rims; and a peat soil in the troughs. This state is commonest in the typical tundra subzone, but is also widespread further to the south.

The sixth stage (VI in Fig. 16.51)

The process of bare-ground overgrowth begins. In the early stages of this local succession (surrounded by mature cover on the rims and in troughs), a specific complex of epedaphic organisms is typical and includes blue-green, green, and yellow-green algae *(Nostoc commune, Schizothrix friesii, Stigonema ocellatum,* species of *Botrydiopsis, Chlamydomonas, Chlorococcum, Ellipsoidion, Gloeocapsa, Microcystis, Neochloris, Scotiellocystis, Scytonema),* crustaceous lichens *(Bilimbia sphaeroides, Cladonia symphycarpia, Lecanora epibryon, Lecidea tornoensis, Lopadium pezizoideum, Pachyospora verrucosa, Pannaria pezizoides, Psoroma hypnorum, Toninia lobulata),* small mosses *(Catoscopium nigritum, Ceratodon purpureus, Ditrichum flexicaule, Hypnum bambergeri, H. revolutum, Myurella julacea, Orthothecium strictum, Polytrichum piliferum, Psilopilum laevigatum, Tortella fragilis, Tortula mucronifolia, T. ruralis),* liverworts *(Anthelia juratzkana, Cephaloziella arctica, Odontoschisma denudatum, Peltolepis grandis, Preissia quadrata, Riccardea pingius, Solenostoma pusilum),* small vascular plants *(Epilobium davuricum, Juncus biglumis, Minuartia rubella, Pinguicula villosa, Sagina intermedia),* and invertebrates. Among the invertebrates are many characteristic inhabitants of bare ground: springtails of the genera *Hypogastrura* and *Tetracan-*

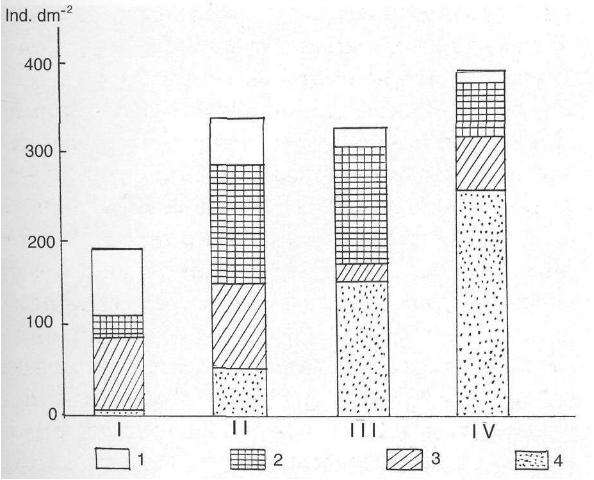

Fig. 16.60. Numbers of different life forms of Collembola in elements of nanorelief in a frost-boil tundra at Tareya, Taymyr, June 1968 (on the basis of 15-30 sample plots). I, patch of bare ground with crust of crustose lichens; II, patch being overgrown with small cushions of mosses and vascular plants; III, patch overgrown with thin continuous moss layer; IV, rim. Life forms: 1, epedaphic; 2, litter-bryobionts; 3, hemiedaphic; 4, euedaphic.

thella; carabid species of the subgenus *Cryobius;* some staphylinid beetles; and bugs of the family Saldidae. The composition of Collembola groupings in different dynamic stages in frost-boil tundras was studied in detail in the Taymyr (Chernov et al., 1971; Ananjeva, 1973). There are marked changes in species composition and life forms of Collembola depending on the degree of development of the plant cover and the soil layer (Fig. 16.60). The consolidated, usually uneven soil surface of the patches is an extremely favorable biotope for many organisms. This biotope is well heated and aerated, sufficiently moistened, and weakly acid, and it contains organic matter. This is why rich algal and microbial groupings develop in the upper soil layer (Parinkina, 1971; Piin et al., 1984). In consequence, there is also a relatively high density of small invertebrates (Collembola, Enchytraeidae, Nematoda).

The combined activity of all these organisms results in a stabilization of the ground because an organogenic crust up to 5 mm thick (partly alive, partly dead) is formed which almost entirely covers the ground. This thin cover, under the action of bulging and cracking of the soil, is periodically destroyed locally, but is also re-established, producing a microsuccessional cycle (stage Via in Fig. 16.52). As a result of general stabilization as well as an increase in the supply of nutrients, the central part covered with the organogenic crust becomes a favorable substrate for all organisms. The process of overgrowth involves vegetative extension of the sedges and *Dryas* spp., spreading of the moss turf, and dispersion of other organisms beyond the edges of the cushion. The organogenic crust becomes a site for the establishment and growth of mosses typical of the rims: *Aulacomnium turgidum, Hylocomium alaskanum,* and *Racomitrium lanuginosum* in dry places and *Hypnum bambergeri* on moist patches. These mosses form a closed vegetation and generate a constant increment in the thickness of the cover, which is also gradually invaded by fruticose lichens. Favorable conditions are created for true soil invertebrates (Enchytraeidae, earthworms, larvae of Tipulidae, hemi- and euedaphic Collembola, etc.) under the organogenic crust. The process of patch overgrowth does not proceed simultaneously. Therefore, it is possible to observe patches with absolutely bare ground as well as a closed cover in a single community of spotty tundra. This state is typical for "plakor" in the typical tundra subzone, but is also frequent in southern tundras.

The seventh stage (VII in Fig. 16.51)

The soil is fully overgrown. A moss turf (with a slightly concave surface) is formed with an admixture of fruticose lichens. The cover has less contrast, but the nanorelief is preserved (the height difference from concave to convex parts is 10-20 cm). The closed turf is made up of mosses, fruticose and foliose lichens, dwarf-shrubs, sedges, and low shrubs. This is the most stable state of the cover. It is characteristic of southern and typical tundras where the "plakor" are sufficiently drained in summer and well covered with snow in winter.

In the southern tundra subzone, low-shrub willows *(Salixpulchra, S. reptans)* and birches *(Betula exilis, B. nana)* are active in the late stages of succession. Their individuals are larger than the elements of the mosaics of the moss cover. In the southern part of the tundra zone, thickets of *Alnaster fruticosus* should be considered as the most advanced stage of the plant cover on the "plakor". In dense thickets, however, a large quantity of litter has accumulated and the snow does not melt until late in the spring. Therefore, the hydrothermal conditions of the soil are unfavorable, the level of permafrost rises, the shrubs die, and the system destroys itself.

Fig. 16.61. Patch of bare ground with roots of shrubs in southern tundra subzone at Kresty, Taymyr.

The eighth stage (VIII in Fig. 16.51)

Cryogenic processes may cause the turf to die. As a result, the bare ground is uncovered at the site of one of the elements of the former frost-boil tundra (Fig. 16.61), and a new succession starts. A "small succession cycle" begins. The integrity of the cover is disturbed locally in general, and the patches of ground are normally solitary. However, simultaneous destruction of the turf at a great number of sites is also possible. Therefore, the frost boils in southern and typical tundras can represent both a stage preceding a closed cover and a stage of retrogression. The latter is evidenced by the "remains" of the soil profile under the patches, which differs from the soil under the rims only by the absence of horizon A_0. Based on a number of indirect indications, the second situation is more typical. In the arctic tundra subzone, patches of bare ground are primary. They are the result of a break in the succession as a consequence of a shortage of vegetation resources for the formation of a closed cover.

The succession sequence on the "plakor" as described extends for an indefinite time and cannot be observed in one place. It proceeds to completion in the southern and typical tundra subzones, while it stops at the stages of net-like or patchy cover in the arctic tundra subzone and in the polar desert.

The processes of plant cover formation are general and occur in a strict sequence by the same groups of plants (Gorodkov, 1956; Tikhomirov, 1957; Matveyeva, 1968; Aleksandrova, 1970; Matveyeva et al., 1973; Piin et al., 1984; Tishkov, 1985a). In cracks it proceeds as follows: small mosses → forbs → grasses, dwarf-shrubs, and mosses → the same + sedges, fruticose and foliose lichens, and low shrubs. The sequence of autotrophs on a flat surface is as follows: blue-green algae, crustaceous epigeous lichens, small mosses, liverworts, and small forbs → mosses, dwarf-shrubs, and sedges → the same + fruticose and crustaceous lichens.

The species composition depends on the location in the "zonal" series. However, the cryptogams are similar throughout the whole tundra zone. The various synecological parameters do not change continuously in the course of the overgrowth of bare ground and the development of continuous plant cover. Thus, taxonomic richness, species diversity, and productivity increase in early succession, reach their maximum at intermediate stages, and then decrease again. The structure of vegetation cover and animal communities in the typical tundra subzone are most complicated in frost-boil tundra, with its patches of bare ground at different stages of overgrowth, and not in communities with a continuous cover. There are no data on the speed of succession, but this process probably extends for hundreds and even thousands of years.

Overgrowth of sands

Large sand masses are not very frequent in the Eurasian tundra zone. They are associated with seas and rivers. The most extensive sand outcrops are found in relatively small islands (Belyi, Sibiryakova, Olenyi, and others), as well as on the peninsulas Yamal and Gydan. Information about the initial stages of sand overgrowth is scarce (Matveyeva, 1980; Matveyeva and Zanokha, 1986). Solitary vascular plants typically occur on unconsolidated sands subject to wind action; the majority of these plants cannot be called psammophils in the narrow sense since they also grow on loams in "zonal" communities.

The nonspecificity of the pioneer flora on the sands is typical of high latitudes. In different regions of the Eurasian Arctic, there can be various species of forbs *(Armeria maritima, Artemisia borealis, Cerastium arvense, C. regelii, Lloydia serotina, Myosotis asiatica, Oxyria digyna, Papaver pulvinatum, Parrya nudicaulis, Potentilla hyparcticd),* grasses *(Deschampsia glauca, Festuca cryophila, Koeleria asiatica, Poa alpigena, P. arctied],* and woodrushes *(Luzula confusa, L. nivalis).* Most typical is the horsetail *(Equisetum arvense* ssp. *boreale).* None of these form a closed cover, and their role in fixing sands is not great. The main role in stabilizing the loose, dispersible substrate is performed by dwarf-shrubs such as *Salix nummularia* and *Dryas punctata,* which form a compact appressed mat. Consolidation of the surface can also be brought about by liverworts such as *Gymnomitrion corallioides* and crustaceous lichens with black thalli which fasten the sand grains together, forming a thin fragile crust. This crust is easily destroyed under the action of winds, snow erosion, and cryogenic processes. Succession is also opposed by the active process of sand deposition. Therefore, the initial stages can last for an indefinitely long time. The gradual growth of the cryptogamic crust and the increase in the size of dwarf-shrub cushions result in the consolidation of the sandy soil. All successions on sands appear to pass through the *Dryas* stage, after which a moss cover of *Hylocomium alaskanum* is gradually formed. In the end, a closed cover of mosses, dwarf-shrubs, and lichens can be formed; however, if cracking of the ground into polygons takes place, then the vegetation becomes differentiated in the same way as in frost boils and polygonal stands on the "plakor". As the plant cover is forming, soil is also developing under it. At late stages of succession of dispersible sands, the vegetation is similar to that of the "zonal" communities on the "plakor", although some distinct features of the floristic composition remain for a long time.

Fig. 16.62. Polygonal mire in the typical tundra subzone at Tareya, Taymyr.

Dynamics of vegetation in the formation of mires

Many varieties of mires occur in the tundra zone (Boch and Masing, 1983). Most typical in the arctic landscape are the polygonal mires (V.N. Andreyev, 1938, 1955; Petrovskyi, 1959; Aleksandrova, 1963; Boch, 1974, 1980; Tyrtikov, 1974). They form a network of large polygons (Fig. 16.62) from 7 x 10 to 20 x 30 m in size, separated by troughs. This pattern results from the formation of polygonal ice wedges. Under the action of cryogenic processes, ice-crack nets are formed in some areas of river floodlands, lake banks, and seaside marshes. In the course of time, the ice wedges become wider and the edges of the polygons rise slightly. The central concave parts of the polygons are saturated or filled with water, while the entire yearly standing crop and deep mineral horizons are involved in the active exchange between plants and soil. In the meadow soils, the activity of soil invertebrates and microorganisms is immeasurably higher than in tundra communities with a well-developed moss cover. Artificial creation and maintenance of meadow communities calls for a radical change in the basic cenotic and trophic relations. Grass establishment in the tundra zone with a constant supply of fertilizers, especially nitrogen, which promote successful competition of herbs, particularly grasses, is the only real way of creating agrocenoses.

Use of the tundra biome resources calls for the application of some specific forms and strategies. Repeatedly stressed are the fragility, the low stability, and poor potentiality for regeneration of tundra ecosystems. All this is easily agreed upon, but it must also be acknowledged that man has not yet fully realized just how vulnerable and powerless tundra nature is when faced with the intrusion of modern civilization. The tundra communities are not merely poorly stable. Their cenotic organization and relationships with abiotic factors induce a resonance effect: a catastrophic increase and widening of negative consequences of anthropogenic impact. The principles of caution, sparing use of resources, preservation, and reservation of the tundra biome should be most systematically applied. The compromises between environmentalists and exploiters under extreme conditions of high latitudes not infrequently turn out to be more ruinous than in any other part of the globe.

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